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全球变化对陆地生态系统枯落物分解的影响

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摘要: 了解枯落物分解对大气二氧化碳浓度增高、气候变暖和降水变化的反应, 对深入理解陆地生态系统土壤有机物形成和碳的固化能力(Carbon sequestration)十分重要。通过分析业已发表的文献、实验室根系分解实验和美国西北部针叶林叶片的分解实验, 旨在评估大气二氧化碳浓度增高、气候变暖和降水变化对陆地生态系统枯落物分解的可能影响。大气二氧化碳浓度增高可通过降低枯落物质量和增加草原生态系统土壤水分间接地影响枯落物分解。根据 17 项研究结果, 大气二氧化碳浓度加倍可导致木本和草本枯落物平均氮含量降低 19.6% 和 9.4%; 木质素/氮比值增高 36.3% 和 5.5%。枯落物质地的降低通常导致枯落物分解减慢。气候变暖一般加速枯落物的分解, 但是用于表示这种促进作用的 Q_{10} 随着温度的增高而降低。全球降水变化对陆地生态系统枯落物分解的影响不但取决于现有水分条件而且还取决于降水变化的程度。以美国西北部地区的针叶林为例, 降水改变对森林生态系统枯落物分解的影响将是多元的, 有的增加, 有的降低, 而有的相对不变。最后, 指出了今后在该领域有待加强的几个研究方面。

关键词: 全球变化; 枯落物; 分解基质质量; 分解速率常数

Effects of global change on litter decomposition in terrestrial ecosystems

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Abstract: Understanding the response of litter decomposition to elevated CO_2 atmospheric concentration, global warming, and change in precipitation is of crucial importance in understanding soil organic matter formation and carbon sequestration in terrestrial ecosystems. In this review, we use published results, laboratory incubation results of decomposing roots, and leaf litter decomposition data in the coniferous forests of the Pacific Northwest of USA to assess the potential effects of global change (e.g., elevated CO_2 atmospheric concentration, global warming, and precipitation change) on litter decomposition in terrestrial ecosystems. Elevated CO_2 concentration influences litter decomposition indirectly by decreasing litter substrate quality and increasing soil moisture content in dry grassland ecosystems. According to 17 publishied studies, doubled ambient CO_2 concentration decreased the average N concentration of tree litters and herbaceous litters by 19.6% and 9.4%, respectively. The average lignin: N ratio of tree litters and herbaceous litters increased 36.3% and 5.5%, respectively, due to CO_2 enrichment. Such substrate quality changes should generally lead to a reduction in the decomposition rate of litters. Global warming directly increases litter decomposition, however, the Q_{10} value used to express this stimulatory effect decreased with increasing temperature. The degree that global precipitation change influences litter decomposition will depend on the potential magnitude of this change as well as the current moisture conditions. Even within a single

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region like Pacific Northwest of USA the responses of litter decomposition to altered rainfall can be divergent, with some sites increasing, others decreasing, and others remaining relatively unchanged. Several research areas are identified for reducing the uncertainites in the effects of global change on litter decomposition in terrestrial ecosystems.

Key words: global change; litter; substrate quality; decomposition rate

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Considerable evidence indicates that global changes such as elevated atmospheric CO_2 concentration, global warming, and change in precipitation is occurring. Global emissions of CO_2 grew by about 5 percent between 1992 and 1995, and are at the highest level ever recorded[1]. The mean global temperature has increased by 0.2～0.3 C during the last 40 years[2,3] and it may increase by another 1.5～4.5 C in the 21st century due to the increasing atmospheric CO_2 concentration[2,4]. Precipitation is also expected to changes. An average 5 to 10 percent increase in overall amount of U.S. rainfall occurred in the last 100 years. The frequency of heavy downpours, in which more than 5 cm of rain falls in a day, has increased by about 20 percent[1].

Given concerns of global climate change there has been increasing interest in determining the capacity of terretrial ecosystems for sequestering carbon from the atmosphere[5～7]. Increased atmospheric CO_2 levels typically lead to increase in photosynthetic rates due to CO_2 fertilization effects[8,9], however, the degree this increased production is sequestrated will depend on where it is allocated. If the increased production is allocated to long-lived plant parts increased carbon stores are expected. If the increased production is allocated to litter then the degree of sequestration will depend on the rate of litter decomposition. Litter decomposition is strongly relevant to soil organic matter formation, carbon sequestration, and soil N availability of ecosystems[10]. Thus, to evaluate whether terrestrial ecosystems can sequester more carbon, one needs to determine how plant production and litter decomposition both respond to global change.

Litter decomposition is profoundly influenced by litter substrate quality, climate, and the decomposer community[11,12]. Substrate quality is known to be a driving factor for decomposition. N and lignin concentrations, lignin:N and C:N ratios have all been proposed as predictors of decomposition rate and lignin:N ratio is thought to be one of the best predictors of litter decomposition rate[13～17]. Temperature and moisture content are regarded as the main climatic factors influencing litter decomposition[11,16,18]. Finally, it is through decomposer organisms that the effects of substrate quality, temperature, and moisture on litter decomposition are expressed. Any major change in substrate quality, climatic environment, and decomposer community will influence litter decomposition.

This review begins with a discussion of how elevated atmospheric CO_2 concentration may influence litter decomposition by changing litter substrate quality, climate, and decomposer organisms of terrestrial ecosystems. We compare the tissue N and lignin concentrations of plants grown in ambient CO_2 concentration with those of plants grown in elevated CO_2 concentration using the results of 17 published studies. We further compare the changes in decomposition rates of plant materials produced in elevated CO_2 with those of plant material produced in ambient air. Secondly, we assess how global warming and rainfall change may influence litter decomposition using the results of short term laboratory incubation of decomposing roots and other published studies. Finally, critical areas for future research are identified.

1　Effects of elevated CO_2 on litter decomposition

Elevated atmospheric CO_2 usually does not have direct effect on litter decomposition of terrestrial ecosystems[19]. However, it can influence litter decomposition indirectly by decreasing litter substrate quality

of plants[21,22], changing soil moisture regimes[8,22], and potentially shifting decomposer community of ecosystems[23].

1.1 General approach

Most research on the effects of elevated CO_2 on decomposition utilize litters of plants grown in pots, open top growth chambers, or closed chambers in which plants are exposed to elevated CO_2[24,25]. More recently, plant litters have been collected from plants grown in Free-Air-Carbon-Dioxide Enrichment (FACE) experiments (Rose Matamala 1999, personal communication). The FACE technique provides the possibility to study ecosystem responses of grasslands and forests to elevated CO_2 including the long-term effect of CO_2 enrichment on litter quality. Natural CO_2 springs can also provide a valuable understanding of long-term responses of plant tissue quality to elevated CO_2[26,27]. After obtaining the litters, decomposition experiments are conducted, most using litterbag techniques at ambient CO_2 environments either in laboratory microcosms[24,28~37] or in the field[26,27,38~44]. Very few decomposition studies have been conducted in elevated CO_2 environments such as FACE rings or around natural CO_2 springs[50]. This may impose some limitations in assessing elevated CO_2 effect on litter decomposition which we will discuss later.

1.2 Decrease in litter substrate quality

Elevated atmospheric CO_2 has been reported to affect substrate quality of plant material[24,28,45,46] (Table 1). In general, increasing CO_2 leads to a decrease in the substrate quality of plant tissues[20,21,47,48]. Among such substrate quality changes, decreased N concentration of plant tissues has been widely reported[24,28,34,41,49,50]. The concentration of structural material like lignin is also expected to increase[19,24,25,51,52]. According to 17 studies, N concentration of tree litters produced under double ambient CO_2 environment decreased from 1.1% to 51.5% with an average decrease of 19.6% (Table 1). Similarly, N concentration of herbaceous litters decreased but by a smaller degree (9.4%) on average. The lignin concentration of tree litters increased 6% on average, ranging from a decrease of 48% to an increase of 62%. For the herbaceous plants examined, lignin concentration increased in almost half of them but decreased in the other half (Table 1). Thus, the responses of lignin concentration of plant materials are not as clear as for N concentration. The lignin:N ratio of the litters produced under elevated CO_2 environment increased 36.3% on average in trees versus 5.5% on average in herbaceous plants (Table 1). This analysis suggests that substrate quality of tree species is more susceptible to elevated atmospheric CO_2 concentration than herbaceous plants. Despite that, response of litter substrate quality varies highly with species within trees or herbs. These decreases in the substrate quality of litters should decrease decomposition rate and thus have a negative feedback on litter decomposition[20,27,45].

1.3 Soil moisture content regimes

Elevated CO_2 often results in increased soil moisture content by decreasing stomatal conductance and plant transpiration in dry terrestrial ecosystems[53~55]. Such effects of elevated CO_2 have been measured in California annual grassland[55], Mediterranean grassland[22], and tallgrass prairie. Field *et al.*[55] found that soil moisture content under elevated CO_2 concentration increased 25% in the surface layer and 50% in the deeper layers in fertile sandstone soil as compared to the control. Increased soil moisture content has been observed to increase litter decomposition in the grassland site[56]. However, soil moisture content increase was not detected in the FACE rings of loblolly pine (*Pinus taeda* L.) forest in North Carolina of USA (Rose Matamala 2000, personal communication). Insufficient studies are available to generalize the effects of elevated CO_2 concentation on soil moisture content of forest ecosystems and the topic deserves further exploration. Generally speaking, the increased soil water availability should have a positive feedback on litter decomposition by enhancing the activities of soil decomposers, especially in dry ecosystems[8,57].

1.4 Decomposer community

The CO_2 concentration in the soil greatly exceeds atmospheric CO_2 concentration[58], therefore a doubling of atmospheric CO_2 concentration is not expected to affect soil microbial composition and structure directly. Hence, the impacts of elevated atmospheric CO_2 concentration on soil microorganisms should largely be indirect[59,60]. One such indirect impact is that soil organisms are commonly carbon-limited and increased carbon availability (e. g., root exudates) generally stimulates microbial growth and activity[19,23,61~64]. Increased dominance of saprophytic fungi in the soil microbial community was reported under elevated atmospheric CO_2 concentration[19,23]. This may enhance decomposition and nutrient cycling of litters. However, most studies found no shift of soil organism community composition in terrestrial ecosystems under long-term CO_2 enrichment treatment[65,66]. Zak *et al*.[65] found no evidence suggesting a shift in the soil organim composition and structure in poplar forest soil under elevated CO_2 atmospheric environment. Elevated atmospheric CO_2 appears to have no significant effect on the composition and function of soil organisms, thus it probably has no effect on litter decomposition of terrestrial ecosystems from the aspect of soil organisms.

1.5 Change in decomposition rates of litters

Decomposition rates of litter produced in elevated atmospheric CO_2 and experimentally decomposed in the laboratory or in the field ambient CO_2 environment were compiled from 16 studies (Table 2). Of the 41 values for decomposition rate, 16 decreased, 7 increased and 18 showed no effect (Table 2). All 15 tree litter comparisons showed a decrease or no change in decomposition rate. In contrast, only 19 values of decomposition rate among the 26 herbaceous litters showed a decrease or no change. Seven of the herbaceous litters even increased decomposition rate. These results are consistent with the substrate quality responses of different life from plants in elevated CO_2 environment with tree species being more susceptible to a decrease in litter substrate quality than herbaceous plants (Table 1). In some studies, the decrease in litter substrate quality does not necessarily lead to a decrease in the litter decomposition. This is in part because the decrease in litter substrate quality is not biologically significant (Table 1).

1.6 Decomposition rate predictions using initial lignin:N ratio of litter

Initial lignin:N ratio is proved to be one of the best predictors of decomposition rate (k) of litters[15,17]. Harmon *et al*.[15] found that the value k of leaf litter was negatively correlated to initial lignin:N ratio (Fig. 1a). It decreased 0.016 per year with each unit of lignin:N ratio increase. We developed a similar model based on fine root litter (Fig. 1b). The value of k decreased 0.041 per year with each unit of lignin:N ratio increase. This suggests that increased lignin:N ratio caused by CO_2 enrichment would lead to a greater decrease in fine root decomposition than that in leaf litter. These empirical models can be used to assess the effects of substrate quality change on litter decomposition due to elevated CO_2 concentration.

The net effects of elevated CO_2 on litter decomposition should be the result of trade-off between CO_2 negative feedback through decreasing substrate quality of litters and CO_2 positive feedback by increasing soil water availability. However, all the decomposition studies examined were carried out at ambient CO_2 environments. Therefore, these studies have limited implications for assessing effects of elevated CO_2 on litter decomposition because they were not conducted in elevated CO_2 environment. Thus the CO_2 positive feedback controls of increased soil moisture content caused by elevated CO_2 on decomposition have not been accounted for[20,27]. Moreover, all these decomposition studies were short-term, ranging from 20 days to 300 days for laboratory microcosm incubations. For the field decomposition studies, most of studies were within a one-year period, the longest lasted 550 days and the shortest was only 61 days (Table 2). This creates a problem because litter decomposition generally lasts much longer with a faster decomposition stage initially

Table 1 Concentrations of N, lignin and lignin:N ratio in plant material grown in ambient air or an elevated atmospheric CO_2 environment[1]

Species	Type[2]	N%			lignin%			lignin:N			References
		Ambient CO_2	Elevated CO_2	Change[3]	Ambient CO_2	Elevated CO_2	Change[3]	Ambient CO_2	Elevated CO_2	Change[3]	
Trees											
Acer pseudoplatnus	L	0.57	0.46	−19.3	9.1	9.8	7.7	16.0	21.3	33.4	[24]
Betula pubescens	L	1.40	0.94	−32.9	13.5	16	18.5	9.6	17.0	76.5	[24]
Betula pubescens	L	1.18	0.88	−25.4	17.7	28.7	62.1	15.0	32.6	117.4	[41]
Betula pubescens	R	2.25	1.93	−14.2							[30]
Castanea sativa	L	1.30	0.63	−51.5	17.1	8.8	−48.5	13.2	14.0	6.2	[29]
Castanea sativa	ST	0.75	0.67	−10.7							[82]
Castanea sativa	R	1.60	1.32	−17.5							[82]
Castanea sativa	GL	1.65	0.98	−40.6							[82]
Cecropia peltata	L	1.35	1.18	−12.6	19.9	21.2	6.5	14.7	18.0	21.9	[42]
Cecropia peltata	GL	1.94	1.77	−8.8							[42]
Elettaria cardamomum	L	0.82	0.68	−17.1	11.9	10.7	−10.1	14.5	15.7	8.4	[42]
Elettaria cardamomum	GL	2.03	1.85	−8.9							[42]
Fagus sylvatica	L	1.25	1.06	−15.2	11.3	12.7	12.4	9.0	12.0	33.3	[44]
Ficus benjamina	L	0.92	0.91	−1.1	11.7	12.9	10.3	12.7	14.2	11.5	[42]
Ficus benjamina	GL	2.34	2.24	−4.3							[42]
Fraxinua excelsior	L	1.14	0.84	−26.3	6.1	7.4	21.3	5.4	8.8	64.6	[24]
Picea abies	B	0.90	0.60	−33.3	22.5	22.8	1.3	25.0	38.0	52.0	[44]
Picea sitchensis	GL	2.95	2.85	−3.4	13.5	17	25.9	4.6	6.0	30.3	[24]
Picea sitchensis	R	1.30	0.90	−30.8							[30]
Quercus alba	L	1.20	0.97	−19.2	4.5	2.9	−35.6	3.8	3.0	−20.3	[83]
Mean		1.4	1.2	−19.6	13.2	14.2	6.0	12.0	16.7	36.3	
Standard deviation		0.6	0.6	13.2	5.4	7.3	28.6	6.0	10.1	36.9	
Herbs											
Andropogon gerardii	S	0.39	0.42	7.7	14.8	15.1	2.0	37.9	36.0	−5.3	[39]
Avena fatua	S	0.67	0.68	1.5	8.07	7.04	−12.8	12.0	10.4	−14.0	[47]
Avena fatua	R	0.58	0.58	0.0	15.93	13.75	−13.7	27.5	23.7	−13.7	[47]
Cares curvula	SS	1.29	1.16	−10.1	8.1	7.7	−4.9	6.3	6.6	5.7	[42]
Carex flaca	GL	1.05	0.99	−5.7	10.5	10.4	−1.0	10.0	10.5	5.1	[42]
Danthonia richardsoni	L				25.8	27.3	5.8				[37]
Danthonia richardsoni	R				43.3	44.3	2.3				[37]

续表 1

Species	Type[2)]	N%			lignin%			lignin:N			References
		Ambient CO_2	Elevated CO_2	Change[3)]	Ambient CO_2	Elevated CO_2	Change[3)]	Ambient CO_2	Elevated CO_2	Change[3)]	
Festuca vivipara	SS	2.70	2.40	−11.1	11.5	11.7	1.7	4.3	4.9	14.5	[43]
Festuca vivipara	R	1.50	1.40	−6.7	28	25	−10.7	18.7	17.9	−4.3	[43]
Gossypium hirsutum	R	3.60	3.00	−16.7	13	11.2	−13.8	3.6	3.7	3.4	[31]
Gossypium hirsutum	S	0.80	0.65	−18.8	24.7	23.7	−4.0	26.8	32.4	20.9	[31]
Gossypium hirsutum	GL	1.70	0.90	−47.1							[49]
Graminoid mixture	SS	1.09	1.06	−2.8	7.6	7.7	1.3	7.0	7.3	4.2	[42]
Graminoid mixture	GL	2.62	2.34	−10.7							[42]
Lolium perenne	R	1.08	0.79	−26.9	8.4	9.5	13.1	7.8	12.0	53.8	[50]
Plantago erecta	S	1.11	1.11	0.0	3.73	3.7	−0.8	3.4	3.3	−0.8	[47]
Plantago erecta	R	0.71	0.62	−12.7	7.4	7.28	−1.6	10.4	11.7	12.7	[47]
Poa pratensis	SS	1.21	1.04	−14.0	11.6	10.9	−6.0	9.6	10.5	9.4	[39]
Poa pratensis	GL	1.38	1.21	−12.3							[84]
Scripus olneyi	SS	0.44	0.40	−9.1	20.5	20.1	−2.0	46.6	50.3	7.9	[35]
Sorghastrum nutans	SS	0.39	0.40	2.6	12.7	12.5	−1.6	32.6	31.3	−4.0	[39]
Spartina patens	S	0.51	0.53	3.9	14.2	14.4	1.4	27.8	27.2	−2.4	[35]
mean		1.2	1.1	−9.4	15.3	14.9	−2.4	17.2	17.6	5.5	
Standard deviation		0.9	0.7	12.3	9.6	9.6	6.9	13.4	13.6	15.6	

1)This table is modified from Couteaux *et al.*[21] and the elevated atmospheric CO_2 treatments used double ambient air or higher CO2 concentration. 2)L=litter, mainly senescent leaf, GL=green leaves, S=shoots, SS=senescent shoots, ST=stem, R=roots, B=branch. 3)Change(%)=100×(value at elevated atmospheric CO_2−value at ambient air)/value at ambient air

Table 2　Change in decomposition rate of plant material grown in elevated CO_2 and decomposed in ambient air[1)]

Species	Type[2)]	Method	Site	Decay period (d)	Change in decay rate(%)[3)]	Reference
Trees						
Acer pseudoplatnus	L	Microcosms	Laboratory	243	=	[24]
Betula pubescens	L	Microcosms	Laboratory	155	−53	[24]
Betula pubescens	L	Litterbags	Field	365	−12	[41]
Betula pubescens	L	Microcosms	Laboratory	91	=	[30]
Betula pubescens	R	Microcosms	Laboratory	91	=	[30]
Castanea sativa	L	Microcosms	Laboratory	300	−23	[21]
Cecropia peltata	L	Litterbags	Field	130	=	[42]
Elettaria cardamomum	L	Litterbags	Field	130	=	[42]
Fagus sylvatica	L	Litterbags	Field	331	−5	[44]
Ficus benjamina	L	Litterbags	Field	130	=	[42]

续表 2

Species	Type[2)]	Method	Site	Decay period (d)	Change in decay rate(%)[3)]	Reference
Fraxinua excelsior	L	Microcosms	Laboratory	170	−26	[24]
Liriodendron tulipifera	L	Litterbags	Field	365	=	[38]
Picea abies	B	Litterbags	Field	331	−3	[44]
Picea sitchensis	GL	Microcosms	Laboratory	155	−9	[24]
Picea sitchensis	R	Microcosms	Laboratory	91	=	[30]
Herbs						
Andropogon gerardii	S	Litterbags	Field	550	=	[39]
Avena fatua	S	Microcosms	Laboratory	152	+10	[36]
Avena fatua	R	Microcosms	Laboratory	152	+8	[36]
Bromus hordeaceus	S	Microcosms	Laboratory	152	+8	[36]
Bromus hordeaceus	R	Microcosms	Laboratory	152	+20	[36]
Carex curvula	SS	Litterbags	Field	61	−6	[42]
Carex flaca	GL	Litterbags	Field	216	=	[42]
Danthonia richardsonii	L	Mixed with soil	Laboratory	297	−34	[37]
Danthonia richardsonii	R	Mixed with soil	Laboratory	150	−22	[37]
Festuca vivipara	SS	Litterbags	Field	400	−10	[43]
Festuca vivipara	R	Litterbags	Field	405	=	[43]
Gossypium hirsutum	R	Microly simeters	Silt loam	59	=	[31]
Gossypium hirsutum	S	Microly simeters	Clay loam	59	=	[31]
Graminoid mixture	SS	Litterbags	Field	216	=	[42]
Graminoid mixture	GL	Litterbags	Field	216	=	[42]
Lolium multiflorum	S	Microcosms	Lab	152	+17	[36]
Lolium multiflorum	R	Microcosms	Lab	152	+26	[36]
Lolium perenne	R	Mixed with soil	Field	460	−14	[50]
Lolium perenne	R	Mixed with soil	Lab	64	−30	[32]
Lolium perenne+ *Triforlium repens*	S+R	Mixed with soil	Lab	20	+5	[33]
Poa pratensis	SS	Litterbags	Field	550	=	[39]
Scripus olneyi	SS	Mescosms	Lab	30	−17	[35]
Sorghastrum nutans	SS	Litterbags	Field	550	=	[39]
Spartina patens	S	Mescosms	Lab	30	=	[35]
Vulpia microstachys	S	Microcosms	Lab	152	−17	[36]
Vulpia microstachys	R	Microcosms	Lab	152	−3	[36]

1) This table is modified from Couteaux *et al*.[21] and the decomposition studies were conducted in ambient CO_2 environment. 2) L=litter, mainly senescent leaf, GL=green leaves, S=shoots, SS=senescent shoots, ST=stem, R=roots, and B=branch. 3) Decomposition rate of litters dervied from plants exposed to elevated CO_2 environment decrease(−), the same(=), or increase(+)compared to the controls

and then slows markedly with time. For example, Chen[17] found the decomposition rates of fine roots after two-year field incubation were 50% lower than the first-year decomposition rate. Thus, long-term litter decomposition experiments in elevated CO_2 environment such as FACE rings are needed to determine the degree of reduced decomposition rates of litters from a range of grassland and forest species grown under elevated CO_2.

2 Effects of global warming on litter decomposition

An increased mean global temperature of 1.5~4.5℃ is expected to occur within the 21st century as a consequence of increased atmospheric CO_2 and other greenhouse gases[2]. Global warming will affect litter decomposition directly and indirectly, but of special concern in this review is the direct stimulation of litter decomposition by global warming. In addition, global warming may indirectly affect litter decomposition by changing species composition[8,39], litter substrate quality[39], soil nutrient availability, and thaw depth in high latitude ecosystems[67]. The effect of global warming on litter decomposition of terrestrial ecosystems by changing species composition and then litter substrate quality may be significant, especially on some grassland ecosystems[8,56,58].

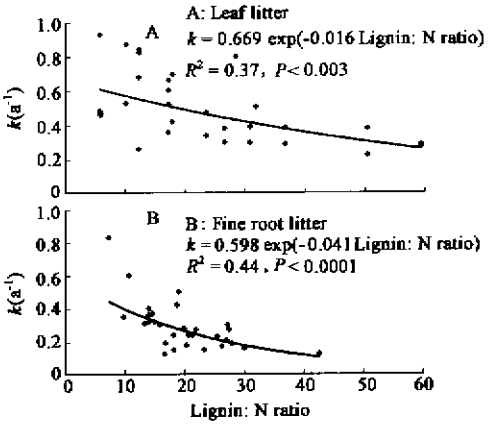

Fig. 1 Decomposition rate (k) as a function of initial lignin:N ratio of litter[1]

A is modified from Harmon *et al.*[15] and B is modified from Chen[17].

2.1 General approach

The most common techniques used to study the impact of global warming on litter decomposition are laboratory incubations, buried heating cables, air-heated open-top and closed chambers, and infrared heaters[8,15,18]. Except for the laboratory incubation method, all these techniques are expensive but easily replicated experiments. There are a few relatively low-cost and easily implemented approaches, including cross-site decomposition experiments and reciprocal transplant technique. Long-term Intersite Decomposition Experiment Team (LIDET) is a good example. The LIDET decomposition experiments have been installed at 28 sites that span a wide array of ecosystems, from moist tundra to warm desert to shortgrass steppe to moist and dry tropical forest across the America[68,69]. This experiment used multiple sites to test, in part, the impact of temperature on long-term decomposition of fine litter. The reciprocal transplant technique is used by swapping low temperature site litter to high temperature site for decomposition and vice versa[70]. These two approaches are useful in testing how global warming will influence litter decomposition. However, the extent of decoupling temperature effect and other controls of litter decomposition remains a concern in these approaches.

2.2 Stimulation of litter decomposition

The general laboratory response of decomposing litters to warming treatments was very similar: enhanced decomposition with increasing temperatures up to an optimum temperature, and retarded decomposition with temperature above that point[18,71~73]. The optimum temperature for decomposition of litters of temperate forests usually was between 30℃ to 40℃[18,72]. Similarly, the respiration of litter of eucalyptus forests reached a peak at 33~34℃[73]. For the Alaska Tundra, the optimum temperature of organic residues was 25℃[71]. Thus, global warming (1.5~4.5℃) should stimulate litter decomposition. The temperature response of this stimulation (usually it is measured by litter respiration) is frequently expressed by

the Q_{10} coefficient: the increase in respiration to a 10 C rise in temperature. It is often assumed to approximate 2.0 for biological systems, but values between 1.3 and 4.0 have been recorded for many temperate and tropical litters over temperature ranges between −10 C and 40 C[18]. Q_{10} value tends to be higher under cold regimes and lower under hot regimes. Thus while de Boois[74] recorded $Q_{10}=2$ response over 5～15 C for microbial respiration in temperate woodland leaf litter, the Q_{10} for litter in the Arctic was 3.7 between 0～10 C[75] and 4 in tundra averaged over 10 C increments from −10～25 C[76]. Even in the same biome, Q_{10} value of litters shows a similar pattern, with higher Q_{10} values at low incubation temperatures and lower values at high incubation temperatures[18]. Chen *et al.*[18] found that the Q_{10} of respiration of decomposing roots in the coniferous forests of the Pacific Northwest of USA was significantly influenced by incubation temperature (Table 3). Moreover, there are strong interactive effects of temperature and moisture on litter respiration[71～73,76]. Flanagan and Veum[71] indicated that at lower moisture contents (<50% of dry weight) temperature increases had little effect on respiration of tundra litters, but at higher moisture contents (100%～225%), respiration was more responsive to temperature changes.

Table 3 Impact of incubation temperature on the Q_{10} of resipiration rate of decomposing woody roots[1)]

	Temperature range (C)			
	5～10	10～15	15～30	30～40
Mean	3.99	2.40	2.02	1.37
Standard deviation	3.12	1.24	0.58	0.68

1) This table is modified from Chen[17].

Despite effects of temperature on Q_{10} a simple constant Q_{10} of 2 has been widely used in modeling warming effects on decomposition of soil organic matter and other organic detritus, regardless of temperature conditions or biome[77,78]. This may lead to a significant understimate of carbon release from litters in a colder climate. Ideally, models should use a Q_{10} value>2 for boreal forests and tundra due to the low annual temperatures, and a value≤2 then for tropical forest or savanna. An example of the Pacific Northwest of USA illustrates the importance of choosing an appropriate Q_{10} value. The carbon release from decomposing litters in ponderosa pine forests at Oregon, USA would be doubled if the annual temperature increases from the current value of 6 C to 10 C and a Q_{10} value of 4 is used. In contrast, if the traditional Q_{10} value of 2 is used the carbon release of decomposing litter would increase only 1.4 fold. Therefore varying the Q_{10} value from 2 and 4 would result in a 60% difference in the carbon released. Modeling global warming effects on decomposing litters of terrestrial ecosystems could be made more realistic by using a temperature dependent Q_{10} value in models. As most previous studies on Q_{10} are from laboratory incubations, more field studies on Q_{10} variation with temperature are needed.

3 Effects of change in rainfall on litter decomposition

Although it is still uncertain how global rainfall will respond to elevated atmospheric CO_2 and global warming, analysis of US rainfall records indicated that an average 5 to 10 percent increase overall in the amount of precipitation occurred in the last 100 years[1,79]. Warmer air will hold more water, therefore some areas may be drier while others may become wetter. Litter decomposition is strongly influenced by litter moisture content[12]. Litter moisture content is positively correlated amounts of rainfall and soil moisture content[17]. However, there are few models that directly predict litter moisture content. Change in global rainfall will have a direct impact on litter decomposition by influencing the respiration of decomposer organisms.

3.1 General approach

Laboratory incubations using different moisture content litters have been used to test the effects of moisture change on litter decomposition[18]. This approach is simple and useful, although the decomposition is not measured under natural environmental conditions. Another approach is field decomposition studies with precipitation manipulation. The Throughfall Displacempent Experiment (TDE) was designed to examine ecosystem responses to long-term decreases in water availability[80]. Litter decomposition was conducted to examine how change in rainfall would influence decomposition rate of litters (Joslin 1998, personal communications). Cross-site decomposition experiments such as LIDET under different moisture content gradient that we described in previous section is another example.

3.2 Moisture effects

Both extremely low and high moisture contents can limit the activity of decomposer organisms[71,75]. According to Chen[17], water was generally not available for the metabolic activity of microbes if moisture content of decomposing woody roots was below 30% (the fiber saturation point). Increasing moisture content enhanced respiration of roots until an optimum moisture range was reached. This optimum moisture content ranged between 100% to 275% depending on the species examined (Fig. 2). When root moisture content was above the optimum range, excess moisture probably retarded decomposition by reducing the diffusion rate of oxygen[81]. Too little or too much water inhibited or even stopped litter respiration due to matric limitation or oxygen diffusion limitation, respectively[17,71,75]. Moreover, there are strong interactive effects of moisture and temperature on litter respiration[71~73,75]. Flanagan and Veum[71] indicated moisture changes had little effect on litter respiration at lower temperatures (<5 C), while at higher temperature (10 ~15 C) respiration was more responsive to moisture changes.

3.3 Effects of rainfall change

The degree that global rainfall change will influence litter decomposition depends on the potential magnitude of this change as well as the current moisture conditions[17]. If the current moisture condition in an ecosystem is optimal for litter decomposition then significant change in rainfall in either direction may result in a decrease in litter decomposition. However, if water is a limiting resource in the ecosystem then increased rainfall will enhance litter decomposition. In contrast, decreased rainfall will further slow down litter decomposition in a water stressed ecosystem. If too much water is available in the ecosystems then decreased rainfall will enhance litter decomposition by improving moisture condition for decomposer organisms. This is exactly what was observed in the woody root decomposition simulation experiment of the Pacific Northwest coniferous forests of USA[17]. Woody root decomposition at the wettest coastal site and the driest site was more responsive to change of rainfall than the site with good moisture condition (Fig. 2). Thus, even within a single region the responses of litter decompositton to altered rainfall can be divergent, with some sites increasing, others decreasing, and others remaining relatively unchanged. In evaluating the impact of altered rainfall on litter decomposition, one should consider the heterogeneous response of litter decomposition among different sites.

4 Future critical research areas

Understanding the responses of litter decomposition to elevated CO_2 concentration, global warming, and change of rainfall is needed at scales ranging from ecosystems to the globe. This review focused on the main mechanisms that how the global change influences litter decomposition based on laboratory incubation or/and field studies of relatively small plot sizes. This knowledge will form the basis to further scaleup. Several research areas are identified for reducing the uncertainties in the effects of global change on litter decomposition in terrestrial ecosystems.

4.1 Long-term litter decomposition experiments under elevated CO_2 environments such as FACE sites

and natural CO_2 springs are needed. Litter decomposition experiments at ambient CO_2 environments do not accounted for the positive feedback of increased soil moisture content caused by elevated CO_2 on decomposition. Moreover, the results from short-term decomposition studies are very limited and are not necessarily correlated to the long-term litter decomposition patterns[17]. The current FACE network provides ideal conditions for cross-site comparisons to fully examine the elevated CO_2 on litter decomposition in different terrestrial ecosystems. To date, more than 10 FACE facilities are operating in the network, mostly in USA. Ecosystems being examined range from a temperate pine plantation, a closed-canopy temperate deciduous forest, a Mediterranean type shrub, temperate grasslands, to agronomic crops.

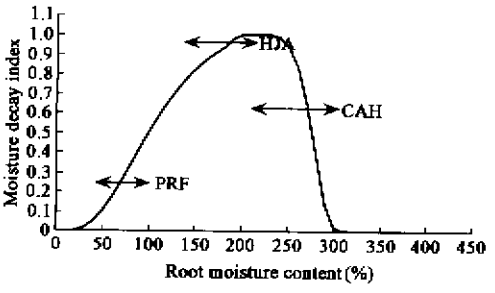

Fig. 2　Moisture decay index as a function of woody root moisture content. Horizontal arrow indicates the root moisture content range between the driest and wettest season at the coastal Cascade Head site (CAH), H. J. Andrews site (HJA), and the driest Pringle Falls site (PRF) at the Pacific Northwest of USA[1]. Fig. 2 is modified from Chen[17] and moisture decay index is a relative index to measure moisture effect on litter decomposition rate and its calculation sees Chen[17].

4.2　Large-scale, cross-site, and long-term litter decomposition experiments under ambient environment are still very valuable in examining the effects of substrate quality and climate on decomposition. This relatively a low cost and easy technique will prove useful when high cost FACE facilities are not available.

4.3　Integrated experiments to test elevated CO_2 concentration, global warming, and increased rainfall on litter decomposition together are essential because these changes will not act alone. Morec over, the interactions among environment factors such as temperature and moisture play important roles in influencing litter decomposition.

4.4　More field studies on variation of Q_{10} value with temperature are needed because most previous studies on Q_{10} are from laboratory incubations.

4.5　In assessing the effect of global warming on litter decomposition, we only reviewed the direct stimulation of litter decomposition by global warming. Global warming could affect litter decomposition indirectly. For example, global warming may change species composition of ecosystems and thus litter substrate quality[8]. Such indirect effects may be very important in grassland ecosystems[35,38]. This topic deserves further exploration.

4.6　Litter moisture content directly influences litter decomposition. However, how litter moisture content quantitatively responds to change in precipitation is not clear. Thus, more studies on moisture balance of litter are needed in predicting effects of change in precipitation on litter decomposition.

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