

Variable Responses of Leaf C, N and P to Climatic Factors in Different Regions and Growth Forms

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Abstract—Plant ecological stoichiometry, which is one of the most important tools to connect the components among different levels of ecosystem, has obtained increasingly extensive concern, especially on its responses to the environmental gradients. Based on the published literatures and datasets, this article focused on reviewing the variable responses of plant foliar ecological stoichiometry to the climatic factors, such as temperature, water, elevated CO₂, and found that foliar ecological stoichiometry responded dynamically to climatic variations among different regions and different growth forms. Then, research status and deficiency were summarized and the expectation on studying the relationships between plant C, N and P ecological stoichiometry and environmental variations which can provide a reference to understand how plants will respond to global change in the future was pointed out.

Keywords—Climatic variations, terrestrial plant, foliar ecological stoichiometry, temperature, precipitation, drought, elevated CO₂

I. INTRODUCTION

AS a new cross-subject, ecological stoichiometry focused on the research of the balance between ecosystem energy and chemistry elements (such as carbon, nitrogen and phosphorus) [1] that connected the individuals, groups and the whole ecosystem, even included the structure and function of ecosystem [2], [3]. At first, it mainly applied in researching aquatic ecosystem [4], [5]. With the extending of study field, terrestrial ecosystem, the more complicated ecosystem, had also been obtained ever-growing attention from the aspect of plant ecological stoichiometry [6]-[8].

C, N and P, which are macro-elements in plants and of the most important nutrient elements, played vital role on plant growth and exhibited irreplaceable leaf chemical traits [1], [9]. Leaf N:P had been verified to be indicator of the type of nutrient limitation [3], [10], which was largely determined by P dynamics rather than N when facing varied environmental factors [10]-[12]. Human activities have significantly changed the environment where the things lived on, such as elevated atmospheric CO₂, nitrogen deposition, warming and altered precipitation. Studying these influences of environmental changes on terrestrial plant C, N and P content, concentration and the stoichiometry can contribute to the exploration of plant species interaction, the range of plant distribution and plant adapting strategy etc. [13].

A lot studies had investigated the relationships between climatic factors and foliar traits, including the influences of irradiance [14], warming, precipitation, drought, elevated CO₂ and N deposition. According to the compiled published literatures, environmental gradients had profoundly altered C, N and P cycles in ecosystems [15]-[17], and the correlations between plant stoichiometry and environmental impacts not only varied in different regions [15], [18]-[20] but also in different plant species [18], [20]-[23], different plant tissues [24]-[28] and different nutrients [16], [29], [30]. Some studies discovered that the N and P content and N:P ratios in leaves presented relationships with climatic factors [12], [15], [18], [31], but inversely, other studies pointed out that there was no relationship between the plant ecological stoichiometry and climatic influences, or the variations of foliar N and C:N ratio mostly attributed to the life form and genus identity rather than climate effects [32]-[35]. Consequently, Sardans considered that the relationships between the plant nutrients contents/concentration, ecological stoichiometry and the environmental effects can vary in different regions [20]. Furthermore, Ordoñez discovered that climate expressed less direct influence on the variance of leaf traits than soil nutrients, but it can highly interact with soil nutrients to indirectly affected leaf stoichiometry [36]. Many researches also had elaborated that when responding to environmental factors, leaf P, which was mainly determined by both plant growth form and environmental factors, had the greatest variability. Leaf N:P came secondly, but leaf N, which was mainly determined by plant growth form, manifested more stability and homeostasis [1], [10], [12].

To well understand how the climatic variations changed the foliar ecological stoichiometry, the responses of leaf nutrient traits in different regions, different growth forms to temperature, precipitation, drought and elevated CO₂ will be proposed, based on the published literatures and datasets. The aims of this study are: (1) to find the different variable mechanisms of plant ecological stoichiometry in different regions, including the discrepancy at global scales in comparison with regional scales, (2) to explore the varying pattern of foliar ecological stoichiometry among different plant growth forms, and (3) to put forward several expectations concerning the effects of environmental variations on plant ecological stoichiometry.

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II. CLIMATIC FACTORS

A. Temperature

1) Carbon

Although at the global scale, C was out of consideration when studying the relationships between foliar chemical traits and climatic changes, C had consistent variation tendency that increased with elevated temperature among most of different regions and growth forms (Table I), the number of species responses come to 87% when we considered C (Fig. 1). Of course, there also existed a reverse tendency that can be found in different growth types and two study sites located in North America [37], [38], and the number account came to 17% (Fig. 1).

2) Nitrogen

From global perspective, Sardans discovered warming can increase, reduce, or had no impair on foliar N depending on the growth type of plant and the climate where it grows [39].

From the aspect of global scale, four authors found leaf N expressed decreasing tendency with growth warming [14]-[16], [40], and two scholars considered that leaf N increased under elevated temperature based on experiments [36], [41], only one study displayed temperature had no effects on leaf N [31].

With the respective of the regional view, in Europe, leaf N of tree showed increasing under elevated temperature at large-scale [42], [43], but the leaf N of moss and shrub in Scottish low-alpine displayed no responses [44], and in Eastern Finland, leaf N of tree inversely expressed reduction when enhancing the environmental temperature [45]. Across the whole China, Eastern China and Qinghai-Tibetan Plateau, leaf N of various plant forms had coincident responses to temperature, and were in line with the global pattern that leaf N showed negative relations to temperature [12], [19], [46]-[48]. However, in Loess Plateau, typical desert of Northern China and Northeast China, the positive relationships between leaf N of various plant forms and temperature had been obtained by investigation [33], [35]. According to the studies in Catalonia by Sardans, consistent positive correlations of foliar N and temperature were found in trees but opposite appearance in shrubs [17], [49]-[52]. In the North America, leaf N of shrubs and herbs in Canada showed no change under warming, but leaf N of other plant forms in USA except Corvallis showed negatively significant relation to warming [25], [37], [38], [53], as well as the herbs in Antarctic [54] (Table I).

Leaf N declined along with warming not only at global scale but also the regional scale. The variation can be verified by the ratio of 4/7 at global scale and 21/36 at regional scale (Fig. 1), and leaf N of different plant forms exhibited no apparent difference from all regions, but in part area, the discrepancy can be found [38]. Furthermore, although temperature reduced leaf N concentrations, the responses still expressed completely opposite changes between green leaf and leaf litter [55], of which we should take account in further research.

3) Phosphorus

On global scale, negative relationships between leaf P and

temperature were elaborated in most studies except for investigation by Aerts [41], but the reason may be just as leaf N, responses of which expressed completely opposite variation between green leaf and leaf litter. Consistent responses of leaf P to warming as global scale were found in most regions, the number of studies account to 13 of 20 studies, and the negative changes also showed significantly, yet the positive variations which were few in number expressed no significant relations [18], [33], [49], [51].

4) Ratios of Nitrogen to Phosphorus

To ratios of N to P, responses to temperature were completely consistent among global scales, as well as regional scales, which showed significantly positive along with elevated temperature, except for three studies which expressed inverse variation, one in Loess Plateau, and two in Catalonia, and three studies that displayed no effects in mountains of Scottish and Catalonia. No obvious differential rule can be discovered in different plant forms. Furthermore, based on the compiled dataset, we can further demonstrate ratios of N to P were mainly determined by leaf P but not leaf N [10]-[12]. Firstly, leaf N:P demonstrated increasing tendency when leaf N and leaf P both decreased in most studies. Secondly, leaf N:P always exhibited increasing variations when leaf P declined despite leaf N increased or decreased along with elevated temperature (Table I). So, leaf N:P had positive relations to warming in most regions and plant forms, it reached 18 in 24 studies (Fig. 1).

Except for the direct research between leaf chemical traits and temperature, indirect studies also had been investigated. In New Zealand, highly significant decreasing of foliar N concentrations of 24 grass species with the increasing altitude were observed, and the altitude had been verified significantly negatively correlating to temperature [56], and as well as in New England, USA [57].

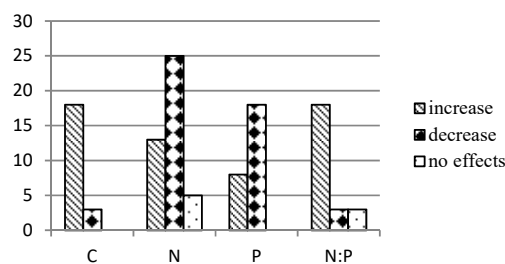


Fig. 1 Number of reported increase, decrease, and no effect of leaf C, N, P and N: P in response to warming

Generally, with the respective of the regional view, the responses of leaf C, N, P and N:P stoichiometry to the temperature presented different variations. Leaf chemical traits in most regions exhibited the agreement with the global scale, and the obvious discrepancy existed among small regions, as well as different plant forms. Actually, we can obtain that different responses to warming of plant ecological stoichiometry can be observed to vary across different regions, growth forms, even though times [58]. In different time, the

responses exhibited highly significant, generally significant or no significant relationships [59]. Of course, warming not only

changed the nutrient concentrations of green leaf but also the senesced leaf and leaf litter [41], [42], [60].

TABLE I
THE RESPONSES OF LEAF C, N, P AND N: P TO TEMPERATURE IN DIFFERENT REGIONS AND GROWTH FORMS

study site	plant	growth form	plant ecological stoichiometry				reference
			C	N	P	N: P	
global	-	-	-	leaf↓	leaf↓*	-	[16]
global	-	-	-	leaf↓***	leaf↓***	leaf↑**	[15]
global	-	-	-	no	leaf↓**	leaf↑**	[31]
global	-	-	-	leaf↑*	leaf↓*	leaf↑*	[36]
global	<i>mangroves</i>	tree	-	leaf↓***	leaf↓***	leaf↑	[40]
global	-	-	-	litter↑*	litter↑	litter↑*	[41]
global	-	-	-	leaf↓**	-	-	[14]
Eurasia	-	tree	-	leaf litter↑***	-	-	[42]
Europe	<i>Norway spruce</i>	tree	-	leaf↑***	leaf↓***	leaf↑***	[43]
Scottish low-alpine	<i>Racomitrium anuginosum</i>	moss	-	no	leaf↓**	no	[44]
	<i>Calluna vulgaris</i>	shrub	-	no	leaf↓**	no	
Eastern Finland	<i>Pinus sylvestris</i>	tree	-	leaf↓	leaf↓**	leaf↑	[45]
China	-	various kinds	-	leaf↓***	leaf↓***	leaf↑	[46]
China	<i>Quercus acutissima</i>	tree	-	leaf↓*	leaf↓*	leaf↑	[48]
North-south transect of eastern China	-	various kinds	-	leaf↓***	leaf↓***	leaf↑	[47]
Eastern China	-	tree	-	leaf↓***	leaf↓***	leaf↑***	[12]
Qinghai-Tibetan Plateau, China	-	herb	-	leaf↓**	leaf↓**	leaf↑**	[19]
Loess Plateau of China	-	various kinds	leaf↑	leaf↑	leaf↑	leaf↓	[33]
Typical desert and desertified regions of northern China	-	shrub	-	leaf↑	leaf↓	leaf↑	[35]
Northeast China	<i>Larix gmelinii Rupr</i>	tree	leaf↑**	leaf↑*	leaf↑	leaf↑**	[18]
Iberian Peninsula, Catalonia	-	tree	leaf↑	leaf↑***	leaf↓***	leaf↑***	[20]
Catalan National Forest	<i>Quercus ilex</i>	tree	leaf↑*	leaf↑**	leaf↑	leaf↑	[51]
	<i>Pinus halepensis</i>		leaf↑**	leaf↓***	leaf↓***	leaf↓	
	<i>Pinus sylvestris</i>		leaf↑	leaf↑	leaf↓***	leaf↑***	
central Catalonia	<i>Globularia alypum</i>	shrub	-	-	leaf↑	-	[49]
	<i>Erica multiflora</i>		-	-	leaf↑*	-	
Garraf mountains in Catalonia	<i>Erica multiflora</i>	shrub	-	leaf↓	leaf↑*	no	[50]
	<i>Globularia alypum</i>		-	leaf↓*	leaf↑	leaf↓*	
	<i>Dorycnium pentaphyllum</i>		-	leaf↓	-	leaf↑	
Ellesmere Island, Nunavut, Canada	<i>Cassiope tetragona</i>	shrub	leaf↓*	no	-	-	[38]
	<i>Eriophorum ngustifolium</i>	herb	leaf↓*	no	-	-	
Northern Minnesota	<i>Populus tremuloides</i>	tree	leaf↑	leaf↑	-	-	[37]
	<i>Betula papyrifera</i>		leaf↑*	leaf↑*	-	-	
	<i>Larix laricina</i>		leaf↑*	leaf↓**	-	-	
	<i>Pinus banksiana</i>		leaf↑	leaf↓*	-	-	
	<i>Picea mariana</i>		leaf↓	leaf↓*	-	-	
McClain County, US	<i>Schizachyium scoparium</i>	grass	leaf↑	leaf↓*	-	-	[25]
	<i>Sporobolus asper</i>		leaf↑	leaf↓*	-	-	
	<i>Dichanthelium oligosnathes</i>		leaf↑	leaf↓*	-	-	
	<i>Ambrosia psilostachyia</i>	forb	leaf↑	leaf↓*	-	-	
	<i>Aster ericoides</i>		leaf↑	leaf↓*	-	-	
Corvallis, OR, USA	<i>Pseudotsuga menziesii</i>	tree	-	leaf↑*	-	-	[53]
Antarctic	<i>Colobanthus quitensis</i>	herb	leaf↑**	leaf↓**	-	-	[54]
	<i>Deschampsia antarctica</i>		leaf↑**	leaf↓**	-	-	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, no-no effect.

B. Precipitation

1) Nitrogen

Whether on large scale or small scale, positive and negative variations of leaf N when responded to the precipitation both can be obtained among trees, forbs, grasses and shrubs, which expressed no obvious rule in different regions. However, it is worth noting that foliar P of herbs in Northern China and Qinghai-Tibet Plateau responded completely apparent

indifference to rainfall [19], [61], which showed significant increasing in both green leaf and senescent leaf along with precipitation addition. And the changes were also remarkable among tree types, which were elaborated by positive responses of *conifers* to precipitation [18], [51], and negative responses of evergreens to precipitation [51], from which more obvious discrepancy emerged in subdivided plant forms. Furthermore, foliar N concentration that expressed highly significant positive correlations with altitude was also positively related to

precipitation [56], and no influences with increasing rainfall also can be found [14], [36].

2) Phosphorus

As well as leaf N, leaf P exhibited different responses to precipitation in small regions, but on large scale, consistent variations that foliar P reduced along with increasing precipitation had been obtained (Table II). According to the study of Reich [15], leaf P increased with increasing latitude, and latitude had negative relations to precipitation, so leaf P should express negative associations with precipitation just as the research of Elser and Ordoñez, which also can be verified by P reduction because of leaching [12]. However, in most of China and Catalonia, various plant forms displayed positive even highly significant relationships with precipitation, which was unable to be explained by leaching.

3) Ratios of Nitrogen to Phosphorus

The influences of precipitation on leaf N: P were also mainly

determined by the variations of leaf P, which verified that P cycling were more variable than N cycling again. In most regions and growth forms, leaf N:P always manifested opposite variations in comparison with changes of leaf P. Leaf N:P always significantly decreased when leaf N and leaf P both increased under elevated precipitation, except for the study that leaf N had moderately significant relationships but leaf P had no significant relationships with precipitation [18]. And leaf N:P declined when leaf P increased no matter leaf N decreased or increased in most regions and plant forms. So leaf N:P also displayed apparent discrepancy among different regions and growth forms according to the variations of leaf P (Table II).

In general, as an important climatic factor, precipitation has very significant influences on variations of leaf chemical traits, not only in green leaves but also in the senesced leaves, from positive and negative directions among different regions and different plant forms.

TABLE II
THE RESPONSES OF LEAF N, P AND N: P TO PRECIPITATION IN DIFFERENT REGIONS AND GROWTH FORMS

study site	plant	growth form	plant ecological stoichiometry			reference
			N	P	N: P	
global	-	-	leaf↓*	leaf↓*	-	[16]
global	-	-	no	leaf↓**	leaf↑**	[36]
Europe	<i>Norway spruce</i>	tree	leaf↓	leaf↓	leaf↓***	[43]
Eurasia	-	tree	leaf litter↑***	-	-	[42]
Northern Sweden	<i>Betula nana</i>	tree	green leaf↓*	-	-	[62]
	<i>Vaccinium uliginosum</i>	tree	senesced leaf↓	-	-	
	<i>Calamagrostis lapponica</i>	grass	green leaf↓*	-	-	
	<i>Rubus chamaemorus</i>	forb	senesced leaf↓	-	-	
			green leaf↓*	-	-	
Eastern China	-	tree	leaf↓**	leaf↓**	leaf↑**	[12]
Loess Plateau of China	-	various kinds	leaf↓	leaf↑	leaf↓*	[33]
Typical desert and desertified regions of northern China	-	shrub	leaf↓	leaf↑*	leaf↓*	[35]
Qinghai-Tibetan Plateau, China	-	herb	leaf↑*	leaf↑**	leaf↓**	[19]
Inner Mongolia Grassland in northern China	<i>Agropyron cristatum</i>	herb	green leaf↑	green leaf↓*	green leaf↑*	[61]
	<i>Stipa grandis</i>	herb	senesced leaf↑*	senesced leaf↓*	senesced leaf↑*	
			green leaf↑*	green leaf↓*	green leaf↑*	
			senesced leaf↑*	senesced leaf↓	senesced leaf↑*	
			green leaf↑*	green leaves↓	green leaf↑*	
			senesced leaf↑*	senesced leaves↓	senesced leaf↑*	
Northeast China	<i>Achnatherum sibiricum</i>	herb	green leaf↑	green leaf↓*	green leaf↑*	[18]
	<i>Cleistogenes squarrosa</i>	herb	senesced leaf↑*	senesced leaf↓	senesced leaf↑*	
	<i>Carex korshinskyi</i>	herb	green leaf↑	green leaf↓	green leaf↑	
Catalan National Forest	<i>Larix gmelinii Rupr</i>	tree	leaf↑**	leaf↑	leaf↑**	[51]
	<i>Quercus ilex</i>		leaf↓**	leaf↓	leaf↓	
	<i>Pinus halepensis</i>	tree	leaf↑***	leaf↑***	leaf↑	
Central Catalonia	<i>Pinus sylvestris</i>		leaf↓	leaf↑***	leaf↓***	[20]
	<i>Globularia alypum</i>	shrub	leaf↑***	leaf↑***	leaf↓***	
South-east Queensland, Australia	<i>mangrove</i>	tree	leaf↓	leaf↑**	-	[63]

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, no-no effect.

C. Drought

1) Carbon

Leaf C in most regions significantly decreased with drought [64]-[67] except for the variation in Lanzhou University [68]

and variation in same regions but different plants, such as in Central Catalonia, the leaf C of *Phillyrea latifolia* and *Hypnum upressiforme* increased with drought, but *Quercus ilex* and *Arbutus unedo* inversely reduced. The variations in different regions showed no obvious discrepancy perhaps because of the

little information of regions, but although the same growth form, in the same region, leaf C of *Quercus ilex* exhibited different responses to drought, which had inverse changes in comparison to other species under drought [20], [67], and the same plant expressed no difference in different place, such as *Phillyrea latifolia* from Central Catalonia and Southern Catalonia (Table III). And in most regions and plant forms litter C expressed opposite variations in comparison with leaf C, except *Arbutus unedo* in different place always showed the same varied direction of leaf C and litter C [64], [65], [67].

2) Nitrogen

Leaf N in most regions presented significant increasing with drought except for *Hypnum upressiforme* in Central Catalonia, *Aubutus unedo* in central Catalonia or Southern Catalonia, *Erica multiflora* and *Globularia alypum* in Garraf Mountains and *Nothofagus dombeyi* in Southern Chile, which also presented that in the same region responses of leaf N to drought varied in different plant forms [69]. Whereas litter N all had positive relationships with drought, leaf N sometimes emerged the same or opposite variations.

More studies had verified that drought treatments exhibited lower plant N than irrigated treatments and these impacts expressed pronouncedly especially to the plant that had higher available N [70].

3) Phosphorus

The responses of leaf P to drought had more detail data than leaf C and leaf N (Table III), and also expressed discrepancy among different regions and different plant forms. Based on the compiled dataset, we can find that responses of leaf P in shrubs to drought displayed stability even in different regions, including the variations of *Globularia alypum* and *Erica multiflora* [49], [52], [71]. However, the responses of leaf P in trees to drought manifested no agreement in different regions, leaf P of *Quercus ilex* and *Phillyrea latifolia* varied along with different regions [72]. And the variations that leaf P had opposite direction compared with leaf N also can be discovered in most regions and plant forms, except some places in Catalonia.

According to the comparison of wetter sites and drier sites in New South Wales, Wright discovered that species from drier sites had higher leaf N and P per dry mass or area [73], but it was not in line with that of every region (Table III).

Because of the limited dataset and literatures, the regions of research on drought are also under restrictions, we cannot compare the responses of leaf chemical traits to drought in large scale with its in regional scales. Although compiling the literatures according to latitudes, the responses rules of leaf C, N, and P to drought along with latitude gradients also cannot be discovered for the same reasons.

TABLE III
THE RESPONSES OF FOLIAR C, N AND P TO DROUGHT IN DIFFERENT REGIONS AND GROWTH FORMS

study site	Plant	Growth form	Plant ecological stoichiometry			Reference
			C	N	P	
South-east Queensland, Australia	<i>mangrove</i>	tree	-	leaf↑	leaf↓***	[63]
South-west China	<i>Populus cathayana</i>	trees	leaf↓*	leaf↑*	leaf↓*	[66]
	<i>Populus cathayana</i>	trees	leaf↓*	leaf↑*	leaf↓*	
Lanzhou University	<i>Triticum aestivum</i>	herb	litter↑*	litter↑*	-	[68]
Central Catalonia	<i>Globularia alypum</i>	shrub	-	-	leaf↓* litter↓	[49]
	<i>Erica multiflora</i>	shrub	-	-	leaf↑ litter↓	
Central Catalonia	<i>Quercus ilex</i>	trees	-	-	leaf↑* litter↑*	[72]
	<i>Phillyrea latifolia</i>	tree	-	-	leaf↑ litter↓	
	<i>Arbutus unedo</i>	tree	-	-	leaf↓ litter↑	
Central Catalonia	<i>Hypnum upressiforme</i>	moss	leaf↑*	leaf↓	leaf↑	[65]
Central Catalonia	<i>Quercus ilex</i>	tree	leaf↓ litter↑	litter↑*	-	[64]
	<i>Phillyrea latifolia</i>	tree	leaf↑ litter↓	leaf↑ litter↑	-	
	<i>Aubutus unedo</i>	tree	leaf↓ litter↓*	leaf↓* litter↑*	-	
Central Catalonia	<i>Quercus ilex</i>	tree	leaf↓	-	leaf↑* litter↑	[71]
Central Catalonia	<i>Phillyrea latifolia</i>	tree	leaf↑	-	leaf↑	
	<i>Arbutus unedo</i>	tree	leaf↓ litter↓*	-	litter↑	
	<i>Quercus ilex</i>	tree	-	-	leaf↓* litter↑*	[74]
Southern Catalonia	<i>Quercus ilex</i>	tree	leaf↓* litter↑	litter↑*	leaf↓ litter↓	[67]
Southern Catalonia	<i>Phillyrea latifolia</i>	tree	leaf↑ litter↓	leaf↑ litter↑	leaf↓ litter↓	
	<i>Arbutus unedo</i>	tree	leaf↓ litter↓*	leaf↓* litter↑*	leaf↑ litter↓	
	<i>Quercus ilex</i>	tree	leaf↑*	leaf↑	leaf↑**	[52]
Catalonia, NE Spain	<i>Erica multiflora</i>	shrub	leaf↑	leaf↑	leaf↑	
Garraf mountains in Catalonia	<i>Erica multiflora</i>	shrub	-	leaf↓*	leaf↑	[49]
	<i>Globularia alypum</i>		-	leaf↓*	leaf↓*	
	<i>Dorynium pentaphyllum</i>		-	leaf↑	-	
Southern Chile	<i>Nothofagus dombeyi</i>	tree	-	leaf↓*	leaf↓*	[69]

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE IV
THE RESPONSES OF FOLIAR C, N AND P TO ELEVATED CO₂ IN DIFFERENT REGIONS AND GROWTH FORMS

study site	plant	growth form	plant ecological stoichiometry			reference
			C	N	P	
Tropical forest in Panama	<i>Elettaria cardamomum</i>	tree	litter↑	litter↓	litter↑	[85]
	<i>Ficus benjamina</i>	tree	litter↓	litter↓	litter↑	
	<i>Cecropia peltata</i>	tree	litter↓	litter↓*	litter↑	
Guangzhou, China	<i>Acmena acuminatissima</i>		-	leaf↓	leaf↑	[11]
	<i>Castanopsis hystrix</i>		-	leaf↓	leaf↑	
	<i>Ormosia pinnata</i>	tree	-	leaf↓	leaf↑	
	<i>Syzygium hancei</i>		-	leaf↓*	leaf↑**	
	<i>Schima superba</i>		-	leaf↓	leaf↑	
Central Florida, USA	<i>Quercus geminata</i>	tree	leaf↑*	leaf↓*	leaf↓	[86]
	<i>Quercus myrtifolia</i>	tree	leaf↑	leaf↓**	no	
Texas, USA	<i>Bothriochloa ischaemum</i>	herb	-	leaf↓*	-	[87]
	<i>Bromus japonicus</i>	herb	-	leaf↓**	-	
Phoenix Arizona, USA	<i>Solanum dimidiatum</i>	shrub	-	leaf↓	-	[88]
	<i>Citrus aurantium</i>	tree	-	leaf↓**	no	
	<i>Cercis canadensis</i>	tree/shrub	leaf litter↓	leaf↓ litter↑	leaf↓ litter↑	
North Carolina, USA	<i>Cornus florida</i>	tree/shrub	leaf litter↓	leaf↑ litter↓	leaf↑ litter↑	[79]
	<i>Acer rubrum</i>	tree	leaf litter↑	leaf↓ litter↓	leaf↑ litter↑	
	<i>Liquidambar styraciflua</i>	tree	leaf litter↑	leaf↓ litter↓	leaf↑ litter↑	
North Carolina, USA	<i>Pinus taeda</i>	tree	leaf litter↑	leaf↓	leaf↓	[89]
	<i>Pinus taeda</i>	tree	-	leaf↓**	no	
Lanzhou University	<i>Triticum aestivum</i>	herb	litter↑	litter↑	-	[68]
Mercury, Nevada, USA	<i>Larrea tridentata</i>	shrub	no	leaf↓*litter↓	leaf↑*litter↑	[77]
	<i>Lycium pallidum</i>	shrub	no	leaf↓*litter↓	leaf↑*litter↑	
	<i>Ambrosia dumosa</i>	shrub	no	litter↑	litter↑	
Central California, USA	<i>Lycium andersonii</i>	shrub	no	litter↓	litter↑	[78]
	<i>Avena</i>	herb	no	litter↓*	-	
Central Portugal	<i>Betula pendula</i>	tree	litter↑	litter↓	litter↓*	[90]
University of Illinois, Chicago, USA	<i>Acer negundo</i>	tree	-	leaf↓*	-	[81]
	<i>Acer platanoides</i>	tree	-	leaf↓*	-	
	<i>Pinus resinosa</i>	tree	-	leaf↑	-	
	<i>Pinus taeda</i>	tree	-	leaf↓	-	
	<i>Quercus bicolor</i>	tree	-	leaf↓*	-	
	<i>Quercus macrocarpa</i>	tree	-	leaf↓*	-	
Edgewater, Maryland	<i>Lindera benzoin</i>	shrub	leaf↑	leaf↓*	-	[91]
Salamanca, Spain	<i>Triticum aestivum</i>	herb	-	leaf↓*	-	[92]
	<i>Populus tremuloides</i>	tree	-	leaf↓	-	
University of Wisconsin Biotron	<i>Betula papyrifera</i>	tree	-	leaf↓***	-	[93]
	<i>Acer saccharum</i>	tree	-	leaf↓	-	
	<i>Erica arborea</i>	tree	leaf↓*	leaf↓	leaf↑*	
Lajatico, Pisa, Italy	<i>Juniperus communis</i>	tree	leaf↓**	leaf↑	leaf↑	[80]
Corvallis, OR, USA	<i>Myrtus communis</i>	tree	leaf↓**	leaf↓***	leaf↓*	[53]
	<i>Pseudotsuga menziesii</i>	tree	-	leaf↓*	-	
Swiss Central Alps	<i>Carex curvula</i>	herb	litter↓	litter↓**	-	[94]
	<i>Carex curvula</i>	herb	litter↓	litter↓*	litter↑	
Temperate grassland in Switzerland	<i>Carex flacca</i>	herb	litter↑	litter↑	litter↓	[85]
	<i>Chestnut</i>	tree	litter↓	litter↑*	-	
Orsay	<i>Populus tremuloides</i>	tree	leaf↑	leaf↓	-	[95]
	<i>Betula papyrifera</i>	tree	leaf↓	leaf↓**	-	
	<i>Larix laricina</i>	tree	leaf↑	leaf↓**	-	
Northern Minnesota	<i>Pinus banksiana</i>	tree	leaf↓	leaf↓	-	[37]
	<i>Picea mariana</i>	tree	leaf↓	leaf↓	-	
Westzaan, Netherland	<i>Vascular plant</i>	herb	-	leaf↓***	leaf↓**	[96]
University of Joensuu, Finland	<i>Salix myrsinifolia</i>	tree	-	leaf↓***	-	[97]
Central Finland	<i>Silver birch</i>	tree	leaf↓*	-	-	[98]
Eastern Finland	<i>Pinus sylvestris</i>	tree	-	leaf↓*	leaf↓	[45]
Central Finland	<i>Betula pendula</i> Roth	tree	-	leaf↓***	leaf↑**	[99]
Gunnarsholt, south Iceland	<i>Populus trichocarpa</i>	tree	-	leaf↓*	-	[100]

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, no-no effect.

D. Elevated CO₂

According to IPCC, elevating atmospheric CO₂ will accumulate 350 to 850 Pg of carbon in the terrestrial biosphere by 2100. And Hungate considered that ecosystem carbon accumulation may be constrained by nitrogen [75]. Early in

1990, Peñuelas found that leaf N content exhibited a significant reduction from 144% to 100% but leaf C content decreases very slightly on average by CO₂ increasing, so overall C:N increased [76].

1) Carbon

Leaf C did not show consistent increase tendency when under elevated CO₂, including the tendency that leaf C reduced or had no variation along with CO₂ elevating, and the decreasing number reached to 14 that surprisingly surpassed the increasing number (Table IV). Among different regions or different plant forms, there all existed three sorts of variations, and even in the same regions and plant forms, different responses to elevated CO₂ were exhibited [37], the reasons may be that leaf C varied among subdivisions of plant forms. Furthermore, responses of leaf C in shrubs and herbs in latitude of 36°-37° in USA displayed no effects by elevated CO₂ [77], [78]. In comparison with leaf C, although litter C also exhibited different varied directions, the influences of elevated CO₂ on litter C showed no significant without exception in any regions or any plant forms.

2) Nitrogen

No surprisingly, the responses of leaf N to elevated CO₂ displayed consistent variations in most regions and plant forms of not only green leaves but also leaf litter (Table IV). In 56 studies, only 7 studies considered leaf N increased with elevated CO₂, and 49 studies verified that leaf N had significantly negative relationships with elevated CO₂ (Fig. 2), although the significance of responses existed obvious discrepancy. However, increasing tendency of leaf N along with elevated CO₂ only had been discovered in some of trees in North Carolina and Chicago of USA and Pisa of Italy [79]-[81], and litter N manifested increasing variations mainly in leaf litter of shrubs and herbs. Furthermore, the effects of elevated CO₂ on leaf N did not demonstrated obvious variation rules along with latitude gradients, except for the consistent declining in low latitudes (Table IV).

3) Phosphorus

Just inversely to leaf N, leaf P exhibited positive relations to elevated CO₂ in most regions, the ratios of response numbers amount to 63% (Fig. 2), and leaf P and litter P demonstrated the same varied directions. Of course, there also existed responses of negative direction and no effects to elevated CO₂ as leaf C. Otherwise, from the compiled dataset, elevated CO₂ had stronger influences on leaf N rather than leaf P, the reason may be that P nutrient also derived from soil nutrients and P cycles mainly were determined by environmental variations, such as weathering and leaching.

In general, elevated CO₂ can highly vary leaf chemical traits among different regions and different plant forms. Loladze obtained the conclusion that high CO₂ can alter plant stoichiometry, because under higher CO₂, plants have higher C fixation rates, which changed internal elemental demands, then rendered not only the variations of C:(other elements) ratios but also the ratios among other elements (e.g. C:N, N:P) [82]. Except for different regions and plant forms, leaf ecological stoichiometry also dynamically responded to elevated CO₂ in different times, Hobbie found that N concentration changes exhibited highly significant, moderately significant or significant correlations with elevated CO₂ based on the

experiments across six disparate years [59], and other leaf chemical traits, such as N:P, C:N and C:P also can be changed by elevated CO₂, the responses of C:N or C:P to elevated CO₂ varied highly, which was found to be increasing, decreasing or remaining the same [83]. Beyond that, green leaves which had significantly lower N concentrations and higher C:N ratios expressed more variability than leaf litter under elevated CO₂ [77]. At last, the reason why leaf N concentration declined under elevated CO₂ had been stated by proposing five hypotheses which included dilution hypotheses, hypotheses of decreased nitrogen uptake and of decreased nitrogen demand, elevated CO₂-mediated nitrogen loss hypothesis and hypothesis of ontogenetic drift in N concentration [84]. Furthermore, as a greenhouse gas, elevated CO₂ exerted relative no different impacts on leaf N (Tables I and III) which significantly reduced leaf N concentrations or contents in leaf biomass. However, the same influences of temperature and elevated CO₂ on variations of leaf C or leaf P did not appear obviously, the reason should be taken account for further study to understand how different leaf chemical traits responded to different climatic factors.

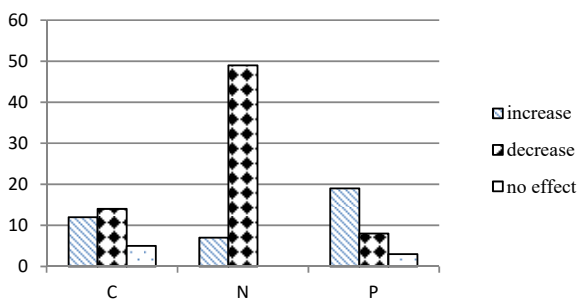


Fig. 2 Number of reported increases, decreases, and no effect of leaf C, N, and P in response to elevated CO₂

III. PROSPECTS FOR FUTURE STUDIES

Of course, climatic factors were a portion of environmental variations that influenced plant tissues traits, and explained between 5% and 25% variations for plant leaf traits [101]. As an important environmental factor, land use also had close relationships with ecological stoichiometry [102], [103], however, the correlations with plant ecological stoichiometry had not been involved and they can be further account for in the future. (Some unexplained variance may be can be explained by land use.)

More factors should be taken into account to study the varied responses of plant ecological stoichiometry. Aerts considered that the influences of climate changes on leaf nutrient concentrations may have close relation to the length of study time [60], so studies should be focused on the dynamic interplay of environmental factors and long-term influences in the future [104]. Furthermore, Durán also discovered that wildfire can altered the nutritional status of forest ecosystem [102], [105], and other researches pointed out soil nutrient levels also play a vitally important part in explaining the responses of plant ecological stoichiometry [12], [106], and coincided climatic factors can exhibit greater overt responses of

plant stoichiometry [39]. At last, except for the linear correlations of leaf N, P and environmental factors, there also exist nonlinear relationships, leaf N or leaf P can express increasing tendency then decreasing when up to a certain temperature or precipitation level or inversely [48], [107], and there was an experiment verified that temperature had larger impact than precipitation on leaf litter [42].

In conclusion, this paper pointed out that future research should be developed as the following aspects: (1) The responses of plant ecological stoichiometry to climatic factors exhibited positive and negative changes, so the effects observed in single-factor studies should be analyzed with more caution and multi-factor climate experiments with interactive influences on plant stoichiometry would be deserved further attention. (2) The range of influential factors should be expanded from macro factors to micro factors, and from natural factors to social or anthropogenic factors, such as burning, land use changes etc. (3) The remove effects of positive and negative responses to different factors should be taken account, as well as the comparison of their magnitude of changes influenced by different climatic/environmental factors.

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