

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

Li Wu

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].

Li Wu is with School of Resources and Environment, Yuxi Normal University, Yuxi, P. R. China (e-mail: liwu2017@yeah.net).

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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.

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].

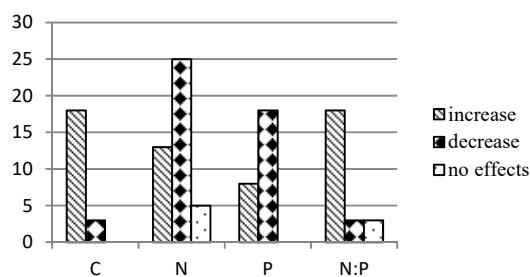


Fig. 1 Number of reported increase, decrease, and no effect of leaf C, N, P and N:P in response to warming

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 psilostachya</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↓ | | | |
| Eastern China | - | tree | green leaf↓* | senesced leaf↓ | | |
| Loess Plateau of China | - | various kinds | leaf↓** | leaf↓** | leaf↑** | [12] |
| Typical desert and desertified regions of northern China | - | shrub | leaf↓ | leaf↑ | leaf↓* | [33] |
| Qinghai-Tibetan Plateau, China | - | herb | leaf↓ | leaf↑* | leaf↓* | [35] |
| Inner Mongolia Grassland in northern China | <i>Agropyron cristatum</i> | herb | leaf↑* | leaf↑** | leaf↓** | [19] |
| | <i>Stipa grandis</i> | herb | green leaf↑ | green leaf↓* | green leaf↑* | |
| | <i>Achnatherum sibiricum</i> | herb | senesced leaf↑* | senesced leaf↓* | senesced leaf↑* | |
| | <i>Cleistogenes squarrosa</i> | herb | green leaf↑* | green leaf↓* | green leaf↑* | |
| | <i>Carex korshinskyi</i> | herb | senesced leaf↑* | senesced leaf↓ | senesced leaf↑* | |
| | <i>Larix gmelinii Rupr</i> | tree | green leaf↑* | green leaves↓ | green leaf↑* | [61] |
| Northeast China | <i>Quercus ilex</i> | tree | senesced leaf↑* | senesced leaves↓ | senesced leaf↑* | |
| Catalan National Forest | <i>Pinus halepensis</i> | tree | green leaf↑ | green leaf↓* | green leaf↑* | |
| | <i>Pinus sylvestris</i> | tree | senesced leaf↑* | senesced leaf↓ | senesced leaf↑* | |
| Central Catalonia | <i>Globularia alypum</i> | shrub | green leaf↑ | green leaf↓ | green leaf↑ | |
| South-east Queensland, Australia | <i>mangrove</i> | tree | senesced leaf↑* | senesced leaf↓ | senesced leaf↑* | |
| | | | leaf↑** | leaf↓ | leaf↑** | [18] |
| | | | leaf↓** | leaf↓ | leaf↓ | |
| | | | leaf↑*** | leaf↑*** | leaf↑ | [51] |
| | | | leaf↓ | leaf↑*** | leaf↓*** | |
| | | | leaf↑*** | leaf↑*** | leaf↓*** | [20] |
| | | | 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↑* | - | |
| | <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↑ | |
| | <i>Erica multiflora</i> | shrub | - | leaf↓* | leaf↑ | [49] |
| | <i>Globularia alypum</i> | shrub | - | leaf↓* | leaf↓* | |
| Southern Chile | <i>Dorynium pentaphyllum</i> | - | - | leaf↑ | - | |
| | <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↑** | |
| Central Florida, USA | <i>Schima superba</i> | | - | leaf↓ | leaf↑ | [86] |
| | <i>Quercus geminata</i> | tree | leaf↑* | leaf↓* | leaf↓ | |
| | <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] |
| | <i>Larrea tridentata</i> | shrub | no | leaf↓*litter↓ | leaf↑*litter↑ | |
| | <i>Lycium pallidum</i> | shrub | no | leaf↓*litter↓ | leaf↑*litter↑ | |
| Mercury, Nevada, USA | <i>Ambrosia dumosa</i> | shrub | no | litter↑ | litter↑ | [77] |
| | <i>Lycium andersonii</i> | shrub | no | litter↓ | litter↑ | |
| Central California, USA | <i>Avena</i> | herb | no | litter↑* | - | [78] |
| | <i>Betula pendula</i> | tree | litter↑ | litter↓ | litter↓* | |
| Central Portugal | <i>Acer negundo</i> | tree | - | leaf↓* | - | [90] |
| | <i>Acer platanoides</i> | tree | - | leaf↓* | - | |
| | <i>Pinus resinosa</i> | tree | - | leaf↑ | - | |
| University of Illinois, Chicago, USA | <i>Pinus taeda</i> | tree | - | leaf↓ | - | [81] |
| | <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] |
| | <i>Myrtus communis</i> | tree | leaf↓** | leaf↓*** | leaf↓* | |
| Corvallis, OR, USA | <i>Pseudotsuga menziesii</i> | tree | - | leaf↓* | - | [53] |
| 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↑* | - | |
| | <i>Populus tremuloides</i> | tree | leaf↑ | leaf↓ | - | |
| Northern Minnesota | <i>Betula papyrifera</i> | tree | leaf↓ | leaf↓** | - | [37] |
| | <i>Larix laricina</i> | tree | leaf↑ | leaf↓** | - | |
| | <i>Pinus banksiana</i> | tree | leaf↓ | leaf↓ | - | |
| Westzaan, Netherland | <i>Picea mariana</i> | tree | leaf↓ | leaf↓ | - | [96] |
| | <i>Vascular plant</i> | herb | - | leaf↓*** | leaf↓** | |
| University of Joensuu, Finland | <i>Salix myrsinifolia</i> | tree | - | leaf↓*** | - | [97] |
| | <i>Silver birch</i> | tree | leaf↓* | - | - | |
| Eastern Finland | <i>Pinus sylvestris</i> | tree | - | leaf↓* | leaf↓ | [45] |
| Central Finland | <i>Betula pendula</i> Roth | tree | - | leaf↓*** | leaf↑** | [99] |
| | <i>Populus trichocarpa</i> | tree | - | leaf↓* | - | |

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

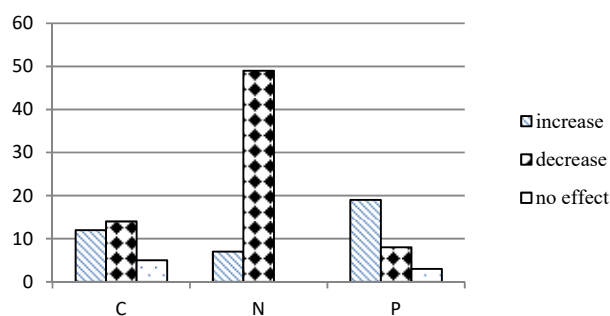


Fig. 2 Number of reported increases, decreases, and no effect of leaf C, N, and P in response to elevated CO₂

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.

REFERENCES

[1] Sterner, R. W. and J. J. Elser. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. NJ, USA, Princeton University Press, 2002.

[2] Elser, J. J., D. DR, et al. "Organism size, life history, and N: P stoichiometry." *Bioscience*, vol.46, pp.674-684, Oct.1996.

[3] Elser, J. J., W. F. Fagan, et al. "Nutritional constraints in terrestrial and freshwater food webs." *Nature*, vol.408, no.6812, pp.578-580, 2000.

[4] Elser, J. J., P. Frost, et al. "Effects of light and nutrients on plankton stoichiometry and biomass in a P-limited lake." *Hydrobiologia*, vol.481, no.1-3, pp.101-112, Aug.2002.

[5] Elser, J. J., M. Kyle, et al. "Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition." *Ecology*, vol.90, no.11, pp.3062-3073, Nov.2009.

[6] Reich, P. B., B. A. Hungate, et al. "Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide." *Annual Review of Ecology, Evolution, and Systematics*, vol.37, pp.611-636, Aug.2006.

[7] Karadaş, C. and D. Kara. "Chemometric approach to evaluate trace metal concentrations in some spices and herbs." *Food Chemistry*, vol.130, no.1, pp.196-202, Jan.2012.

[8] Qiu, L., X. Wei, et al. "Nutrient stoichiometry of three plant species under a natural nutrient gradient of a semiarid small watershed." *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science*, vol.63, no.3, pp.231-240, Nov.2012.

[9] Chapin III, S., P. A. Matson, et al. "Principles of terrestrial ecosystem ecology", Springer New York, 2002.

[10] Güsewell, S. and W. Koerselman. "Variation in nitrogen and phosphorus concentrations of wetland plants." *Perspectives in Plant Ecology, Evolution and Systematics*, vol.5, no.1, pp.37-61, 2002.

[11] Huang, W., G. Zhou, et al. "Effects of elevated carbon dioxide and nitrogen addition on foliar stoichiometry of nitrogen and phosphorus of five tree species in subtropical model forest ecosystems." *Environmental Pollution*, 168, pp.113-120, 2012.

[12] Chen, Y., W. Han, et al. "Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form." *Ecography*, vol.36, no.2, pp.178-184, 2013.

[13] Hong, J. T., J. B. Wu, et al. "Effects of global climate change on the C, N, and P stoichiometry of terrestrial plants." *Chinese Journal of Applied Ecology*, vol.24, no.9, pp.2658-2665, 2013.

[14] Wright, I. J., P. B. Reich, et al. "Modulation of leaf economic traits and trait relationships by climate." *Global Ecology and Biogeography*, vol.14, no.5, pp.411-421, 2005.

[15] Reich, P. B. and J. Oleksyn. "Global patterns of plant leaf N and P in relation to temperature and latitude." *Proceedings of the National*

Academy of Sciences, vol.101, no.30, pp.11001-11006, 2004.

[16] Elser, J. J., W. F. Fagan, et al. "Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change." *New Phytologist*, vol.186, no.3, pp.593-608, 2010.

[17] Sardans, J. and J. Peñuelas. "The Role of Plants in the Effects of Global Change on Nutrient Availability and Stoichiometry in the Plant-Soil System." *Plant Physiology*, vol.160, no.4, pp.1741-1761, 2012.

[18] Ren, S. J., G. R. Yu, et al. "Spatial patterns for variations in leaf nutrient contents of Dahurian Larch (*Larix gmelinii* Rupr.)." *Acta Ecologica Sinica*, vol.29, no.4, pp.1899-1906, 2009.

[19] Yang, K., J. H. Huang, et al. "Canopy leaf N and P stoichiometry in grassland communities of Qinghai-Tibetan Plateau, China." *Chinese Journal of Plant Ecology*, vol.34, no.1, pp.17-22, 2010.

[20] Sardans, J. and J. Peñuelas. "Tree growth changes with climate and forest type are associated with relative allocation of nutrients, especially phosphorus, to leaves and wood." *Global Ecology and Biogeography*, vol.22, no.4, pp.494-507, 2013.

[21] He, J. S., D. F. B. Flynn, et al. "CO₂ and nitrogen, but not population density, alter the size and C/N ratio of *Phytolacca americana* seeds." *Functional Ecology*, vol.19, no.3, pp.437-444, 2005.

[22] Novotny, A. M., J. D. Schade, et al. "Stoichiometric response of nitrogen-fixing and non-fixing dicots to manipulations of CO₂, nitrogen, and diversity." *Oecologia*, vol.151, no.4, pp.687-696, 2006.

[23] Zhao, Y. S. and X. Hou. "Foliar stoichiometry under different mycorrhizal types in relation to temperature and precipitation in grassland." *Journal of Plant Ecology*, vol.6, no.4, pp.270-276, 2012.

[24] Cotrufo, M. F., I. Phil, et al. "Elevated CO₂ reduces the nitrogen concentration of plant tissues." *Global Change Biology*, no.4, pp.43-54, 1998.

[25] An, Y., S. Wan, et al. "Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming." *Global Change Biology*, vol.11, no.10, pp.1733-1744, 2005.

[26] Esmeyer-Liu, A. J., R. Aerts, et al. "Nitrogen enrichment lowers *Betula pendula* green and yellow leaf stoichiometry irrespective of effects of elevated carbon dioxide." *Plant and Soil*, vol.316, no.1-2, pp.311-322, 2008.

[27] Stevens, C. J., C. Duprè, et al. "The impact of nitrogen deposition on acid grasslands in the Atlantic region of Europe." *Environmental Pollution*, vol.159, no.10, pp.2243-2250, 2011.

[28] Yang, Y. H., Y. Q. Luo, et al. "Terrestrial C: N stoichiometry in response to elevated CO₂ and N addition: a synthesis of two meta-analyses." *Plant and Soil*, vol.343, no.1-2, pp.393-400, 2011.

[29] Reich, P. B., J. Oleksyn, et al. "Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species." *Oecologia*, vol.160, no.2, pp.207-212, 2009.

[30] Dijkstra, F. A., E. Pendall, et al. "Climate change alters stoichiometry of phosphorus and nitrogen in a semiarid grassland." *New Phytologist*, vol.196, pp.807-815, 2012.

[31] Kerkhoff, A. J., B. J. Enquist, et al. "Plant allometry, stoichiometry and the temperature-dependence of primary productivity." *Global Ecology and Biogeography*, vol.14, no.6, pp.585-598, 2005.

[32] He, J.-S., J. Fang, et al. "Stoichiometry and large-scale patterns of leaf carbon and nitrogen in the grassland biomes of China." *Oecologia*, vol.149, no.1, pp.115-122, 2006.

[33] Zheng, S. X., P. Zhou, et al. "Spatial patterns of leaf nutrient traits of the plants in the Loess Plateau of China." *Trees*, vol.21, no.3, pp.357-370, 2007.

[34] Aerts, R., T. V. Callaghan, et al. "Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog." *Functional Ecology*, vol.23, no.4, pp.680-688, 2009.

[35] Li, Y. L., W. Mao, et al. "Leaf nitrogen and phosphorus stoichiometry in typical desert and desertified regions, north China." *Environmental Science*, vol.31, no.8, pp.1716-1725, 2010.

[36] Ordoñez, J. C., P. M. van Bodegom, et al. "A global study of relationships between leaf traits, climate and soil measures of nutrient fertility." *Global Ecology and Biogeography*, vol.18, no.2, pp.137-149, 2009.

[37] Tjoelker, M. G., P. B. Reich, et al. "Changes in leaf nitrogen and carbohydrates underlie temperature and CO₂ acclimation of dark respiration in five boreal tree species." *Plant, Cell and Environment*, no.22, pp.767-778, 1999.

[38] Hudson, J. M. G., G. H. R. Henry, et al. "Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming." *Global Change Biology*, vol.17, no.2, pp.1013-1021, 2011.

[39] Sardans, J., A. Rivas-Ubach, et al. "The C: N: P stoichiometry of organisms and ecosystems in a changing world: a review and

- perspectives." *Perspectives in Plant Ecology, Evolution and Systematics*, vol.14, no.1, pp.33-47, 2012.
- [40] Lovelock, C., I. Feller, et al. "Testing the growth rate vs. geochemical hypothesis for latitudinal variation in plant nutrients." *Ecology Letters*, vol.10, no.12, pp.1154-1163, 2007.
- [41] Aerts, R. "Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship." *OIKOS*, vol.79, no.3, pp.439-449, 1997.
- [42] Liu, C., B. Berg, et al. "Leaf litter nitrogen concentration as related to climatic factors in Eurasian forests." *Global Ecology and Biogeography*, vol.15, no.5, pp.438-444, 2006.
- [43] Kang, H., H. Zhuang, et al. "Variation in leaf nitrogen and phosphorus stoichiometry in *Picea abies* across Europe: An analysis based on local observations." *Forest Ecology and Management*, vol.261, no.2, pp.195-202, 2011.
- [44] Britton, A. and J. Fisher. "NP stoichiometry of low-alpine heathland: Usefulness for bio-monitoring and prediction of pollution impacts." *Biological Conservation*, vol.138, no.1-2, pp.100-108, 2007.
- [45] Luomala, E.-M., K. Laitinen, et al. "Stomatal density, anatomy and nutrient concentrations of Scots pine needles are affected by elevated CO₂ and temperature." *Plant, Cell and Environment*, no.28, pp.733-749, 2005.
- [46] Han, W. X., J. Y. Fang, et al. "Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China." *New Phytologist*, vol.168, no.2, pp.377-385, 2005.
- [47] Ren, S. J., G. R. Yu, et al. "Leaf nitrogen and phosphorus stoichiometry across 654 terrestrial plant species in NSTEC." *Environmental Science*, vol.28, no.12, pp.2665-2672, 2007.
- [48] Wu, T., G. G. Wang, et al. "Patterns of leaf nitrogen and phosphorus stoichiometry among *Quercus acutissima* provenances across China." *Ecological Complexity*, vol.17, no.1, pp.32-39, 2014.
- [49] Sardans, J., J. Peñuelas, et al. "Drought and warming induced changes in P and K concentration and accumulation in plant biomass and soil in a Mediterranean shrubland." *Plant and Soil*, vol.306, no.1-2, pp.261-271, 2008.
- [50] Sardans, J., J. Peñuelas, et al. "Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland." *Global Change Biology*, vol.14, no.10, pp.2304-2316, 2008.
- [51] Sardans, J., A. Rivas-Ubach, et al. "Factors affecting nutrient concentration and stoichiometry of forest trees in Catalonia (NE Spain)." *Forest Ecology and Management*, vol.262, no.11, pp.2024-2034, 2011.
- [52] Sardans, J., A. Rivas-Ubach, et al. "Field-simulated droughts affect elemental leaf stoichiometry in Mediterranean forests and shrublands." *Acta Oecologica*, vol.50, pp.20-31, 2013.
- [53] Lewis, J., M. Lucash, et al. "Relationships between needle nitrogen concentration and photosynthetic responses of Douglas-fir seedlings to elevated CO₂ and temperature." *New Phytologist*, vol.162, no.2, pp.355-364, 2004.
- [54] Day, T. A., C. T. Ruhland, et al. "Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra." *Global Change Biology*, vol.14, no.8, pp.1827-1843, 2008.
- [55] Norby, R. J., T. M. Long, et al. "Nitrogen resorption in senescing tree leaves in a warmer, CO₂-enriched atmosphere." *Plant and Soil*, vol.224, no.1, pp.15-29, 2000.
- [56] Craine, J. and W. Lee. "Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand." *Oecologia*, vol.134, no.4, pp.471-478, 2003.
- [57] Gotelli, N. J., P. J. Mouser, et al. "Geographic variation in nutrient availability, stoichiometry, and metal concentrations of plants and pore-water in ombrotrophic bogs in New England, USA." *WETLANDS*, vol.28, no.3, pp.827-840, 2008.
- [58] Arft, A., M. Walker, et al. "Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment." *Ecological monographs*, vol.69, no.4, pp.491-511, 1999.
- [59] Hobbie, E. A., D. M. Olszyk, et al. "Foliar nitrogen concentration and natural abundance of N-15 suggest nitrogen allocation patterns of Douglas-fir and mycorrhizal fungi during development in elevated carbon dioxide concentration and temperature." *Tree Physiology*, vol.21, no.15, pp.1113-1122, 2001.
- [60] Aerts, R., J. Cornelissen, et al. "Climate change has only a minor impact on nutrient resorption parameters in a high-latitude peatland." *Oecologia*, vol.151, no.1, pp.132-139, 2007.
- [61] Lü, X.-T., D.-L. Kong, et al. "Nitrogen and water availability interact to affect leaf stoichiometry in a semi-arid grassland." *Oecologia*, vol.168, no.2, pp.301-310, 2011.
- [62] Aerts, R., B. Wallen, et al. "Growth-limiting nutrients in Sphagnum-dominated bogs subject to low and high atmospheric nitrogen supply." *Journal of ecology*, vol.80, pp.131-140, 1992.
- [63] Adame, M. F., B. Virdis, et al. "Effect of geomorphological setting and rainfall on nutrient exchange in mangroves during tidal inundation." *Marine and Freshwater Research*, vol.61, no.10, pp.1197-1206, 2010.
- [64] Sardans, J. and J. Peñuelas. "Drought-induced changes in C and N Stoichiometry in a *Quercus ilex* Mediterranean Forest." *Forest Science*, vol.54, no.5, pp.513-522, 2008.
- [65] Sardans, J. and J. Peñuelas. "Drought changes nutrient sources, content and stoichiometry in the bryophyte *Hypnum cupressiforme* Hedw. growing in a Mediterranean forest." *Journal of Bryology*, vol.30, no.1, pp.59-65, 2008.
- [66] Lu, Y., B. Duan, et al. "Intraspecific variation in drought response of *Populus cathayana* grown under ambient and enhanced UV-B radiation." *Annals of Forest Science*, vol.66, no.6, pp.613-613, 2009.
- [67] Sardans, J. and J. Peñuelas. "Soil enzyme activity in a Mediterranean forest after six years of drought." *Soil Science Society of America Journal*, vol.74, no.3, pp.838, 2010.
- [68] Liao, J., Z. Hou, et al. "Effects of elevated CO₂ and drought on chemical composition and decomposition of spring wheat (*Triticum aestivum*)." *Functional Plant Biology*, vol.29, pp.891-897, 2002.
- [69] Alvarez, M., D. Huygens, et al. "Ectomycorrhizal fungi enhance nitrogen and phosphorus nutrition of *Nothofagus dombeyi* under drought conditions by regulating assimilative enzyme activities." *Physiologia Plantarum*, vol.136, no.4, pp.426-436, 2009.
- [70] Gonzalez-Dugo, V., J.-L. Durand, et al. "Water deficit and nitrogen nutrition of crops. A review." *Agronomy for sustainable development*, vol.30, no.3, pp.529-544, 2010.
- [71] Sardans, J., J. Peñuelas, et al. "Experimental drought reduced acid and alkaline phosphatase activity and increased organic extra Tab. P in soil in a *Quercus ilex* Mediterranean forest." *European Journal of Soil Biology*, vol.44, no.5-6, pp.509-520, 2008.
- [72] Sardans, J. and J. Peñuelas. "Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest." *Functional Ecology*, vol.21, no.2, pp.191-201, 2007.
- [73] Wright, I. J., P. Reich, et al. "Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low- rainfall and high- and low- nutrient habitats." *Functional Ecology*, vol.15, no.4, pp.423-434, 2001.
- [74] Sardans, J. and J. Peñuelas. "Increasing drought decreases phosphorus availability in an evergreen Mediterranean forest." *Plant and Soil*, vol.267, no.1-2, pp.367-377, 2004.
- [75] Hungate, B. A., J. S. Dukes, et al. "Nitrogen and climate change." *Science*, vol.302, no.5650, pp.1512-1513, 2003.
- [76] Peñuelas, J. and R. Matamala. "Changes in N and S leaf content, stomatal density and specific leaf area of 14 plant species during the last three centuries of CO₂ increase." *Journal of Experimental Botany*, vol.41, no.9, pp.1119-1124, 1990.
- [77] Billings, S. A., S. F. Zitzer, et al. "Effects of elevated carbon dioxide on green leaf tissue and leaf litter quality in an intact Mojave Desert ecosystem." *Global Change Biology*, vol.9, no.5, pp.729-735, (2003).
- [78] Henry, H. A. L., E. E. Cleland, et al. "Interactive effects of elevated CO₂, N deposition and climate change on plant litter quality in a California annual grassland." *Oecologia*, vol.142, no.3, pp.465-473, 2004.
- [79] Finzi, A. C., A. S. Allen, et al. "Forest litter production, chemistry, and decomposition following two years of free-air CO₂ enrichment." *Ecology*, vol.82, no.2, pp.470-484, 2001.
- [80] Penuelas, J., I. Filella, et al. "Leaf mineral concentrations of *Erica arborea*, *Juniperus communis* and *Myrtus communis* growing in the proximity of a natural CO₂." *Global Change Biology*, vol.7, no.3, pp.291-301, 2001.
- [81] Zerihun, A. and H. Bassirirad. "Interspecies variation in nitrogen uptake kinetic responses of temperate forest species to elevated CO₂: potential causes and consequences." *Global Change Biology*, vol.7, no.2, pp.211-222, 2001.
- [82] Loladze, I. "Rising atmospheric CO₂ and human nutrition: toward globally imbalanced plant stoichiometry?" *Trends in Ecology & Evolution*, vol.17, no.10, pp.457-461, 2002.
- [83] Gifford, R. M., D. J. Barrett, et al. "The effects of elevated CO₂ on the C: N and C: P mass ratios of plant tissues." *Plant and Soil*, vol.224, no.1, pp.1-14, 2000.
- [84] Taub, D. R. and X. Wang. "Why are nitrogen concentrations in plant tissues lower under elevated CO₂? A critical examination of the hypotheses." *Journal of Integrative Plant Biology*, vol.50, no.11, pp.1365-1374, 2008.

- [85] Hirschel, G., C. Korner, et al. "Will rising atmospheric CO₂ affect leaf litter quality and in situ decomposition rates in native plant communities." *Oecologia*, vol.110, no.3, pp.387-392, 1997.
- [86] Johnson, D. W., B. A. Hungate, et al. "The effects of elevated CO₂ on nutrient distribution in a fire-adapted scrub oak forest." *Ecological Applications*, vol.13, no.5, pp.1388-1399, 2003.
- [87] Anderson, L. J., H. Maherali, et al. "Gas exchange and photosynthetic acclimation over subambient to elevated CO₂ in a C3-C4 grassland." *Global Change Biology*, vol.7, no.6, pp.693-707, Aug.2001.
- [88] Penuelas, J., S. B. Idso, et al. "Effects of long-term atmospheric CO₂ enrichment on the mineral concentration of Citrus aurantium leaves." *New Phytologist*, vol.135, no.3, pp.439-444, Mar.1997.
- [89] Finzi, A. C., E. H. DeLucia, et al. "Canopy N and P dynamics of a southeastern US pine forest under elevated CO₂ " *Biogeochemistry*, vol.69, no.3, pp.363-378, 2004.
- [90] Elser, J. J. "Ecological stoichiometry: from sea to lake to land." *Trends in Ecology & Evolution*, vol.15, no.10, pp.393-394, 2000.
- [91] Cipollini, M. L., B. G. Drake, et al. "Effects of elevated CO₂ on growth and carbon nutrient balance in the deciduous woody shrub *Lindera benzoin* (L.) Blume (Lauraceae)." *Oecologia*, vol.96, no.3, pp.339-346, Mar.1993.
- [92] Del Pozo, A., P. Pérez, et al. "Gas exchange acclimation to elevated CO₂ in upper-sunlit and lower-shaded canopy leaves in relation to nitrogen acquisition and partitioning in wheat grown in field chambers." *Environmental and Experimental Botany*, vol.59, no.3, pp.371-380, 2007.
- [93] Agrell, J., E. P. McDonald, et al. "Effects of CO₂ and light on tree phytochemistry and insect performance." *OIKOS*, vol.88, no.2, pp.259-272, Feb.2000.
- [94] Arnone, J. A. and G. Hirschel. "Does fertilizer application alter the effects of elevated CO₂ on Carex leaf litter quality and in situ decomposition in an alpine grassland." *Acta Ecologica*, vol.18, no.3, pp.201-206, 1997.
- [95] Couteaux, M.-M., M. Mousseau, et al. "Increased atmospheric CO₂ and litter Quality Decomposition of Sweet Chestnut Leaf Litter with Animal Food Webs of Different Complexities." *OIKOS*, vol.61, no.1, pp.54-64, May.1991.
- [96] Milla, R., J. H. C. Cornelissen, et al. "Vascular plant responses to elevated CO₂ in a temperate lowland Sphagnum peatland." *Plant and Climate Change*, vol.41, pp.13-26, Dec. 2004.
- [97] Julkunen-Tiitto, R., J. Tahvanainen, et al. "Increased CO₂ and nutrient status changes affect phytomass and the production of plant defensive secondary chemicals in *Salix myrsinifolia* (Salisb.)." *Oecologia*, vol.95, no.4, pp.495-498, May.1993.
- [98] Riikonen, J., T. Holopainen, et al. "Leaf photosynthetic characteristics of silver birch during three years of exposure to elevated concentrations of CO₂ and O₃ in the field." *Tree Physiology*, vol.25, pp.621-632, 2005.
- [99] Kasurinen, A., J. Riikonen, et al. "Chemical composition and decomposition of silver birch leaf litter produced under elevated CO₂ and O₃." *Plant and Soil*, vol.282, no.1-2, pp.261-280, 2006.
- [100] Sigurdsson, B. D., H. Thorgeirsson, et al. "Growth and dry-matter partitioning of young *Populus trichocarpa* in response to carbon dioxide concentration and mineral nutrient availability." *Tree Physiology*, vol.21, pp.941-950, 2000.
- [101] Reich, P. B., I. J. Wright, et al. "Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis." *Ecological Applications*, vol.17, no.7, pp.1982-1988, 2007.
- [102] Durán, J., A. Rodríguez, et al. "Changes in leaf nutrient traits in a wildfire chronosequence." *Plant and Soil*, vol.331, no.1-2, pp.69-77, 2010.
- [103] Wang, W., J. Sardans, et al. "Responses of soil nutrient concentrations and stoichiometry to different human land uses in a subtropical tidal wetland." *Geoderma*, pp.459-470, Nov.2014.
- [104] Dormann, C. and S. Woodin. "Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments." *Functional Ecology*, vol.16, no.1, pp.4-17, 2002.
- [105] Wang, X.-G., X.-T. Lü, et al. "Responses of nutrient concentrations and stoichiometry of senesced leaves in dominant plants to nitrogen addition and prescribed burning in a temperate steppe." *Ecological Engineering*, vol.70, pp.154-161, 2014.
- [106] Cunningham, S. A., B. Summerhayes, et al. "Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients." *Ecological monographs*, vol.69, no.4, pp.569-588, 1999.
- [107] Song, Z., H. Liu, et al. "Ecological stoichiometry of N: P: Si in China's grasslands." *Plant and Soil*, vol.380, no.1-2, pp. 165-179. Mar.2014.