

Issues and prospects of belowground ecology with special reference to global climate change

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Abstract The theory of ecology is based on over 100 a of research and investigation, all centered on aboveground patterns and processes. However, as contemporary ecologists are increasingly acknowledging, belowground structures, functions, and processes are some of the most poorly understood areas in ecology. This lack of understanding of belowground ecological processes seriously restricts the advance of global change research. The interdisciplinary field of belowground ecology began to flourish in the 1990s, along with the expansion of global change research, and quickly gained momentum. Belowground ecology aims to investigate belowground structures, functions, and processes, as well as their relationships with corresponding aboveground features, emphasizing the responses of belowground systems under global change conditions. Key research areas include root ecology, belowground animals, and soil microorganisms. This review summarizes and analyzes the relationships between above- and belowground ecosystems, root ecology, root biogeography, belowground biodiversity, as well as research areas with particular challenges and progress. This commentary emphasizes certain theoretical issues concerning the responses of belowground processes to global change, and concludes that belowground ecology is a critical research priority in the 21st century.

Keywords: global change, root ecology, root biogeography, belowground biodiversity, ecosystem processes, belowground ecology.

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After more than 100 a of research and investigation, today's ecologists have finally begun to acknowledge that the functioning of terrestrial ecosystems relies to a great degree on the distribution patterns and processes of carbon (C), as well as the corresponding biogeochemical cycles^[1]. Penetrating research has been conducted on terrestrial ecosystems' aboveground portions for some time, but belowground portions remain poorly understood^[2,3]. This has created a serious inadequacy in ecosystem process research^[4]. The influence of belowground systems on ecosystem functioning stems not only from the provision

of water and nutrients, but also from the rich biodiversity in these systems which maintains ecosystem functioning, and even more importantly, from their central position in carbon distribution and processes of terrestrial ecosystems^[1,5]. Belowground ecosystem processes (hereafter referred to as belowground processes) are the "bottleneck" for contemporary ecosystem process research, being the least well understood facet of ecosystem function research, especially with regard to their decisive role in carbon processes^[2,6]. The reality of global change creates an urgent demand for ecologists to clarify the mechanisms of belowground processes' influence on terrestrial ecosystems^[7]. This is the background from which belowground ecology has arisen. Different academic disciplines have contributed research into ecosystems' belowground structure, function, and processes, as well as their relationship with aboveground systems. Furthermore, a variety of research specialties have been applied to predict how the influence of belowground systems will change under global change conditions. The compilation of this information will allow ecologists to begin to understand the true nature of ecosystem function and processes. Here it must be stated, belowground ecology deals with a broad range of research fields, including root ecology, soil ecology, soil fauna, and soil microbial ecology. However, this commentary most importantly summarizes and analyzes the links between above- and belowground ecosystems, root ecology, root biogeography, belowground biodiversity and related issues, emphasizing belowground C and N processes as well as key progress made in understanding the influence of global change on belowground ecosystems.

1 Connections between above- and belowground ecosystems

All terrestrial ecosystems incorporate mutually dependant producers and decomposers. Through aboveground ecosystem processes (hereafter referred to as aboveground processes), producers provide organic material to the whole system, while decomposers operate through belowground processes to decompose litter and other waste material, releasing nutrient elements, thus completing the cycle for the whole system. Producers and decomposers form the foundation of the food chain for consumers, the former for herbivores aboveground, the latter for detritivores belowground^[8]. The relationships between each link of the food chain, as well as the interactions between above and belowground processes, determine to a great extent ecosystem function and processes^[9,10]. Since ecosystem response to global change relies largely on the tight relationship between above- and belowground processes, studying these processes as a whole will be the important direction for ecosystem research at present^[11].

As research has already shown, plants mainly influence soil organisms and underground processes via the

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provision of resources (most importantly as a C source) as well as through each species' ecophysiological traits. This vein of research has demonstrated that () at the ecosystem scale, net primary productivity (NPP) is likely the most important controlling factor of soil organisms and belowground processes^[9]. The recent research of Valentini et al.^[12] and Högberg et al.^[13] into the above- and belowground distribution of carbon in North European and North American forests provides one example: the carbon metabolized by soil organisms is provided solely by the belowground distribution of photosynthates; () relationships between aboveground species, in particular the activity of herbivores, can influence soil organisms and belowground processes^[9,14]. Recently, Bardgett et al.^[14] proposed three mechanisms by which herbivore activity could affect belowground processes, namely through changing resource quality, resource quantity, or altering the functional group composition of plant communities. Insect feeding on plants may also induce changes in plant secondary metabolites, which could in turn influence soil organism activity; () the structure and composition of plant communities under global change conditions will likely experience change^[15-17], likely greatly influencing decomposer activity^[18]. This type of effect is mainly based on the characteristics of plant litter and root exudates, particularly the chemical composition of these substances^[19]. As recent evidence indicates, through coevolutionary processes plants can "select" decomposers that facilitate decomposition of their own residues^[20], a form of mutualism between plants and decomposers; and () aboveground ecosystems can also influence soil organisms and belowground processes through other processes. For example, early successional species and late successional species differ in their physical effects on soil organisms, as well as in their nutrient use efficiencies^[5,14]. Such differences can change the spatial and temporal structure of the decomposer food chain.

Soil organisms also can influence the structures, functions, and processes of aboveground ecosystems^[21-23]. Such influences are mainly manifested as follows: () The interactions between decomposers and other soil organisms, through nutrient turnover, modify the availability of nutrients to plants, thus influencing plant development, resource allocation, and chemical composition (such as nitrogen content)^[19,24]. () As experiments have shown, the size, frequency, and distribution of individual organisms and the structure of the belowground food chain can influence plant development^[25,26]. For example, the consumption of roots by belowground herbivores can alter the above- and belowground distribution pattern of carbon, in particular by stimulating plant production of chemical defense compounds^[23]. Similarly, rhizosphere microbes can stimulate root systems to produce large quantities of exudates^[21]. () Some soil organisms can influence plant

development, community structure, and succession by altering the interspecific relationships between plants^[27-30].

() Soil organisms that have a transformative effect on the underground environment (ecosystem engineers), such as earthworms and termites, can change the physical structure of soil. This crucially influences the species composition of aboveground communities^[31,32].

As these examples demonstrate, the relationship between above- and belowground ecosystems is intimate. Therefore, bringing together the research from both spheres is not only a requirement for the development of ecosystem ecology, but also necessary for a complete understanding of ecosystem structure and function.

2 Root ecology

Above- and belowground ecosystem processes are linked essentially by root systems. However, root systems, and especially fine roots, are probably the least well understood plant organs. Root systems act as the source for nutrients and water, and the sink for produced carbon, and have become one of the most closely studied topics in ecosystem ecology and global change research^[2,33]. This is due to the observation that, for a given ecosystem, the morphology, architecture, and distribution of the roots of dominant plants, particularly the turnover of fine roots^[19], determine a great extent ecosystem carbon processes, water balance, as well as elemental biogeochemical cycles. Recent research on 9 North American tree species indicates that root order has notable influences on root parameters, such as specific root length (SRL, m/g) and N content, thus influencing ecosystem C and N cycles^[34].

Belowground net primary productivity (BNPP) composes a relatively large proportion of total ecosystem productivity. Despite much research effort directed at root systems, the contribution of BNPP remains the least clearly understood component of terrestrial ecosystems^[35,36]. According to estimates, BNPP composes 20%—80% of the total NPP, although there clearly exists large uncertainty^[37]. For example, in the *Leymus chinense* and *Stipa grandis* grasslands of China's Inner Mongolia, root biomass composes 81% and 73% of total biomass, respectively^[38], while BNPP can differ by a factor of 2 between years in an alpine meadow^[39]. On a global perspective, grassland BNPP contributes 24%—87% to total NPP^[40], while in forest ecosystems the contribution ranges between 7%—76%^[41]. This wide range is due to different ecosystem structures which give rise to different above- and belowground carbon distributions^[35], as well as different rates of fine root turnover between communities, which leads to differences in rates of photosynthate consumption^[42]. However, it has also been suggested that these large differences are largely due to differences in measurement methodologies^[43]. How root system productivity will change under global change conditions is an even greater unknown^[44]. For instance, Aber et al.^[45] used

nitrogen balance and biomass methods to measure the productivity of fine roots of 13 coniferous and broad-leaved tree species in North America, finding ranges in productivity within single species (e.g. *Quercus rubra*) of up to 10 times. Among the 13 species, root productivity varied on average by a factor of two. Root system research not only has great technical challenges, but at present still does not have any universally accepted methods, and still lacks solid theoretical background. Thus, how root systems influence community productivity, elemental cycles, and ecosystem patterns and processes will be key areas in future ecosystem ecology research, providing great research opportunities in the future.

In conducting research into belowground ecology processes, and in particular root system research, destructive sampling methods are essential. If using temporally sequential measurements, it is necessary to use a great number of experimental units or replicates. Because of this, sampling strategy for root systems has been a difficult problem for ecologists. Four major reasons contribute to the large uncertainty in measurements of root system: () it is difficult to discriminate between root systems of different plants or of different ages, especially for herbaceous plants; () we lack effective measures to differentiate living and dead roots, and the former method of using shape or color to differentiate often creates large errors^[46]; () the turnover processes of root development, senescence, death, and decomposition lack effective monitoring methods^[47]; () ecophysiological processes of fine roots are influenced to a large extent by soil nutrients, moisture, and rhizosphere microorganisms. For example, mycorrhiza can stimulate P assimilation of deciduous pine root systems by 20%—23%^[48], and root systems, according to levels of soil heterogeneity, can express tremendous structural and functional plasticity.

For grasslands and annual herbaceous communities, many methods of measuring annual net primary productivity (ANPP) have been used^[49]. However, the measurement of BNPP presents many more difficulties^[37], especially with regard to forest ecosystems. Despite several approaches for estimating BNPP, such as biomass, stable isotope analysis, carbon or nitrogen balance, and minirhizotron methods^[49], it remains unfeasible to efficiently estimate belowground ecosystem carbon allocation or predict its processes^[43].

For root systems, lack of an effective sampling method complicates research into root ecology processes. However, research into the effects of root systems in ecosystems can advance by taking advantage of the importance of functional traits in root systems. In particular, the competition between interspecies root systems is symmetric^[50]. This trait is unique to belowground systems, since in aboveground systems the shading effect bestows disproportionately larger dominance on relatively large plants.

For example, belowground competition in Japanese ash (*Fraxinus mandshurica*) sometimes relates closely only with nutrient status and moisture levels^[51,52]. Therefore, the use of the relationships between functional traits to study root effects on ecosystems represents an important future research direction.

3 Root biogeography

Traditional plant biogeography has mainly focused on large-scale distribution patterns of vegetation, both past and present^[53], as well as the probable changes in these distribution patterns under global change scenarios^[54]. However, plant biogeography research has concentrated mostly on how patterns of aboveground vegetation structures respond to geographic environmental gradients, with very few studies focusing on belowground structures, namely geographic analysis of root systems. In China for example, Feng et al.^[55] summarized the biomass and productivity of China's main forest types, and Fang et al.^[56] investigated changes in carbon storage and carbon density in different regions of China over 50 a, but estimates of China's forest belowground biomass and C pool have yet to be made with authority. Thus, theories of root biogeography^[57] receive great attention upon their proposal. Belowground biomass, productivity, root turnover rate, and vertical distribution patterns, as well as composition of rhizosphere microorganism, all change with differences in vegetation types^[58–61]. Research into the relationships between the geographic differentiations in these root parameters and controlling factors (such as temperature, rainfall, and soil types) is crucial for root biogeography.

Global change as defined by fundamental changes in temperature, rainfall, and other climatic factors are unprecedented for the present ecosystems^[62]. Root biogeography has advanced at the speed of global change research. At the plant species level, Canadell et al.^[58] summarized data on the distribution of rooting depth of 253 species of woody and herbaceous plants. Maximum rooting depths ranged from 0.3 m in tundra areas to 68 m in deserts. Of the species analyzed, 77% rooted deeper than 2 m, 20% deeper than 5 m, and at least 8.7% rooted deeper than 10 m. In temperate grasslands, average rooting depth was 2.6 ± 0.2 m. From these results, it can be seen that ecosystem models commonly underestimate the effect of root systems on the carbon cycle^[42]. At the ecosystem level, Schulze et al.^[63] traced a rainfall gradient, from 770 mm/a forests, 520—290 mm/a shrub areas, 160 mm/a *Stipa* grasslands, down to 125 mm/a deserts, in order to investigate whether or not rooting depth correlates with rainfall, i.e. if rooting depth can compensate for insufficient rainfall. Their results indicate that, despite a decrease in average above- and belowground community biomass and leaf area index, water-use efficiency did not change markedly along the rainfall gradient. In soil profiles, 90% of belowground biomass was distributed between 0.5 and 0.8 m.

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Furthermore, there was no prominent difference in this measurement between forests and grasslands, showing no compensatory effect. At the biome level, Jackson et al.^[59] investigated the root distribution in biomes across the globe. Their results indicated that tundra, northern coniferous forests and temperate grasslands have the shallowest root systems, with 80%—90% of root systems distributed at 0.3 m deep into the soil. Among all biomes, the biomass and productivity of fine roots in tropical ecosystems was the highest, with relatively short average lifespan and the fastest turnover rate. Furthermore, fine root biomass and productivity in boreal ecosystems was the lowest, with longer average lifespan and slow turnover rate^[36,34].

Several investigations of root systems have been conducted in China. For example, the fine root turnover rate for *Leymus chinense* grasslands was found to be 0.55 a^{-1} ^[65], while that of alpine meadows only 0.37 a^{-1} ^[39]. Wang et al. analyzed data from 250 published reports, finding the root productivity of China's temperate forests (latitudes 25—40°N) was the highest ($2599 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$), followed by sub-tropical forests ($1597 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$), with that of cold-temperate forests the smallest ($1375 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$) (Wang et al., unpublished data). These results indicate that climate controls the patterns of belowground productivity in terrestrial ecosystems.

Under global change conditions, the scope of climate factors deciding plant species distribution will change. From tropical to boreal regions, soil physical, chemical, and biological processes will also gradually experience change^[19], such as nitrogen mineralization^[17]. Root biogeography research needs to address how these changes will influence the large-scale belowground productivity, as well as patterns and processes of carbon allocation. Large-scale root biogeography studies provide several important research directions for global change biology. In particular these include how root biomass, root turnover rate, vertical distribution patterns, and rooting depth change with vegetation type, climate and human activity, as well as forecasting how root characteristics will change under future climate change conditions.

4 Belowground biodiversity

Research concerning mechanisms of biodiversity have traditionally and without exception concentrated on aboveground portions of plants^[66,67]. Recently, discussion of belowground biodiversity or soil biodiversity has become more frequent^[68], especially in discussing the response of belowground processes to global change. From a global perspective, invertebrates overwhelm all other groups in number of species. Among invertebrates, a large number of them spend some portion of their life history underground^[9]. Soil organisms include soil fungi, bacteria, actinomycetes, as well as annelids, earthworms, and protozoans. This range of organisms ensures that many terrestrial ecosystems have greater biodiversity belowground

than the above. Despite our currently slight understanding of soil biodiversity, the importance of its regulation of ecosystem processes (such as litter decomposition) is well known. Evidence now shows that high habitat heterogeneity and resource availability can enhance soil biodiversity^[68,69]. In terms of the wide variety of species types in the soil, biodiversity decreases monotonically with increasing disturbance, not following the “hump-shaped” pattern which has been often found in aboveground ecosystems^[9]. Therefore, the “intermediate disturbance hypothesis” cannot be applied to soil organisms.

High aboveground species diversity can provide litter material for belowground organisms which is diverse in quality and type. Furthermore, resource heterogeneity can give rise to diversity in decomposers^[70]. Experiments have shown that there exists a unique relationship between some decomposers and the litter material they survive on^[68]. Plants, through root exudates, can also develop co-evolutionary relationships with soil microbes, promoting diversity in other soil organisms. In addition, a wide variety of soil organisms, including termites, earthworms, and ants, as well as decomposed roots, influence the physical characteristics of the soil, providing space for a diversity of other soil organisms. Due to the difficulties in assessing belowground biodiversity, and the large number of species awaiting identification, research into how above- and belowground biodiversity relate will facilitate the assessment of belowground biodiversity and how aboveground determines belowground diversity, with important implications for biodiversity conservation. Future belowground biodiversity research will ask: () Does high aboveground biodiversity necessarily predict high belowground biodiversity? What is the relationship between the two? () If above- and belowground diversity have a determinate relationship at a given scale, will that relationship be maintained at other scales? () Since above- and belowground systems operate under different environmental conditions, do they exhibit analogous responses to environmental gradients? () As aboveground biodiversity experiences disturbance, what kind of modification will occur in belowground biodiversity?

From these relationships it will be possible to deduce whether or not above- and belowground biodiversity exhibit corresponding mechanisms and strategies for recovery.

Due to the limits of observation, sampling, and control, the previous experimental research into biodiversity and ecosystem function rarely considered soil biodiversity, particularly overlooking the influence of soil biodiversity on aboveground plant diversity (feedback)^[71]. Recent experiments have explored this aspect of biodiversity from several perspectives. van der Heijden et al.^[30] showed that high mycorrhizal diversity can lead to high plant diversity. Bradford et al.^[72] used the Ecotron experimental facility to

establish a series of artificial grasslands, each with different levels of soil organism diversity, under a series of climatic conditions. Their results showed that soil biotic community influenced the aboveground community species composition, soil microorganisms, root biomass and mycorrhizal fungus propagation. In addition, De Dyn's Microcosm experiments^[28] have demonstrated that the addition of invertebrates in grassland soil not only can accelerate secondary succession, but also can increase community biodiversity. As with all research into the relationship between biodiversity and productivity, the shortcomings of these experiments stem from time limitations and imperfect research methods. Reynolds et al.^[73] recently proposed that two microbiological processes are likely critical to plant community structure and dynamics, namely that microbes (especially mycorrhizal fungi) exert influence on both plant niche differentiation in resource use as well as on the dynamic feedback between plant and soil communities. This provides a new path for researching mechanisms of species coexistence.

5 Responses of belowground processes to global change

() The effect of soil carbon pool. Global climate change has become increasingly apparent in recent years^[62]. Research into the response of above ground systems to global change has already developed impressively and reached some important conclusions^[74]. However, belowground responses are only weakly understood^[75], despite their equal importance with aboveground systems. Recent research has shown that the terrestrial biosphere is a vast carbon sink, especially northern hemisphere forests^[56,76-79]. These forests play an important role in buffering increases in atmospheric CO₂ concentration ([CO₂]), although large uncertainty about these measurements exists^[56,76], and the soil processes are the sources of this uncertainty^[80]. According to estimates, the carbon pool in the first 1 m of soil may reach 1500—1600 Pg (1 Pg = 10¹⁶ g), more than atmospheric (750 Pg) and terrestrial ecosystem (560 Pg) pools combined^[19]. Therefore, soil carbon pool is critical in slowing the anthropogenic increase of atmospheric [CO₂], and conversely, release of soil carbon will further accelerate the increase of atmospheric [CO₂].

In natural ecosystems, carbon generally enters soil via litter, root turnover, or individual plant death, forming soil organic carbon. Carbon is returned to the atmosphere primarily in the form of CO₂ resulting from soil respiration (including root respiration and soil organism respiration), with a net flux of 75 Pg C·a⁻¹^[81], second only to global net gross primary production of 105 Pg C·a⁻¹^[82]. Therefore, whether or not soils will be a net sink or source essentially depends on the relative CO₂ dependencies or responsiveness of above- and belowground litter inputs and soil organic C decomposition rates and the time scale at which each operates.

() Response to [CO₂] increase. The direct effects of [CO₂] increase on soil should be few, because soil [CO₂] itself is already high compared to that of the atmosphere^[83]. Indirect effects between plants and soil organisms are likely to give rise to several modes of feedback. Litter increase and nitrogen content decrease are commonly observed under increased [CO₂] conditions, which may give rise to either positive or negative feedback on atmospheric [CO₂]^[84]. Strain et al.^[85] first proposed the "litter quality hypothesis", stating that plants grown in elevated [CO₂] will produce litter with reduced N content, producing a negative feedback between plants and atmospheric [CO₂]. The feedback results from a lower decomposition rate of litter, allowing soil to act as a C sink. However, due to an increase in litter quantity and increased root exudates under elevated [CO₂], positive feedback is also likely^[5,84]. Furthermore, the shift in plant assemblage structure resulting from CO₂ enrichment^[18], which can have dramatic effects on litter chemistry and C accumulation in soil, may act as either positive or negative feedback.

Schlesinger et al.^[80] used FACE (free air CO₂ enrichment) techniques to investigate the response of young loblolly pine (*Pinus taeda*) forests in the American South to a 200 ppm increase in [CO₂]. They observed a prominent initial increase in litter C reserves, but due to the rapid C turnover rate a new balance was quickly established, resulting in only a small increase in C reserves. Additionally, He et al.^[86] found that under different nutrient provision conditions [CO₂] increase creates a variety of C allocation patterns in herbaceous plant communities. It is presently unclear whether or not these responses trends differ between coniferous and broad-leaved forests, or whether this trend is representative of other ecosystem types. Our research has found that [CO₂] increase alters patterns of seed C and N allocation (He et al., unpublished data). In temperate grassland ecosystems, several experiments show an increase in soil organic matter under [CO₂] doubling^[87]. Experimental evidence shows that this type of soil organic carbon increase in perennial ryegrass (*Lolium perenne*) grasslands is due to a disproportionate increases in NPP relative to decomposition rate^[88]. However, in an 8-a OTC (open-top chamber) [CO₂] increase experiment in a North American grassland, above- and belowground productivity increases occurred mainly in drought periods. Furthermore, the average increase over many years was not substantial^[89]. This indicates that negative impact of elevated CO₂ on decomposition and nutrient availability may depend on soil water availability. Recently, meta-analysis has shown that under [CO₂] doubling conditions, mature green leaf N content is reduced by 16% compared to natural [CO₂] conditions, but in naturally senescing leaf litter this reduction is only 7.1%^[90]. However, mass loss and respiration rates from litter produced in elevated CO₂ are difficult to ascertain^[90].

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At present it remains unclear if different ecosystems all exhibit this trend towards reduced leaf or litter N content. Lacking knowledge of how litter decomposition responds to $[\text{CO}_2]$ increase hampers the ability of forecasting overall ecosystem response to $[\text{CO}_2]$ increase. Thus, the response of litter decomposition to $[\text{CO}_2]$ increasing conditions is a key future research direction.

() Response to global warming. Temperature is a major factor modifying terrestrial ecosystem biogeochemical processes^[17]. Important carbon cycle processes, such as plant carbon assimilation and allocation, litter accumulation and decomposition, soil respiration and carbon release, are all modified to some extent by temperature^[19]. The sensitivity of soil organisms to temperature is clearly greater than that of aboveground organisms, since even small increases in temperature range can alter belowground physiological processes^[91]. A recent meta-analysis of 32 research sites representing tundra, low tundra, grassland, and forests, show that across all sites and years, 2—9 a of experimental warming in the range 0.3—6.0 significantly increased soil respiration rates by 20% and plant productivity by 19%^[92]. Meta-analysis also shows that, although the degree of response in different ecosystem types varies, the stimulation of soil respiration by soil warming is consistently greater than the enhancement of NPP, likely leading to a decrease in soil C storage. However, these results are based on experiments only 2—9 a in duration. Research has indicated that the sensitivity of soil respiration to temperature can acclimate under consistent warming^[93], which will weaken the positive feedback effect. Different ecosystems respond differently to soil warming. For instance, increasing soil temperatures in forests can produce an increase in soil respiration greater than that of grasslands or tundra, while the same temperature increase can lead to increasing NPP in tundra beyond that of forests or grasslands^[92]. In addition, increasing temperatures will alter the composition of soil microbe and soil animal communities, which will make the prediction depending more on ecosystem types.

() Soil organism feedback on atmospheric $[\text{CO}_2]$. Soil microorganisms mainly concentrate around roots^[21], in order to obtain carbon from root exudates and litter, and thus initiating the belowground food chain^[94]. These organisms create feedback in response to increasing $[\text{CO}_2]$ via reciprocal effects between above- and belowground litter, in a still-unknown fashion. Increasing $[\text{CO}_2]$ is likely to () change plant community composition, () change chemical composition of litter and root exudates, particularly via increasing C/N^[74,90], thus altering the type and constitution of soil organisms' food. As soil organisms are likely to respond differently to these changes, an increase in atmospheric $[\text{CO}_2]$ will influence soil biodiversity by modifying litter type and chemical composition, thereby influencing ecosystem C and N cycles. This im-

plies that mycorrhizal fungi will also experience change under increasing $[\text{CO}_2]$ scenarios^[7,88]. For example, the responses of mutualistic symbionts (mycorrhiza and rhizobia) to high CO_2 are highly sensitive^[88]. A doubling of $[\text{CO}_2]$ can modify arbuscular mycorrhizae type^[95] and the configuration of symbiotic structures^[96]. Climate change, such as higher wintertime temperatures and altered rainfall patterns, can also modify the richness of soil fungi species^[97]. Furthermore, mycorrhiza have decisive influence on the quality of litter material belowground^[98].

Högberg et al.^[13] recently used girdling techniques to skillfully terminate the supply of current photosynthate to root and mycorrhizae, while ensuring the preservation of the root-microorganism-soil system. Their results demonstrated that mycorrhizal respiration contributes at least 50% of total soil CO_2 flux. Further research has shown that of the belowground C allocated by plants, 75% is consumed by soil respiration, leaving only 25% for root development^[99]. This indicates that an alteration of soil organism communities will have a large effect on the whole ecosystem C balance. In a controlled experiment using a solar dome, Fitter^[100] demonstrated that an increase in $[\text{CO}_2]$ did not significantly influence aboveground biomass in a grassland ecosystem. However, root biomass increased by 50%, and root turnover also increased greatly. Using the Ecotron experimental facility to investigate ecosystem implications of elevated $[\text{CO}_2]$, Jones^[101] showed that the distribution of photosynthetically-fixed C in an artificial grassland shifted to the belowground portion. This led rhizosphere microbes to stimulate the provision of greater quantities of root-secreted organic materials, while at the same time increasing root development. These results also show that, despite no obvious change in the biomass of soil microorganisms, the composition of soil fungi was altered, causing an increase in the rate of cellulose decomposition. Since soil animals rely greatly on fungi, it can be speculated that $[\text{CO}_2]$ increase will influence soil animal diversity.

In sum, compared with aboveground systems, under increased $[\text{CO}_2]$ conditions, plants' belowground allocation of C is a complicated ecophysiological process^[6,44], and is a key link in modifying the response of soil organisms to atmospheric $[\text{CO}_2]$ ^[6]. It can be estimated that due to large differences in the root structure and function, ecosystem responses to global change will depend on ecosystem types. On one hand, higher $[\text{CO}_2]$ will input more C below ground, however, at the same time soil respiration will also be stimulated^[81], countering that effect. From another perspective, the reduction in ecosystem carbon storage due to temperature increase will be greater than the increase in NPP. At the same time, soil organisms feed back to both $[\text{CO}_2]$ and temperature increases, although the sensitivity of soil organisms to temperature can be reduced by acclimation. Thus, at present the net effect

of CO₂ and temperature on soil organic C storage and belowground processes is yet unclear. However, without a doubt, research and resolution of these questions has critical theoretical value for the understanding of the mechanisms of belowground processes response to global change.

6 Conclusions

After more than 100 a, aboveground ecological research has revealed the rich diversity of the natural world's ecosystems, and has provided valuable experience for the field of ecology as a whole. Along with the development of global change research, belowground ecology will enter the mainstream of 21st century ecology, since it will reveal what seem now to be intractable mysteries in ecosystems. It emphasizes the interrelationship between physical, chemical, and physiological processes of belowground ecosystems at different scales, as well as their relationship with aboveground processes, and focuses on roots, belowground animals, and soil microorganisms. Half of ecology is belowground. Belowground ecology is a broadly unknown field, urgently requiring research. The advance of modern techniques gives ecologists the confidence and ability to tackle these research questions, but theory, method, and applied techniques remain great challenges, awaiting the attention of creative and talented ecologists.

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