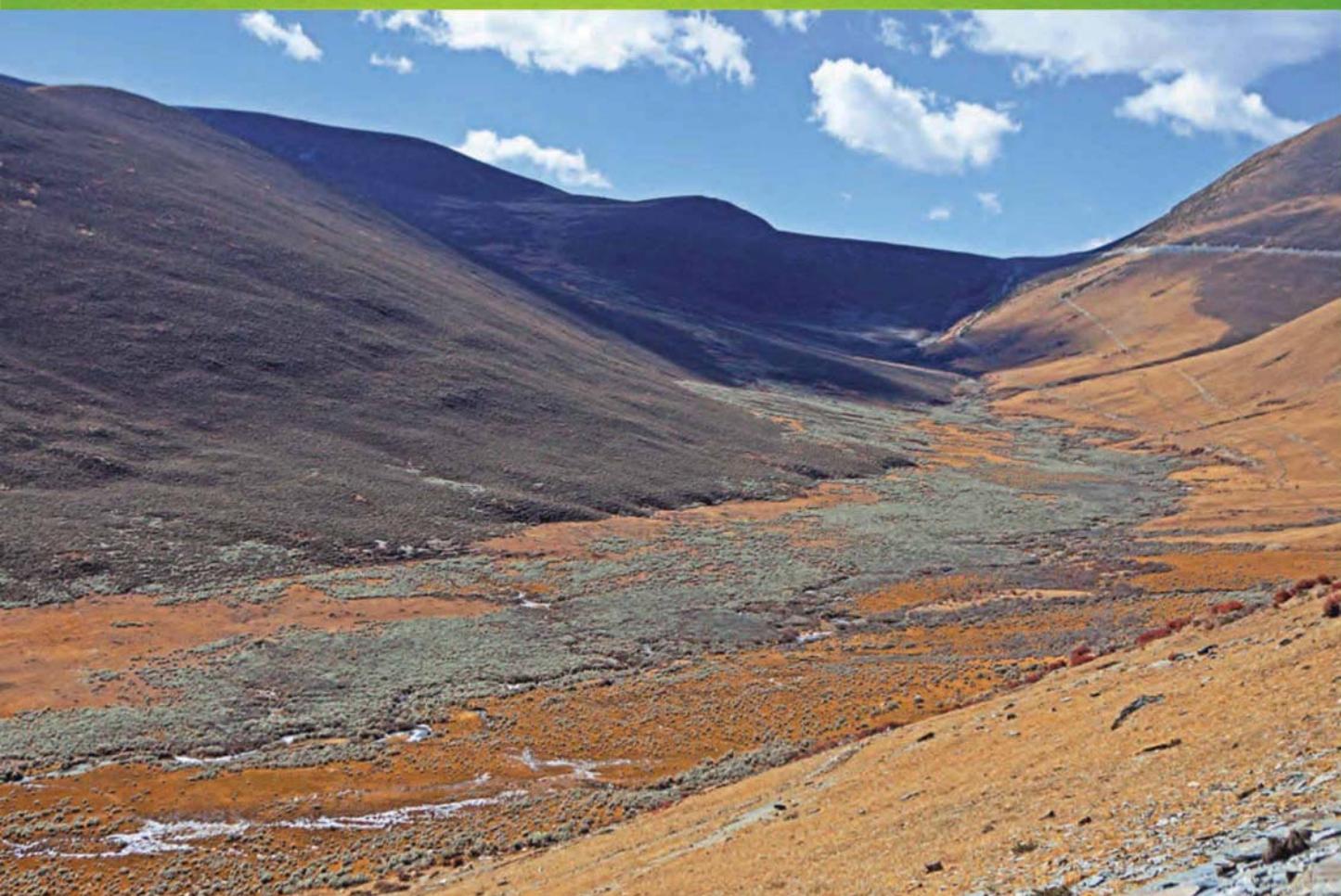


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封面图说: 川西高山地带土壤及植被——青藏高原东缘川西的高山地带坡面上为草地, 沟谷地带由于低平且水分较充足, 生长有很多灌丛。川西地区大约在海拔 4000m 左右为林线, 以下则分布有亚高山森林。亚高山森林是以冷、云杉属为建群种或优势种的暗针叶林为主体的森林植被。作为高海拔低温生态系统, 高山-亚高山地带土壤碳被认为是我国重要的土壤碳库。有研究表明, 易氧化有机碳含量与海拔高度呈显著正相关, 显示高海拔有利于土壤碳的固存。因而, 这里的表层土壤总有机碳含量随着海拔的升高而增加。

彩图及图说提供: 陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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生态化学计量学特征及其应用研究进展

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摘要: 生态化学计量学已成为生态学研究的热点问题。作为一门新兴学科, 综观国内外最新研究进展, 相关研究目前尚存在着许多不足。基于此, 从全球与区域尺度、功能群尺度及个体水平3个方面阐述生态化学计量学特征, 从空间、时间、生境和植物类型等生物与非生物因素综述生态化学计量学特征的驱动因素。并讨论生态化学计量学特征在限制性养分判断、生态系统稳定性、生长率与C:N:P关系中的应用。

关键词: 生态化学计量学; 限制性养分; 内稳定性; C:N:P

Reviews on the ecological stoichiometry characteristics and its applications

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Abstract: It is necessary to construct a unified theoretical framework of ecology in view of the rapid developments in modern ecology. Ecological stoichiometry is the discipline to study the balance between multiple chemical elements in ecological processes, and unify the research of different levels. Ecological stoichiometry is a theory, a thinking way and a tool that should permeate all aspects of ecology.

Currently, studies on ecological stoichiometry are relatively few in China as compared to elsewhere. Studies mainly focus on the C, N, P ecological stoichiometric characteristics and its driving factors, especially in forest and grassland ecosystems. Ecological stoichiometric characteristics in different regions and ecosystem types were different, but at relatively smaller scale, the differences were less. Compared with the other parts of the world, terrestrial ecosystem phosphorus deficiency in China appeared higher for C:P and N:P ratios.

Ecological stoichiometry characteristics on the level of functional group appeared that herbaceous N:P was smaller than that of wood. The mode of living plant, litter and soil showed that litter ecological stoichiometry was similar to living plant and the soil ecological stoichiometry was changed with the order of soil. Ecological stoichiometry characteristics on the level of individual showed that the correlation of plant leaves, stem and root ecological stoichiometry that appeared variable as the plant grows.

Seen from the environmental factors that influenced the ecological stoichiometry, contain latitude, hydrothermal conditions, pedogenesis, human disturbance etc.

Ecological stoichiometry had been applied on many areas of ecology and biology. For example, N:P stoichiometry was one of the most important indicators of limited nutrient conditions, but the criterion of the indication of ecological stoichiometry in various ecosystem were different, and it was necessary to further clarify its applicability. Second, use the ecological stoichiometric homeostasis to clarify the effect of environmental change on ecosystem structure, function and stability, which varied with the change of nutrient availability, fertilization, species and growth stage. Third, taken the

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C:N:P as the most import index of the plant growth rate, relationship between growth rate and C:N:P was proposed based on the growth rate hypothesis, and then linked cell and genetics with growth rate.

Seen from the newest research advance, the relative research was fewer for the new subject. For the reason, the ecological stoichiometry characteristics is clarified on global and regional scale, group scale and individual scale. In order to deepen the understanding of ecological stoichiometry characteristics and its driving factors, quantitatively assess limited nutrient and homeostasis of ecological stoichiometry in ecosystems, forecast community, ecosystem structure and stability evolution trend, strengthen the understanding of relationship between growth rate and ecological stoichiometry characteristics, the newest research advance was reviewed. This is consistent with the controlling factors including biotic and abiotic factors at spatial and temporal scales, habitat and plant types. At the same time, application of ecological stoichiometry characteristic on limited nutrient, ecosystem homeostasis and the relation between growth rate and C:N:P variation are discussed. It will be necessary for achieving optimal management of ecosystems and their reasonable protection, maintaining the regional ecological security and sustainable development.

Key Words: ecological stoichiometry; limited nutrient; homeostasis; C:N:P

随着现代生态学的快速发展,构建统一的理论框架十分必要^[1]。从分子到生态系统都是元素按照一定比例组成的,生态化学计量学正是研究生态过程中多重化学元素平衡关系的学科^[2],并从元素比率的角度把这些不同层次的研究结果统一起来^[3],成为生态学研究的主要方法和研究热点。

自从 Elser 等^[2]首先明确提出生态化学计量学的概念以来,在验证不同生态系统是否存在恒定的生态化学计量学特征^[4]、生态系统限制养分的判断^[5]以及 C:N:P 与生物生长率的关系^[6]等方面开展了大量的研究。2002 年 Sterner 和 Elser^[3]出版了第一部生态化学计量学专著(Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere),以及分别于 2004 年和 2005 年在 Ecology 和 Oikos 发表了生态化学计量学专题,标志着生态化学计量学已经成为一门较为系统的、基本成熟的学科。在国内,Zhang 等^[7]最早对生态化学计量学做了综述,随后曾德慧和陈广生^[8]、王绍强和于贵瑞^[9]、贺金生和韩兴国^[1]、程滨等^[10]、杨慧敏和王冬梅^[11]分别从不同侧面对生态化学计量学的研究进展进行了综述。关于生态化学计量学的实验研究,近年来在国内得到了迅速发展,主要集中在区域 C:N:P 生态化学计量学特征及其驱动因素方面,以森林生态系统和草原生态系统的研究成果居多^[12-17],也有关于以生态化学计量学特征判断草原生态系统限制性养分的研究^[18]。内稳定性理论和生长速率理论是生态化学计量学存在的重要基础。化学计量内稳定性与物种优势度、稳定性有显著的相关关系,对于生态系统结构、功能和稳定性研究有重要意义。生物体的 C:N:P 与生长率有很强的关系,在此基础上,产生了“生长率假说”,对于拓展生态化学计量学理论意义重大。生态化学计量学是一种理论、一种思维,也是一种工具^[1],应向生态学的各个方面渗透,并拓展到不同的生态系统类型。基于此,本文从全球与区域尺度、功能群尺度及个体水平三个方面,并从空间、时间、生境和植物类型等因素对生态化学计量学研究的最新进展作一综述,以期为国内外同行开展相关研究提供参考。

1 生态化学计量学特征及其驱动因素

1.1 生态化学计量学特征

生态化学计量学特征从尺度上划分可以分为全球与区域尺度、功能群或生态系统尺度以及个体水平。在全球与区域尺度关于生态化学计量学特征的研究中,Redfield^[19]首次证明了海洋浮游生物具有恒定的 C、N、P 组成,Elser 等^[4]研究表明陆地节肢动物和海洋节肢动物具有相近的 N:P 比率。随后诸多学者开始在陆地生态系统验证全球以及区域尺度的生态化学计量学特征(表 1)。从表 1 可以看出,对于不同区域、不同生态系统类型其生态化学计量学特征有所差异,但在相对接近的区域,不同生态系统类型的生态化学计量特征之间差别较小。此外,无论是中国陆地植物生态化学计量学特征的均值还是单独的森林生态系统、草地生态系统生态化学计量特征中的 C:P 和 N:P 都高于全球陆地生态系统的平均水平,这说明与世界其它地区相比,我国陆地生态系统缺磷的现象更为明显。

在功能群尺度关于生态化学计量学特征也开展了大量的研究工作,并从生活型、生活史、光合途径等方面进行了比较(表 2)。表 2 显示,在生活型方面,从较大的区域来看,针叶林的 C:N 高于阔叶林,而 C:P 和 N:P 低于阔叶林,但在局地尺度可能有所不同;常绿林的 N:P 高于落叶林;总体来看,草本的 N:P 低于木本。在生活史方面,不同植物之间的 N:P 也存在着一定的差异,特别是蕨类植物的 N:P 明显高于其它植物类型。在光合途径方面,仅有的研究表明 C₃ 植物的 N:P 高于 C₄ 植物。枯落物生态化学计量学特征与植物活体的规律相似。土壤的生态化学计量特征均表现为森林低于草原、沙漠低于极寒高原,而且随着土纲的变化,其生态化学计量学特征也发生改变。

表1 全球与区域尺度生态化学计量学(质量比)特征

Table 1 Ecological stoichiometry (mass ratio) characteristics in the global and regional levels

类型 Types	物种数 Species	碳氮比 C:N	碳磷比 C:P	氮磷比 N:P	文献 References
全球陆生植物 Global terrestrial plants	395	30.9	374.7	12.6	[4]
中国陆生植物 Chinese terrestrial plants	753	—	—	14.4	[12]
全球森林生态系统植物 Global forest ecosystem plants	55*	37.1	469.2	12.6	[20]
中国森林生态系统植物 Chinese forest ecosystem plants	4*	28.5	513.0	18.0	[21]
中国东部地区陆生植物 Terrestrial plants of eastern China	654	—	—	15.4	[14]
中国北方典型荒漠及荒漠化地区植物 The typical desert and desertification area plants of northern China	214	—	—	15.8	[22]
中国草地植物 Chinese grassland plants	213	17.9	273.9	15.3	[13,23]
全球森林生态系统凋落物 Global forest ecosystems litter	55*	57.3	1175.6	20.3	[20]
中国森林生态系统凋落物 Chinese forest ecosystems litter	4	44.8	1132.5	25.0	[21]
全球陆地(0—10 cm)土壤 Global land (0—10 cm) soil layer	186	12.3	72.0	5.9	[24]
中国陆地(0—10 cm)土壤 Chinese land (0—10 cm) soil layer	133	12.3	52.7	3.9	[25]

* 生态系统类型数量

表2 不同功能群生态化学计量学(质量比)特征

Table 2 Ecological stoichiometry (mass ratio) characteristics in the different functional groups

类型 Types	碳氮比 C:N	碳磷比 C:P	氮磷比 N:P	文献 References
全球温带阔叶林 Global temperate broadleaf forest	30.1(29)	357.0(28)	12.7(28)	[20]
全球温带针叶林 Global temperate coniferous forest	51.0(19)	476.8(19)	9.8(20)	[20]
全球热带森林 Global tropical forest	30.4(7)	951.1(12)	19.6(7)	[20]
中国草本植物 Chinese herbs	—	—	13.5(240)	[12]
中国灌木植物 Chinese shrubs	—	—	14.7(135)	[12]
中国常绿林 Chinese evergreen forest	—	—	15.2(149)	[12]
中国落叶林 Chinese deciduous forest	—	—	14.8(126)	[12]
中国针叶林 Chinese coniferous forest	—	—	13.0(27)	[12]
中国阔叶林 Chinese broadleaf forest	—	—	15.1(255)	[12]
长白山温带针阔混交林 Temperate needle broad-leaved mixed forest in the Changbaishan	24.7(21)	321.0(21)	13.0(21)	[21]
鼎湖山亚热带常绿阔叶林 Subtropical evergreen broad-leaved forest in the Dinghushan	25.5(21)	561.0(21)	22.0(21)	[21]
西双版纳热带季雨林 Tropical monsoon forest in the Xishuangbanna	23.3(36)	442.0(36)	19.0(36)	[21]
千烟洲亚热带人工针叶林 Subtropical coniferous plantation forest in the Qianyanzhou	40.4(48)	728.0(48)	18.0(48)	[21]
中国东部地区草本 Herb of eastern China	—	—	13.0(218)	[14]
中国东部地区木本 Woody plant of eastern China	—	—	13.8(349)	[14]
中国东部地区常绿木本 Evergreen woody plant of eastern China	—	—	14.7(245)	[14]
中国东部地区落叶木本 Deciduous woody plant of eastern China	—	—	12.8(154)	[14]
中国东部地区针叶木本 Coniferous woody plant of eastern China	—	—	12.0(44)	[14]
中国东部地区阔叶木本 Broadleaf woody plant of eastern China	—	—	14.1(305)	[14]
珠江三角洲针阔混交林 Coniferous and broad-leaved mixed forest in Pearl River Delta	51.4(5)	553.0(5)	10.9(5)	[17]
珠江三角洲针叶林 Coniferous forest in Pearl River Delta	47.4(4)	727.5(4)	15.7(4)	[17]
珠江三角洲常绿阔叶林 Evergreen broad-leaved forest in Pearl River Delta	45.6(10)	412.2(10)	9.5(10)	[17]
中国种子植物 Chinese seed plant	—	—	14.3(529)	[12]
中国蕨类植物 Chinese fern	—	—	17.6(18)	[12]
中国裸子植物 Chinese gymnosperm	—	—	13.0(27)	[12]
中国被子植物 Chinese angiosperm	—	—	14.3(502)	[12]

续表

类型 Types	碳氮比 C:N	碳磷比 C:P	氮磷比 N:P	文献 References
中国单子叶植物 Chinese monocotyledon	—	—	13.1(109)	[12]
中国双子叶植物 Chinese dicotyledon	—	—	14.6(419)	[12]
中国C ₃ 草本植物 Chinese C ₃ herb	—	—	13.6(204)	[12]
中国C ₄ 草本植物 Chinese C ₄ herb	—	—	13.0(36)	[12]
中国内蒙古草本植物 Herbs in the Inner Mongolia of China	18.7(55)	—	16.4(129)	[13,23]
中国新疆草本植物 Herbs in the Xinjiang of China	18.8(69)	—	13.4(139)	[13,23]
中国西藏草本植物 Herbs in the Tibet of China	17.0(110)	—	15.7(257)	[13,23]
中国草本植物 Chinese herb	16.0(103)	—	14.2(181)	[13,23]
中国木本植物 Chinese woody plant	19.2(38)	—	15.9(83)	[13,23]
中国豆科植物 Chinese leguminous plant	13.9(31)	—	19.0(58)	[13,23]
中国非豆科植物 Chinese non-legume	18.5(182)	—	14.8(467)	[13,23]
全球温带阔叶林凋落物 Global temperate broad-leaved forest litter	50.1(34)	659.0(28)	13.1(30)	[20]
全球温带针叶林凋落物 Global temperate coniferous forest litter	75.3(25)	910.8(19)	11.7(20)	[20]
全球热带森林凋落物 Global tropical forest litter	51.7(47)	1593.3(57)	28.3(50)	[20]
长白山温带针阔混交林凋落物 Temperate needle broad-leaved mixed forest litter in the Changbaishan	39.4(14)	552.0(14)	14.0(14)	[21]
鼎湖山亚热带常绿阔叶林凋落物 Subtropical evergreen broad-leaved forest litter in the Dinghushan	37.3(6)	1305.0(6)	35.0(6)	[21]
西双版纳热带季雨林凋落物 Tropical monsoon forest litter in the Xishuangbanna	30.1(12)	723.0(12)	24.0(12)	[21]
千烟洲亚热带人工针叶林凋落物 Subtropical coniferous plantation forest litter in the Qianyanzhou	72.2(48)	1950.0(48)	27.0(48)	[21]
全球草地 0—10 cm 土壤 Global grassland 0—10 cm soils layer	11.8(75)	64.3(72)	5.6(150)	[24]
全球森林 0—10 cm 土壤 Global forest 0—10 cm soil layer	12.4(55)	81.9(47)	6.6(47)	[24]
中国温带沙漠 Chinese temperate desert	10.5(319)	12.4(319)	1.2(319)	[26]
中国极寒高原 Chinese frigid highland	11.7(749)	24.0(749)	2.7(749)	[25]
中国有机土 Chinese histosols	14.9(16)	131.6(16)	8.0(16)	[25]
中国旱成土 Chinese aridisols	9.6(300)	11.2(300)	1.2(300)	[25]
中国淋溶土 Chinese alfisols	10.4(614)	24.6(614)	2.5(614)	[25]

表中数据表示平均值,括号内为样本量

关于更小尺度(属、种和个体)生态化学计量特征的研究也涌现一些成果。王维奇等^[27]研究表明闽江河口湿地互花米草植物体地上器官 C:N、C:P 和 N:P 高于短叶茳芏;周鹏等^[28]对温带草原主要优势植物不同器官间功能性状的关联研究中发现,草类植物细根 N:P 与叶片无差异,而远高于生殖结构;徐冰等^[29]对内蒙古锡林河流域典型草原植物叶片与细根性状在种间及种内水平上的关联的研究表明,草类细根 N:P 为 7.8,低于叶片 N:P(16.7);Kerkhoff 等^[30]对不同生活史和生活型的种子植物氮磷变化比例的研究显示 N:P 在叶片、茎、生殖结构和根之间均表现出正相关;王冬梅和杨惠敏^[31]研究了 4 种牧草不同生长期的 C:N 生态化学计量特征,结果发现叶的 C:N 生态化学计量比低于茎和根。

此外,生态化学计量学特征的时间变化也比较明显,杨惠敏和王冬梅^[11]比较详尽地介绍了这一特征。吴统贵等^[16]对杭州湾湿地植物 N:P 生态化学计量学特征的研究表明,在生长初期其值较小,在生长旺盛期先升高后降低,随后在成熟期逐渐增加并趋于稳定。杨阔等^[32]对青藏高原草地植物群落冠层叶片氮磷生态化学计量学特征的分析中,发现 N:P 具有明显的年际变化规律。从更长的时间尺度看,植物的演替过程对植物的生态化学计量学特征也有深刻影响,但演替类型和演替阶段的不同,生态化学计量学特征的变化趋势也不一致^[33]。

1.2 生态化学计量学特征的驱动因素

生态化学计量学特征因尺度、生境、植物类型等环境与非环境因素的变化而发生改变。Reich 和 Oleksyn^[34]对全球尺度 N:P 变异性的研究表明,植物体中 N:P 比随着温度和土壤基质年龄的生物地理梯度的变化而改变。McGroddy 等^[20]对全球森林生态系统的研究表明,不管是叶片还是凋落物的 N:P 都是随着纬度的增加而降低。王晶苑等^[21]对中国从温带到热带的 4 种森林类型主要优势植物的 C:N:P 化学计量特征的研究表明,亚热带常绿阔叶林的植物活体与凋落物 C:N:P 均表现为最高,温带针阔混交林的最低,也表现出一定的纬度方向上的变化规律。区域固有的特性使得影响其生态化学计量学特征的因素也有

所不同,如 He 等^[13,23]研究表明,在内蒙古温带草原植物生长主要受到降水的限制,西藏高寒草原主要受到温度限制,新疆山地草原可能是由二者共同决定的。基于区域固有限制性因素的变化,使其生态化学计量学特征的调节因素也将发生改变^[12]。Tian 等^[25]在对我国土壤的 C:N:P 比值的研究中发现,水热条件和成土作用是控制土壤生态化学特征的主要因素。此外,随着人类干扰的加剧,破坏了 C,N,P 循环^[35-36],进而改变着生态过程^[10],但不同区域对人类活动响应的趋势的不一致性,也将会造成 C:N:P 比的重新匹配。由此表明,C:N:P 比的变异性到底有多大,还不是很确定,正如 Reich 和 Oleksyn^[34]所阐述,尚需进一步开展植物活体、枯落物和土壤 C:N:P 的时空特征变异性方面的分析与探讨。

综上所述,不同尺度、功能群类型、环境条件改变都将对生态化学计量学特征造成影响,但从当前的主要研究看,森林和草地生态系统的研究成果居多,且以宏观尺度研究较多,湿地作为自然界生产力最高的生态系统之一,与森林和海洋并称为全球三大生态系统,但其生态系统特征与其它系统存在着明显的差别,因此,应给予特别的重视。

2 生态化学计量学特征在限制性养分判断中的应用

由于人类活动的增强,土地利用方式的转变已造成大面积陆地生态系统养分的失衡,深刻影响着植物的初级生产力^[37]。虽然对各种生态系统类型的恢复与保护逐渐增强,但关于限制性养分的研究却未给以足够的重视。严格地说,施肥试验是检验种群和群落水平养分限制的唯一准确方法^[38-39]。但施肥试验周期长、对样地产生干扰,寻求能快捷的反映养分限制的简单指标一直是生态学和植物营养学的关键问题之一。Aerts 和 Chapin^[40]研究认为叶片对 N,P 养分缺乏的适应可体现在叶片 N:P 化学计量比的变化上。因此,N:P 化学计量比可作为当前限制性养分判断的指标之一。

Han 等^[13]和任书杰^[14]的研究表明我国陆地植物的 N:P 高于全球平均值^[4],说明我国陆地植物相对国外更缺磷。同样,用生态化学计量学方法,Elser 等^[41]认为全球陆地、海洋和淡水生态系统均是受到磷的限制。但随着研究的深入,这些指标的不稳定日益显露出来,国内外对这些指标的应用也从盲从趋于谨慎。因此,这些养分限制诊断指标的敏感性和适用性因研究对象不同而存在差异^[18,42]。Koerselman 和 Meuleman^[5]选取不同植物进行的施肥实验表明,在群落水平上,N:P>16 表示 P 限制,N:P<14 是 N 限制。但是,同一个群落内,有的物种是 N 限制,有的物种则是 P 限制,所以 N:P 不能用来表示物种水平的限制元素。Güsewell 等^[43]对湿地植物的施肥实验表明,N:P>20 时,添加 P 肥,群落有显著的变化,而 N:P<20 时,添加 N 肥或者同时添加 N 和 P 都没有显著的变化,N:P 不能用来揭示 N 限制或者是 P 限制。此外,Zhang 等^[18]对我国内蒙古羊草草原的施肥实验表明,N:P>23 时是 P 限制,而 N:P<21 时是 N 限制。

由此表明,不同的生态系统养分限制的生态化学计量学标准存在差异,用统一的标准来衡量生态系统的限制性养分并不合适,应结合施肥试验,彻底弄清影响这一指标适用性的因素及影响机制。

3 生态化学计量内稳定性

化学计量内稳定性是化学计量生态学的核心概念^[3],其强弱与物种的生态策略和适应性有关^[44]。从国内外研究来看,这方面研究属于一个新兴的领域,研究成果十分匮乏。已有的研究表明,动物的生态化学计量内稳定性相对较强,但变化范围也较大,P 的内稳定性指数为 4—40^[45],P:C 的内稳定性指数为 16—161^[44]。Yu 等^[46]对内蒙古羊草草原 12 种植物的研究表明,维管植物内稳定性指数具有很大的变动范围(1.9—14.5)。总体来看,从早期的原核生物到后期的原核生物,再到单细胞真核生物和多细胞真核生物,内稳定性可能是逐渐增强的^[47],藻类和真菌的内稳定性低于低等植物,低等植物低于高等植物,植物低于动物^[3]。与此同时,不同元素的内稳定性也不相同,如 Karimi 和 Folt^[48]对淡水无脊椎动物的研究,N,C,P 的内稳定性指数分别是 34.1、13.8 和 7.7。一般来说,大量元素的内稳定性高于微量元素,微量元素高于非必要元素^[3]。此外,关于植物生态化学计量内稳定性的影响因子研究表明,养分的供应状况和光的强度^[42],施肥^[49]、物种、器官(地上和地下)、生长发育阶段和元素^[46]都会影响到植物的生态化学计量内稳定性。

关于生态化学计量内稳定的生态学和进化学意义,得到学者们的高度重视^[3],因为这个指标反映了生物对环境变化的生理和生化的适应^[50-51],其强弱与物种的生态策略和适应性有关^[44],但研究成果十分有限。Yu 等^[52]在内蒙古羊草草原的实验表明,生态化学计量内稳定性高的物种具有较高的优势度和稳定性,这说明生态化学计量内稳定性是生态系统结构、功能和稳定性维持的重要机理,但环境条件(如氮肥添加)可能会改变生态化学计量内稳定性与生态系统特性的关系^[53]。由于不同的生态系统类型间存在巨大差异,生态化学计量内稳定性在湿地生态系统的特征亟待研究。

4 生长率与 C:N:P 关系

生物体最基本的组成是元素,特别是 C,N,P,生物的生长过程实质上是对这些元素的积聚与相对比例的调节过程^[51]。因此,生长率是能够从整体上描述生物生活史策略的核心指标^[54],Sterner 和 Elser^[3]认为,生物体的 C:N:P 与生长率有很强的关系,在此基础上,产生了生长率假说,即生物体的快速生长需要大量的核糖体 RNA 合成蛋白质,由于核糖体 RNA 中含有大量的 P,从而使得生长率高的生物具有较低的 C:P 和 N:P^[2-3]。这一理论的诞生,把细胞和基因机理与生长率这样的宏观生态结果统一起来,对于拓展与完善生态化学计量学理论意义重大^[2]。在此之后,掀起了相关研究的热潮,其有效性在不同的生物类型与生态系统之中进行验证。已有的研究成果中,在浮游动物、节肢动物和细菌研究中得到验证^[4,55-57]。但由于植物具有贮存物质的功能以及 RNA 中的 P 占植物全磷的比例较低^[55],使得高等植物是否符合生长率假说更具不确定性。有些研究表明植物

生长符合生长率假说^[51,58-59],也有一些研究不支持生长率假说^[6]。因此,植物中N:P与生长率的关系还有待进一步验证^[51]。在极其有限的研究中,一些学者还探讨了是否养分供应决定着维管植物符合生长率假说与否,研究结果表明营养条件可以改变N:P与生长率的关系,即在P限制条件下,桦树幼苗N:P与生长率负相关,而N限制下,N:P与生长率正相关^[60]。

此外,生长率的快慢也调节着其与N:P的关系。对热带树木和藤蔓植物的研究表明,N:P与生长率正相关,而高生长率时,N:P与生长率负相关^[61]。在湿地生态系统红树植物研究表明,红树科的两种植物物种间N:P与生长率负相关,而物种内没有发现规律^[62]。

5 结语

生态化学计量学是当今研究的热点与核心问题,受到了国内外学者的广泛关注,通过综述国内外最近研究进展,主要得出以下几点认识:

- (1)在全球与区域尺度上,不同区域、不同生态系统类型其生态化学计量学特征有所差异,但在相对接近的区域,不同生态系统类型的生态化学计量特征之间差别较小。与世界其他地区相比,我国陆地生态系统缺磷现象更为明显;
- (2)不同功能群生态化学计量学的特征在生活型、生活史、光合途径方面表现出一定的规律性,总体表现为草本的N:P低于木本,枯落物与植物活体生态化学计量学特征规律相似,土壤的生态化学计量学特征随着土纲的变化而变化;
- (3)个体水平的生态化学计量学特征表现出植物叶片、茎、生殖结构和根存在关联性,并存在明显的时间变化规律;
- (4)纬度、水热条件、成土作用、区域固有的特性及人类干扰是生态化学计量学特征重要的驱动因素;
- (5)在生态化学计量学的应用方面,N:P化学计量比是当前限制性养分判断的重要指标之一,应结合施肥实验作进一步的诊断。因研究对象不同,限制性养分判断指标的适应性存在差异。不同生态系统养分限制的生态化学计量学标准存在差异,尚需进一步弄清这一指标适用性的影响因素及机制;化学计量内稳定性总体表现为低等生物向高等生物增强的趋势,其强弱与物种的生态策略和适应性有关,具有重要的生态学和进化学意义。养分的供应状况、施肥、物种及生长发育阶段等是生态化学计量内稳定性的重要影响因子;在生长率与C:N:P关系的基础上提出了生长率假说,将细胞和基因机理与生长率联系起来,对完善生态化学计量学理论意义重大,有待在不同生物类型与生态系统中进一步的验证。

综上所述,目前关于生态化学计量学的研究仍然存在着很多不足之处。因此,系统深入地研究生态系统生态化学计量学特征与驱动因素、生态化学计量学特征对限制性养分的指示标准、生态化学计量内稳定性与影响因子的综合评价、生态化学计量内稳定性对生态系统结构、功能和稳定性的维持机制、生态化学计量学特征与植物生长率的关系等,对于深入认识和理解生态系统生态化学计量学特征及其驱动力,定量评估生态系统的限制性养分与生态化学计量内稳定性,预测群落、生态系统结构与稳定性的演变趋势,深化生长率与生态化学计量学特征的关系的认识,实现生态系统的优化管理和合理保护、维护区域生态安全和实现可持续发展等方面均具有十分重要的理论和现实意义。

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