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Ecological Response to Global Change: Changes in C:N:P Stoichiometry in Environmental Adaptations of Plants

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Abstract

This review aims to discuss the state of the art of the stoichiometric ratio of foliar nutrients and their impact on adaptive mechanisms of plants to environmental change. Plant stoichiometry is an excellent way to study the multiple ratios across the nutrients in plants and their ecological interactions with the environment. It plays an important role in clarifying the responses of plants to various changes and their adaptation to different environments. However, anthropic activity can change the stoichiometric ratios of plants. In recent decades, anthropic activities have altered the cycle of nitrogen (N), phosphorous (P) and carbon (C) in plants. This is due to excessive fertilizer application, increased global warming and increased atmospheric CO₂ emissions, which can quickly limit the increase of production in plants, as they affect the process of acclimatization, which involves a series of changes in plant metabolism at different levels of organization (molecular, biochemical, anatomical and morphological). In this sense, in this new scenario of changes, new plant responses to stoichiometric changes and adaptive processes in the ecosystem have to be reviewed.

Keywords: plant species, multiple ratios, adverse habitats, ecological processes, ecosystem

1. Introduction

The increase in warming and droughts and the high concentrations of atmospheric CO₂ can change the contents and the stoichiometry of nitrogen (N) and phosphorous (P) in plants [1], and they can have an indirect impact on soil and nutrient availability. This increase in high

CO₂ concentrations induces changes in plants, especially in C3 plants, with an increase in the uptake of carbon (C), which may lead to a reduction of transpiration [2], because CO₂ absorption promotes stomata closure [3], which may limit the ability of plants to assimilate N [4].

The high absorption of CO₂ may also lead to a gradual limitation of nutrients that can quickly limit the increase in plant production [5], because it affects the process of acclimatization that involves a series of changes in plant metabolism at different levels of organization (molecular, biochemical, anatomical and morphological) [6].

In recent decades, anthropic activities have altered the P cycle; excessive doses of fertilizers are being used, thus inducing an increase in the input of this nutrient into terrestrial and aquatic ecosystems [7, 8]. Increased application of P may alter the balance between C, N and P in plants, and thus change the C:N:P stoichiometry ratios [8] and reduce the C:P ratio in plant tissues [9, 10]. Another concern is the change in N and P cycles, which can cause several consequences to the environment [11–13].

In this scenario, environmental responses of plants to global changes have a negative character with future losses to food production worldwide. Therefore, it is necessary to recognize the new stoichiometry (C:N:P ratios) that occurs in plants in this new scenario in order to try to identify a plant-environment interaction that may allow an increase in food production and that will allow greater food security in the future.

The interactions that occur between elements are complex and their effects reflect the mineral composition of plants. An alternative to study the multiple ratios between elements in a plant is to focus on stoichiometric ratios that are considered to be an important biological indicator for elucidating plant responses to various changes and their adaptation to different environments [14].

Moreover, the study of plant stoichiometry can influence ecological processes, and thus modulate the structure and function of the ecosystem [15, 16]. It can also effectively indicate changes in C, N and P cycles [17].

The carbon (C):nitrogen (N):phosphorus (P) ratio is one of the most investigated topics in stoichiometry, because N and P limit plant growth and C is the structural basis of plants: they account for 50% of plant dry mass [18].

These elements are strongly linked to the biochemical functioning of plants. P is an important element in the production of ribosomes; it is involved in the synthesis of proteins containing N and C. There are, therefore, fundamental biochemical reasons for using these elements in appropriate proportions [19].

In plants, C:N and C:P ratios represent the ability of photosynthetic fixation of C through N or P accumulation. Also, the N:P ratio can be used as an indicator to study plant nutrient limitation in adverse habitats [20].

Therefore, the proportions of leaf N and P in plant biomass can be an indicator of vegetation composition and nutrient limitation at the community level [21, 22]. An N:P < 14 ratio indicates N limitation, whereas an index >16 suggests P limitation [21]. An ideal N:P ratio is considered to be 10–20, on a mass basis [22].

In view of the above, the present chapter sought to study patterns and values and discuss the stoichiometric changes C:N:P occurring in plants in response to global changes and their implications in the adaptive mechanisms of plants to the environment.

2. Climatic effect

The climate exerts a strong control on plant growth and hence it influences plant stoichiometry. Changes in growth rate can be caused by changes in the availability of elements as a result of changes in temperature, latitude, drought and warming. Thus, one of the challenges in the future should elucidate the reasons and implications of this variability which may alter the success of resident plant species.

2.1. Latitude

Latitude is a climatic parameter that can influence stoichiometric ratios. In this scenario, three analyses of leaf N:P patterns indicated that the N:P ratio is approximately half when latitude in the Equator is 70° (**Figure 1**) [23, 24].

The reason for this trend can be explained by N concentrations (N:C) which are approximately constant for latitudes, increasing P concentrations as latitude changes. This is indicative of a trend in N:P [23].

A study that analysed foliar N:P ratio as a function of latitude showed that this ratio increases with temperature [25]. This increase in temperature towards the Equator occurs because P is

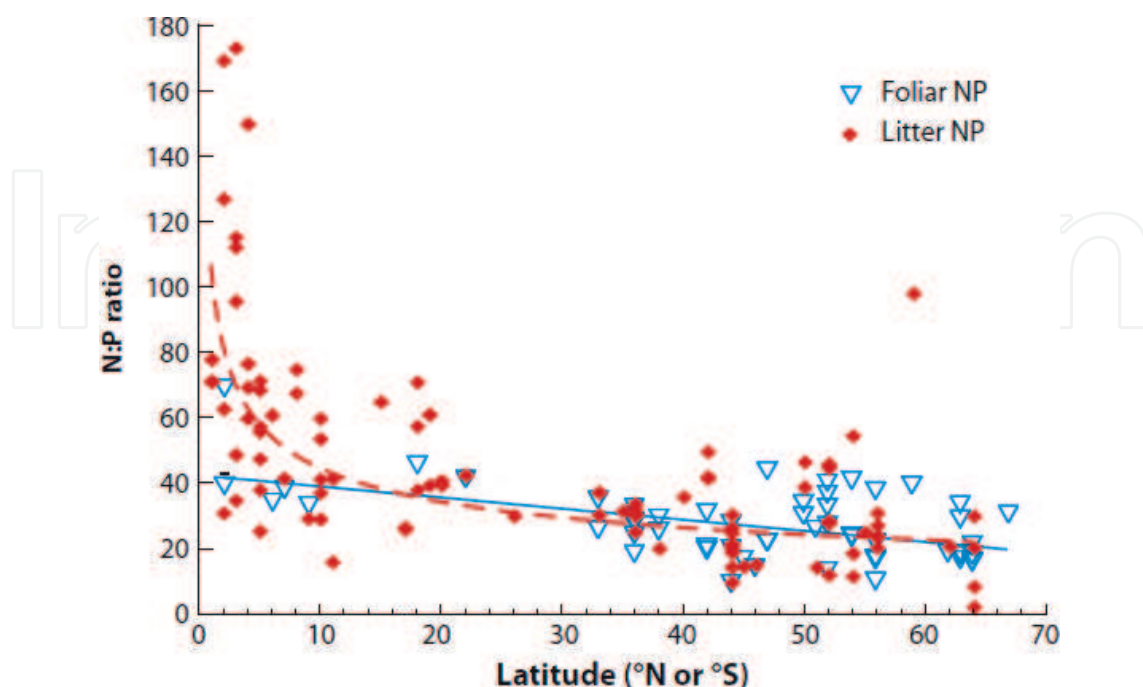


Figure 1. Variation in N:P (molar ratio) in foliage (open triangles) and litter (solid diamonds) as a function of latitude [23].

an important limiting nutrient in tropical soils and N is the main limiting nutrient in temperate regions and high-latitude soils.

2.2. Light

Differences in the exposure of plants to sunlight can also affect their stoichiometry. One study compared the N:P ratio of sunlight-exposed leaves and shade-exposed leaves of two species of *Quercus ilex* and *Quercus coccifera* plants in Spain [26]. In both species, the sunlight-exposed leaves had about twice as much concentration of P compared with the shade-exposed leaves, while there were minor differences in the concentrations of N. The P:N ratio was also higher in the sunlight-exposed leaves than in the shade-exposed ones.

This result indicates that the two plant species may show ability to adequately respond to changes in environmental factors by means of phenotypic plasticity, which is positively related to the ecological distribution of species.

2.3. Drought

Long periods of water stress often cause a reduction in plant growth [27], but plants respond with increased absorption of water and improved mechanisms for water use efficiency. The events caused by water stress initiate physiological responses in plants which often affect ecosystems and nutrient cycling [28, 29].

Mathematical models predict an increase in water deficit in various areas of the world. The effects of increased water deficit differ across ecosystems and species. In semi-arid areas, drought reduces the C:N ratio in the roots of the species *Quercus ilex* [30, 31].

In other plant species, drought increased the C:N and C:P ratios of leaves of shrubs and trees in the Mediterranean, as a result of protection mechanisms [32, 33] associated with the presence of leaves whose structure is drought-tolerant [34].

In moist temperate ecosystems, the C:N ratio can decrease moderately because plants increase the uptake of N and reduce their growth [35].

Thus, evidence suggests that drought tends to increase C:N ratios of photosynthetic tissue in semi-arid environments, but the effects are not so clear in moist ecosystems (**Figure 2**), in which drought may affect various aspects of plants.

In dry regions, the increase in C:N ratios can combine with increases in response to CO₂ concentrations, which suggests synergy that increases the C:N ratio (and, probably, the C:P ratio) and slows the N and P cycles, thus reducing the availability of N and P and their concentrations in the biomass [32, 36].

2.4. Warming

The increase in ambient temperature can increase the mineralization of organic C and, thus, increase the amount of atmospheric CO₂ [37]. This may explain why several studies have not detected an effect of high ambient temperatures on the C:N ratios of some plants (**Figure 2**).

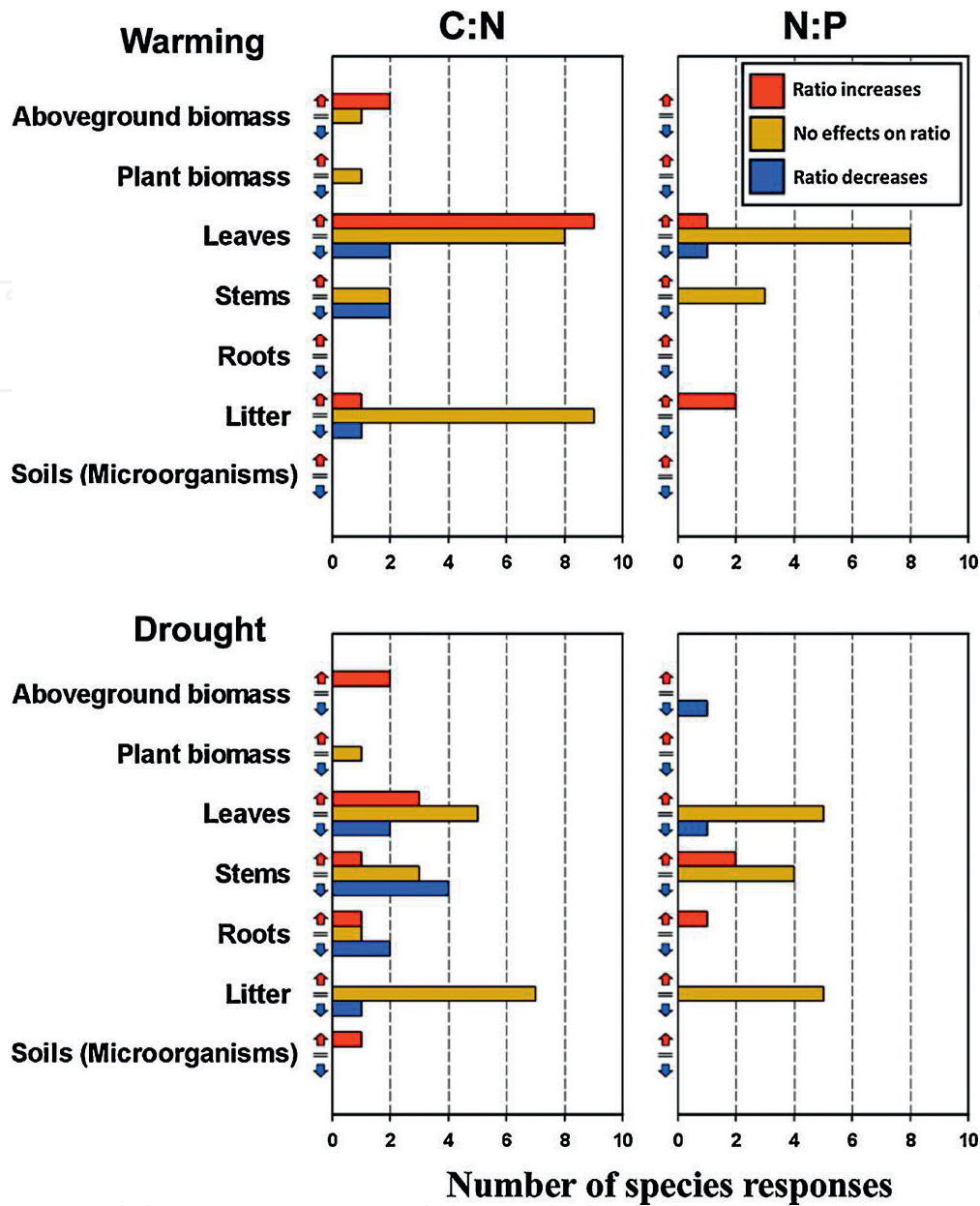


Figure 2. Reported increases, decreases and absence of change in C:N and N:P ratios in response to warming or drought [13].

Plant respiratory responses to warming may affect the availability of light, water and CO₂, and plant responses may differ across species and organs [38]. Thus, evidence suggests that the rise in temperature predicted by climate models will increase the C:N and C:P ratios of plants based on mechanisms of water stress resistance or water-use efficiency. This increase of C:N and C:P ratios caused by warming coincides in semi-arid regions.

In cold ecosystems that are not limited by water, the effects of warming on C:N ratios of plants are not well understood. However, some studies have shown that warming has changed the C:N ratios of plants, increasing production capacity and nutrient absorption of plants [39]. Other studies in pastures in cold regions have not found any effects [40] or have reported an increase in the C:N ratio associated with an effect of dilution by an increase in biomass production [41].

3. Variations in C:N:P ratios in plants

3.1. Growth rate and N:P stoichiometry in plants

The applicability of growth rate (GR) to plants has been attracting interest because leaves have high concentrations of nutrients (N and P). However, only a few experimental studies have assessed GR for particular plant species.

A study with seedlings of the species *Betula pendula* with P limitation showed a decrease in N:P ratios and high relative growth rates; however, plants with N limitation did not show this pattern [42], probably because of P storage under N limitation.

A study with 14 pine species grown with high levels of nutrients in a greenhouse [43] reported faster plant growth, which was correlated with nutrient concentrations and a decrease in the protein RNA.

Finally, when the researchers compared the seedlings for growth rates among the 14 species under high-nutrient conditions, they found no correlation with N:P ratios or the protein RNA [43].

The results of Ågren [42] and Matzek and Vitousek [43] suggest that the basic prediction of GR (a negative correlation between N:P and growth rate) may not be useful for plants when nutrients, especially P, are not limiting factors.

Thus, studies have concluded that although the vegetable protein:RNA ratio affects the speed and efficiency of growth; it does not determine, by itself, leaf N:P stoichiometry. Thus, it seems that the advances and understanding of interactions between N:P stoichiometry and growth require both additional studies and development of models that represent the potential storage of nutrients, especially P [44].

The correlation between N and P observed in leaves has been recently confirmed in other important plant organs [45]. A study using a high number of species [46] found that, as in leaves, N and P concentrations are correlated in roots, stems and in reproductive tissues.

High concentrations of P and low N:P ratios are linked with growth rate [14]. The effects of high CO₂ concentrations on plants and C:P ratios and, in particular, on N:P ratios, still are not clear [47] and deserve further study because N and P are essential in living systems and their relationship is associated with changes in the structure of the ecosystem [14]. In fact, it is important to increase our understanding of changes in the mineralization of N and P in plants and in the soil under high CO₂ concentrations because N and P are important in the composition of litter and soil decomposition rates [48]. A meta-analysis showed that added N significantly decreased the C:N ratio of photosynthetic tissues of woody plants ($P < 0.05$, $n = 25$) and herbaceous species ($P < 0.05$, $n = 6$). On average, N reduced the C:N ratios of photosynthetic tissues by 25% ($P < 0.05$, $n = 31$) (**Figure 3**).

In 20 of 36 species, the addition of N increased the N:P ratio of photosynthetic tissues; in 15 species, the N:P ratios were not changed and, in one species, the ratio decreased. The addition of N increased the N:P ratios of the photosynthetic tissues of woody plants ($P < 0.05$, $n = 10$) and herbaceous species ($P < 0.05$, $n = 12$) (**Figure 3**).

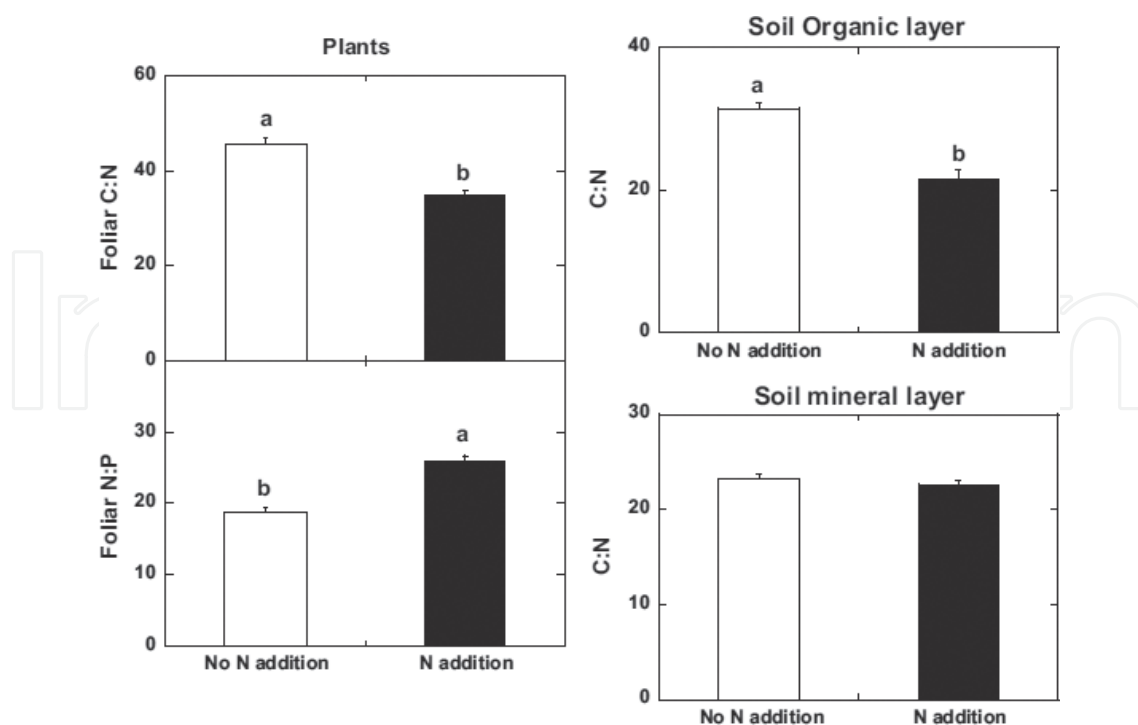


Figure 3. Leaf C:N and N:P ratios of plants growing in the environment and in the N-addition treatment. Metadata analysis of 31 different experimental results in the case of leaf C:N ratio and of 22 different experimental results in the case of leaf N:P ratio. Soil organic and inorganic C:N ratios under ambient conditions and in the N-addition treatment. The only studies that were taken into account were those that provided the mean (\pm S.E.) of leaf C:N and C:P ratios of plants, and soil C:N ratios growing under ambient conditions and in the N-addition treatment. Meta-analyses were made by using the MetaWin Package, which is based on the knowledge of control and treatment results (mean \pm SD) in each study (considering each species being studied). Different letters indicate statistically different values ($P < 0.05$) [13].

3.2. Plant stoichiometry

Plant stoichiometric is a technique that allows investigating energy flow and cycling of materials in ecosystems [49], stoichiometric flexibility, physiological adjustment of C:N:P ratios which may improve plant performance in response to environmental changes [50]. Therefore, it is important to investigate the patterns of stoichiometric values and their flexibility within and among plant species [51].

However, this technique may present some disadvantages regarding the variability that occurs in plant C:N:P stoichiometry in several habitats and emerges from two interaction processes: (1) macro-scale constraints caused by specific geographic environment (climate and soil), and (2) fundamental physiological constraints resulting from growth, development, metabolism, phenology and life history [23].

Moreover, plant size, which changes as a result of seasonal development, may influence the rate indicated by the metabolic scale theory [52, 53], which in turn affects the stoichiometric ratios through metabolic changes [1].

Sampling time is another factor that may compromise the success of this technique, because sampling ranges from months to years, and the effects of organ size within a period of the year of the study are often not kept constant [25, 54].

Thus, a study developed to evaluate the C:N:P stoichiometric flexibility as of the date of sampling was developed by Zhang et al. [55] in field conditions in Mongolia. Three plant species were selected: *Leymus chinensis* (perennial C3 plant); *Cleistogenes squarrosa* (perennial C4 plant) and *Chenopodium glaucum* (annual C3 plant).

To study the effects of sampling date, 30 individual plants of each species were collected at 15-day intervals, from 10 July to 25 August 2006, for a total of four sampling dates.

The authors found that the C:N, C:P and N:P ratios in the leaf tissue increased over time compared with the study species, except for the species *Chenopodium glaucum* (Figure 4a–c) [55].

For the species *Leymus chinensis*, the C:N, C:P and N:P ratios were the highest among the three species and they increased over time, with the exception of the N:P ratio until the last date of

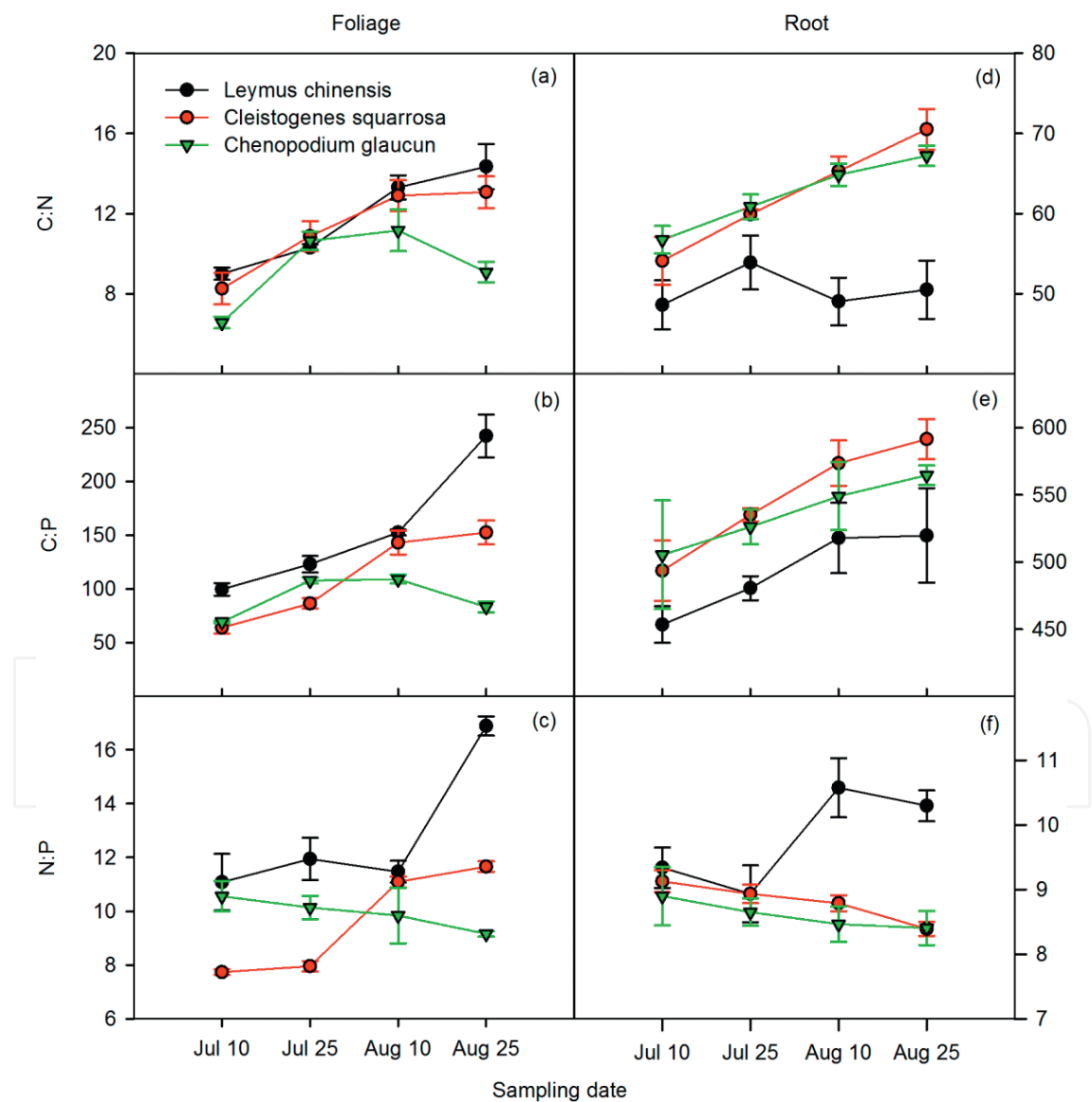


Figure 4. Change in C:N (a), C:P (b), N:P (c) ratios for leaf (left) and C:N (d), C:P (e), N:P (f) root (right) tissues over time for three grassland species in the sand culture study. Error of mean [49].

sampling (**Figure 4c**). However, for *Chenopodium glaucum*, the C:N and C:P ratios increased for the first two sampling dates and then decreased after 10 August 2006 (**Figure 4a and b**) [55].

Thus, the study suggests that leaf sampling at different times may influence the stoichiometric ratios of the plant, particularly C:N and C:P ratios of leaves [55].

In general, the C:N and C:P ratios of leaves increased with increasing sampling date within the study periods. This increase was probably driven by the increase in plant size (C content); as plants get older, the C-enriched material accumulates, which leads to a 'dilution' of N and P contents over time [56, 57].

Thus, over time, C:N and C:P ratios may increase because of reduced nutrient allocation to older leaves and to nutrient dilution as the leaf area and root systems increase over time [55].

C:N:P stoichiometric ratios in plants can also be altered depending on the application of beneficial elements in agriculture, e.g. silicon (Si).

In this scenario, a study was conducted in a greenhouse in Jaboticabal, São Paulo State, Brazil, in which a rice crop was combined with the application of Si sources (Nano silica and soluble silicon) and concentrations of Si (0, 605, 1210, 103 and 2420 g ha⁻¹ Si, applied on the seeding furrow). They found that Si availability did not affect the C:N:P stoichiometric ratio in the shoot of rice plants, although there were higher stoichiometric C:N:P ratios in the concentration of 1210 and 2420 g ha⁻¹ Si, when soluble silicon was used (**Table 1**) [58].

In this study, the stoichiometric ratio found refers to the average, excluding the panicle, and this probably resulted in the absence of more pronounced effects of the treatments applied [58].

There are strong associations between the absorption of Si, N and P, and a study on silicon sources and grass species emphasized that the responses varied according to the sources of silicon in use [59]. In an experiment with *Phragmites australis* [60], it is reported that Si availability can have significant effects on stoichiometric C:N:P ratios in different tissues (leaf blades, sheaths and stems).

Elements	Treatments (g ha ⁻¹)	Stoichiometry
C:N:P	Nano silica: 0	188:15:1
	Nano silica: 605	191:16:1
	Nano silica: 1210	183:15:1
	Nano silica: 2420	197:16:1
	Soluble silicon: 0	188:15:1
	Soluble silicon: 605	183:15:1
	Soluble silicon: 1210	199:17:1
	Soluble silicon: 2420	199:17:1

Table 1. Stoichiometry of nutrients affected by sources and doses of silicon applied in the seeding furrow of rice [58].

4. Global changes and plants: a perspective of stoichiometric scaling

Global changes can affect the stoichiometry of plants and of the ecosystem through changes in C:P and C:N ratios, which can alter food quality, affect the nutrient cycle, impoverish the nutrient composition of the ecosystem and increase the risk of extinction of species.

4.1. Atmospheric CO₂

There is strong evidence on the relationship between atmospheric CO₂ concentration and plant stoichiometry. It is expected that the increases of atmospheric CO₂ will stimulate the plant photosynthesis and, perhaps, growth and overall production.

As a result, there is potential for C sequestration in plant biomass as atmospheric CO₂ increases [61]. However, the length of plant growth in any location is probably influenced by the resources available in the soil, particularly N [62].

Atmospheric CO₂ fixation tends to increase the root/plant ratio [63] and leaf area [64], which will influence the C:N:P ratios of the entire plant and, ultimately, photosynthetic capacity [65].

At the molecular level, rubisco, a key photosynthetic enzyme, operates more efficiently at higher levels of CO₂ emissions (intracellular levels), especially in C₃ plants [66], by minimizing the need for gene expression of the enzyme to compensate for the losses to photorespiration [67]. The resources (for example, N) which are not used to produce rubisco can then be diverted to increase production [68].

In general, a higher concentration of CO₂ should result in a greater C:N ratio in plant biomass and increases in plant size [69].

4.2. Global warming

Global warming will likely influence plant stoichiometry, plant species, community primary production through impacts on phenology and plant growth conditions [61].

However, these effects will be moderated by drought. For example, in the long term, warming with increasing drought conditions in the Amazon can induce massive changes in biomass carbon [62].

However, restrictions on the use of nutrients [45] and changes in development and the way plants share resources across the types of tissue [70] suggest changes in C concentrations on a large scale; they will also be accompanied by absolute changes in levels of soil nutrients.

4.3. Varying increases in supplementation with N and P

The majority of terrestrial ecosystems has historically been adapted to a natural limitation of key nutrients [71]. Combustion of fossil fuels, use of fertilizers, agricultural production of legumes [72], deforestation and changes in land [73] allowed for a large-scale duplication of input of biologically available N in ecosystems around the world. The anthropogenic effects

of P in the biosphere appear to be even greater, because the cycle of this nutrient was amplified four times by human action [74].

In the short term, more availability of N and P can increase the productivity of plant species through a greater leaf area index [65] among other routes, and biomass [18]. In the long term, increases mediated by nutrient deposition in the soil can shape community composition differentially, changing the growth rate and the success of resident plant species [75].

5. Methodology

Data from the published literature on the ecological response to global change were collected: C:N:P stoichiometry changes in plant environmental adaptations. The information on the climatic effect of latitude was obtained from information on variation in N:P (molar ratio) in foliage (open triangles) and litter (solid diamonds) as a function of latitude [23].

Regarding the light climatic factor, data were selected and collected on differences in the exposure of plants to sunlight that can affect plant stoichiometry. This study was based on the work of Valladares et al. [26].

Regarding the dry climatic factor, the information collection was made considering that the effects of the water deficit differed between ecosystems and species, based on scientific studies [30–35].

For the climate heating factor, information on the effect of temperature, respiratory responses to heating and on cold ecosystems the effects of heating on the C:N ratios [38–41] were addressed.

The variations in the C:N:P ratios in plants were plotted from the collection of information on growth rate and N:P stoichiometry in plants that were based primarily on works of [42, 43], and plant stoichiometry in the information collected mainly from the work of [49, 50, 55, 58].

Finally, global and plant changes: a perspective of stoichiometric design, atmospheric CO₂ was studied; Global warming and variable increases in N and P supplementation, from the collection of relevant information, based on published scientific articles on the subject.

6. Conclusions and future perspectives

This chapter addressed the main issues regarding the ecological response to global change: C:N:P stoichiometry changes in plant environmental adaptations, based on recent scientific findings that can guide students and researchers in their studies and enable future research.

Plant stoichiometry is becoming an excellent measure to study the multiple ratios that occur between plant nutrients and their ecological interactions with the environment. It plays an important role in elucidating a plant's responses to various changes and adaptation to different environments. However, anthropic activity can change stoichiometric ratios of plants.

In recent decades, anthropic activities have altered the cycle of N, P and C, mainly with the use of high doses of fertilizers, increased global warming, droughts, increased atmospheric CO₂ emissions. This increase has altered stoichiometric relations among the nutrients in plant tissues and their availability, thus influencing the structure of ecosystems.

In this sense, future research needs to review the new responses of plants in relation to stoichiometric changes and processes adaptive to the ecosystem to this new scenario of changes.

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