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Bożena Denisow, Faculty of Horticulture and Landscape Architecture, University of Life Sciences in Lublin, Poland

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INVITED REVIEW

Plant–insect interactions: the role of ecological stoichiometry

Michał Filipiak*, January Weiner

Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Cracow, Poland

* Corresponding author. Email: michal.filipiak@uj.edu.pl

Abstract

The energy budget of organisms is a primary factor used to generate hypotheses in ecosystem ecology and evolutionary theory. Therefore, previous studies have focused on the energy costs and benefits of adaptations, the efficiency of energy acquisition and investment, and energy budget limitations. The maintenance of stoichiometric balance is equally important because inconsistency between the chemical composition of the consumer's tissues and that of its food sources strongly affects the major life-history traits of the consumer and may influence the consumer's fitness and shape plant–herbivore interactions. In this short review, the framework of ecological stoichiometry is introduced, focusing on plant–insect interactions in terrestrial ecosystems. The use of the trophic stoichiometric ratio (TSR) index is presented as a useful tool for indicating the chemical elements that are scarce in food and have the potential to limit the growth and development of herbivores, thereby influencing plant – herbivorous insect interactions. As an example, the elemental composition and stoichiometry of a pollen consumer (mason bee *Osmia bicornis*) and its preferred pollen are compared. The growth and development of *O. bicornis* may be colimited by the scarcity of K, Na, and N in pollen, whereas the development of the cocoon might be colimited by the scarcity of P, Mg, K, Na, Zn, Ca, and N. A literature review of the elemental composition of pollen shows high taxonomical variability in the concentrations of bee-limiting elements. The optimized collection of pollen species based on the elemental composition may represent a strategy used by bees to overcome stoichiometric mismatches, influencing their interactions with plants. It is concluded that the dependence of life-history traits on food stoichiometry should be considered when discussing life history evolution and plant–herbivore interactions. The TSR index may serve as a convenient and powerful tool in studies investigating plant-insect interactions.

Keywords

ecological stoichiometry; plant; insect; plant–herbivore; fitness; life history; bee; pollen

Background

Herbivores rely on diets rich in energy but scarce in the components used for body building and body maintenance. Thus, the development and growth of herbivores may primarily depend on food quality and body-building matter availability in addition to energy [1–4], cf. [5]. Although matter quality has been recognized as an important factor shaping ecological interactions [1–3,6–8], energy has been the main focus of ecologists in recent decades; however, less attention has been focused on the element-specific requirements for the growth, development, and maintenance of the adult body [1–4]. A framework of ecological stoichiometry can consider both energy and matter in the study of ecological interactions [1,2,4,9]. In this short review, we

demonstrate how ecological stoichiometry can provide important insights into plant–herbivore interactions in terrestrial ecosystems and summarize recent advances in ecological stoichiometry. Subsequently, a case study on the ecological stoichiometry of a plant–insect interaction as exemplified by a bee feeding on pollen is presented.

Chemical elements are the most basic and fundamental building blocks that compose all living matter. Organisms are built of diverse, heterogeneous, and composite matter. Despite the diversity and complexity of structures, forms, and functions, all organisms consist of exactly the same building blocks of approximately 25 chemical elements, and these blocks are completed and maintained with the use of energy [1–3]. These elements, however, compose the bodies of living organisms in various proportions, what is crucial for ecological interactions and influence the function of whole ecosystems (e.g., [1,2,4,9–12]). The most influential feature of the elements that shape ecological interactions is that specific atoms must not be transformed into different atoms during processed by the organism. This feature is a consequence of the law of conservation of mass, meaning that every developing organism has at its disposal only the building material that is offered by its environment as a resource. In the case of herbivores, this material consists of a few elements available in excess (e.g., C, H, and O) and a deficit of others (e.g., P, N, and Na [1,3]). Even if potential food is available in excess, the mismatch between the elemental composition of the food and the requirements of the herbivore imposes a limitation on the growth and development of the herbivore [1,4,13,14]. Moreover, growth and development are colimited by the scarcity of several elements in addition to the most limiting element [3,15].

Ecological stoichiometry is an elementary approach to balancing energy and matter flow

Maintaining the balance between matter supply and demand for growth is crucial for the development of an organism. Hence, limitations imposed by the differences between demand and supply may determine the fitness of an organism and influence its ecological interactions [1–4]. The framework of ecological stoichiometry was introduced to elucidate the ecological interactions resulting from the fundamental need for elements and energy. Ecological stoichiometry extends the traditional approach focused on energy flows by introducing the concepts of mass flow and element cycling in ecosystems [1,2,4,9]. In this context, key life-history traits (growth rate, body size, trophic position, etc.) related to body composition are expressed as simple variations in elemental content that represent the major molecules and structures. Organisms are only supplied with accessible food containing given quantities of particular elements [1]. Consequently, all herbivores are faced with a high threshold of stoichiometric mismatches between the chemical composition of their tissues and their food; therefore, they must overcome the fundamental differences in the elemental ratios between their body tissues and their food [1,4,9], cf. [16,17]. Such incompatibility between food and its consumer may result in limited energy budgets, hampered growth rates, decreased reproduction and survivorship. In other words, stoichiometric mismatches influence the consumer's fitness. Therefore, any adaptation that enables herbivores to overcome the stoichiometric mismatches should be favored by natural selection. Accordingly, stoichiometric mismatch is an important factor that shapes plant–herbivore interactions [10,18–22], cf. [23].

The framework of ecological stoichiometry was envisioned in the works of Wiernadski [6,24], Liebig et al. [25], Lotka [26], Tilman [7], and Reiners [8]; postulated explicitly as a fruitful approach by Sterner and Hessen [4], Elser et al. [14,27,28]; and described in detail in the seminal book of Sterner and Elser [1]. The synthesis written by Sterner and Hessen [4], which focuses on nutrient limitations of aquatic herbivores, was recognized as a landmark paper that stimulated ecologists to broaden the understanding of producer–consumer interactions while considering ecological stoichiometry [29]. The essential ideas and living-systems characteristics of ecological stoichiometry are as follows: (*i*) the law of conservation of mass and immutable atoms flowing through the food chain; (*ii*) the capability of living organisms to transform organic substances; (*iii*) stoichiometric stability (“homeostasis”), in which every species

has a unique composition of chemical elements in the body tissues, with heterotrophs showing a lower level of variability than autotrophs; and *(iv)* consumer-driven nutrient recycling (CNR), in which the flow of matter through the food chain is regulated by the elemental body composition of species, thereby composing particular links in the chain (for reviews see: [1,9,28,30–35]). In the context of plant–animal interactions in terrestrial ecosystems, two components are particularly important: *(i)* the threshold of stoichiometric mismatch [9,16,17] that must be surpassed by herbivores (presented above) and *(ii)* stoichiometric idiosyncrasies of plant matter in terrestrial ecosystems, i.e., C richness causing the threshold of stoichiometric mismatch to be particularly high for land herbivores because of high ratios of C to other elements typical of terrestrial plant matter [14,32].

Plant–herbivore interactions in the framework of ecological stoichiometry

The differences between the elemental body compositions of plants and herbivores determine the nutritional limitations imposed on the consumer's growth and development and affect the consumer's fitness [1,4,28]. Consequently, the growth and development of an herbivore are likely limited by the difference between the demand and supply of every chemical element composing its body. P limitation has probably been the most extensively studied within the framework of ecological stoichiometry. P plays an important role in the growth of organisms because it is a major component of rRNA. The “growth-rate hypothesis” (GRH [1,27,28]) postulates a positive correlation between P concentration, growth rate and body size. C:N:P ratios have been considered in studies examining the GRH, and a number of reports have demonstrated that the relationship between C:N:P ratios in organisms and their food controls the life-history traits of consumers (e.g., [36–39]). Therefore, the body size of an organism is considered an important factor in shaping its stoichiometry (detailed reviews in: [1,9,28,30–35]). Another elemental limitation extensively studied in the context of ecological stoichiometry is related to N demand as well as the N:P and C:N ratios of consumers and their food [1,9]. Reports have suggested that terrestrial herbivores experience a higher degree of N limitation than aquatic herbivores [1,14,32,33]. Additionally, the N and P concentrations in consumers' bodies are related to the trophic position, with higher concentrations observed in consumers feeding on animals than consumers feeding on plant matter [33,40–43]. The consumer's stoichiometry has even broader implications considering plant–animal interactions as predicted by the CNR concept. The elemental body composition of a heterotroph (consumer) is homeostatic; thus, the specific stoichiometry of the body must be maintained. Therefore, a given amount of every element is assimilated from the food (plant material) to the consumer's body, and a specific percentage of that element is excreted. This balance affects the growth of the autotrophs that constitute the herbivore's food because the autotrophs rely on the nutrients recycled and excreted by the herbivore. A study of this linkage was conducted by Elser et al. [44], who experimentally demonstrated that a producer's growth is limited by the consumer's nutrient recycling. The study also found that the communities of consumers that differ in their N:P stoichiometry differently influence producer communities by grazing on species of different stoichiometry while also excreting chemical elements in different ratios. This difference subsequently affects the nutritional limitations of producers (for a detailed analysis see [45]). This phenomenon regulates the flow of matter in ecosystems [46–49]. A nutritional limitation may also travel up the food chain [50]. One of the fundamental processes in forest ecosystems is litter decomposition, which is regulated by litter stoichiometry and the stoichiometric demands of litter consumers and decomposers [51–55]. In addition, population dynamics may be regulated stoichiometrically [30,56,57]. Therefore, the stoichiometric limitations imposed on herbivores and the plant–herbivore interactions resulting from these limitations may have consequences for the functioning of the whole food web. Recent reports have indicated that our understanding of elemental limitations in the sense of Liebig's law, where only the most limiting nutrient shapes ecological interactions, is too simplified; rather, multielemental (or multiresources if macronutrients are considered) colimitation likely

occurs and shapes these interactions [3,58–61]. Additionally, a small number of studies have merged the limiting effects of stoichiometry with particular organic compounds because even if a type of organic matter is always composed of a fixed ratio of elements, the elements alone may be invested in various constituents that can influence the consumer's fitness [11,12,62,63].

The analysis of the literature related to ecological stoichiometry (e.g., [1,3,9,11–13,28,30–35,43,55,58,60,64–69]) and the associated citations show that ecological stoichiometry has been extensively employed in studies in aquatic ecosystems, whereas it has rarely been used in terrestrial ecosystems, including in studies of plant–animal interactions. Moreover, although C:N:P ratios have been broadly studied, the importance of all 25 elements that build living matter has been neglected. In the case of terrestrial ecosystems, Na appears to be a particularly important element. Na limits the growth and development of herbivores because of its scarcity in plants; however, it should not be studied separately from other potentially colimiting elements [3,58]. N and Na concentrations in host plants represent factors that shape the life history evolution as well as the fitness of butterflies [68]. A direct relationship between soil P availability, plant stoichiometry, and herbivore population dynamics was described by Schade et al. [13]. Additionally, the influence of plant and herbivore stoichiometry on plant–herbivore interactions in both directions has been demonstrated theoretically [20,21,60] and experimentally [18], and these interactions may help explain the patterns of biological invasions [70]. Lemoine et al. [33] compared the C:N:P resource–consumer stoichiometry within an entirely terrestrial community, and the results suggest that the colimitation of herbivore development is a result of N and P scarcity in plant tissues. Multielemental colimitation has been demonstrated to shape the life histories and feeding strategies of woodboring beetles [71–73], and such a limitation may influence growth, development, and feeding strategies of detritivores [74]. Possible mechanisms that might connect ecological stoichiometry with plant–animal interactions in land ecosystems have been described by Mulder et al. [75], who focused on understanding the biodiversity–ecosystem functional relationship and considered stoichiometry an important trait that shapes within-ecosystem relationships. Abbas et al. [76] suggested that plant elemental compositions, which vary with changes in the composition of plant communities, may have consequences for herbivore abundance. Hence, herbivore communities may be regulated by changes in the stoichiometry of its food source plant communities. Sitters and Venterink [19] highlighted gaps in our understanding of the feedback among herbivores, plants, and soil nutrient cycling and noticed that (i) stoichiometric mismatches play a role in herbivore-induced changes in resource quality and quantity, (ii) stoichiometric mismatches influence plant–herbivore interactions in both directions while also affecting soil nutrient cycling, and (iii) stoichiometry-dependent mechanisms are poorly understood because of scarce data. Host plant quality has been recognized as a key determinant of the fecundity of herbivorous insects [23]. Hence, the fitness of a herbivorous insect is likely strongly related to the nutritional value of its host plant. Plant–insect interactions have been comprehensively described in this context by Awmack and Leather [23]. What should be emphasized, however, is the bidirectional trajectory of this relationship in which plant quality affects the life strategies of herbivorous insects and the insects' actions modify the plant quality. Moreover, this relationship also influences higher trophic levels [23]. Much remains to be learned about the role of multielemental colimitation of herbivorous insect growth and development in shaping plant–insect interactions in terrestrial ecosystems.

Studying the effects of colimitation of a variety of elements on growth and development raises serious technical difficulties because it requires large-scale feeding experiments that utilize a large number of variables (food enriched/depleted in various amounts of an element but similar in concentrations of organic compounds, a large number of elements, etc.). This problem, however, may be eliminated by using a theoretical approach. A simple mathematical comparison of the ratios of certain elements may be sufficient to detect the elements that may colimit the growth and development of an organism feeding on the chosen food [73]. This approach allows for comparisons between various herbivores that feed on various foods and inhabit various environments, and it also considers optional variables that would not be possible without performing long, ongoing, expensive and unfeasible feeding trails.

Trophic stoichiometric ratio (TSR) – the index of stoichiometric mismatches

The fundamental index in ecological stoichiometry is the threshold elemental ratio (TER). This index allows for the calculation of the limiting effect imposed on an organism by stoichiometric mismatches. The threshold elemental ratio is the lowest atomic ratio of C : other element in food at which the consumer's development is not limited by the scarcity of C (i.e., energy) but is limited by the scarcity of the non-C element in the food [1,9,16,17,77]. The basis for calculating the TER represents the consumer's requirement for any non-C element during growth and development. This requirement is represented by utilizing the consumer's consumption rate, assimilation rate, and respiration rates of C and the non-C element. Hence, considered are both (i) energy budget, measured as the C balance, and (ii) the budget of any non-C element.

The TER is understood as follows [1,16,17,77]:

$$TER_x = (GGE_x/GGE_C)(C:X)_{i+1}$$

where GGE_x is the gross growth efficiency of element x , GGE_C is the gross growth efficiency of carbon, i is the trophic level, C is the concentration of carbon, and X is the concentration of element x .

If:

$$(C:X)_i \geq TER_x$$

then element x may become a limiting factor for growth at trophic level $i+1$.

Following Hessen et al. [9], the TER for any C:X ratio, where X is any element other than C, may be calculated as follows:

$$TER_x = \{A_x/[(I_C A_C - R_C)/I_C]\}(C:X)_{i+1}$$

where A_x and A_C are the assimilation rates for elements X and C , respectively, I_C is the C ingestion rate; R_C is the C respiration rate; and $(C:X)_{i+1}$ is the atomic ratio of C:X in the consumer's body.

However, in the case of herbivorous invertebrates, utilizing this index for certain elements is technically impossible. The gross growth efficiencies should be experimentally measured using laboratory feeding trials in growing animals. Such data are extremely scarce, particularly for elements other than N and P. For organisms that feed on extremely nutritionally scarce food and present low growth rates and larval development as long as several years (e.g., wood eaters), obtaining all of the necessary data is practically impossible. In practical terms, the TER index for invertebrates can only be estimated using arbitrary assumptions [17,78,79]. To allow for the identification of multiple elements that colimit the development of an organism and facilitate comparisons between various taxa, habitats, food and life histories, the trophic stoichiometric ratio (TSR) was developed. The TSR is a simplified version of the TER that solely utilizes the data of the elemental composition of the organism and its food, and feeding experiments are not required [73]. The TSR was based on the following:

$$(C:X)_i/(C:X)_{i+1} \geq GGE_x/GGE_C$$

The minimum balanced ratio of GGE_x/GGE_C can be estimated as $1/0.25 = 4$ assuming that 75% of the consumed carbon is released as CO_2 while the other consumed elements are incorporated with 100% efficiency. Hence, it is conservatively assumed that for $(C:X)_i/(C:X)_{i+1} \geq 4.0$, the element x may impose a constraint on growth [73]. Therefore, the TSR is calculated as follows:

$$TSR_x = (C:X)_{\text{food}}/(C:X)_{\text{consumer}}$$

where C is the concentration of carbon and X is the concentration of element x .

A $TSR_x \geq 4$ indicates a possible limitation posed on growth and development of an organism that feeds on the given food, caused by the scarcity of element X in the food. The higher the TSR value, the more severe the limiting effect. The TSR is not meant to represent the actual measured TER of a given element; however, it serves as a relative index indicating a potential stoichiometric mismatch. Various elements may be differentially acquired, assimilated, reused, and excreted. The TSR index compares the elemental composition of an animal's body and the food eaten (not the food assimilated).

The absorbed matter has a different elemental composition than the ingested matter, but to absorb this and to void the non-digestible surplus is the physiological effort which is proportional to the difference between the food eaten and food assimilated and the stoichiometric mismatch represented by TSR index is proportional to that. Because the TSR index assumes that non-carbon elements are assimilated from food at a maximum rate (100%), the actual mismatches in natural situations may only be greater than the estimated TSR values. Therefore, the TSR index serves as a conservative but convenient tool that facilitates the detection of elements that colimit development and comparisons of the severity of the limitations imposed by various foods on different consumers. On that basis, testable hypotheses can be generated to better understand both (i) the biomass and nutrient flow within and between ecosystems and (ii) the nutritional ecology of organisms and the relationship between organisms and their various food sources, including plant–insect interactions (e.g., [71–74]).

Stoichiometric mismatches may affect life-history traits of a pollen eater – an example of the use of ecological stoichiometry in the study of plant–insect interactions

Pollen is commonly regarded as a concentrated, exceptionally rich source of sustenance for herbivores. However, the elemental composition of pollen has mainly been studied in relation to human diet supplementation. Thus, the function of pollen with respect to ecological stoichiometry is poorly understood (e.g., [80–86]). The limited data on pollen elemental composition and the more abundant data on its organic compounds (e.g., [87–91]) indicate that pollen is likely an excellent food, and its composition might be qualitatively comparable to animal tissue. Thus, herbivores foraging on pollen should easily be able to maintain their stoichiometric balance. Three questions arise: (i) what are actual requirements of pollen eaters, concerning various elements? And given this into account, (ii) what are actual amounts of various elements in pollen of different plant species? Finally, (iii) how does the diversity of pollen stoichiometry influence the life history and development of pollen eaters? To resolve these issues, we must determine how the pollen stoichiometric composition fits into the biomass building stoichiometry of pollen eaters. Food nutritional quality is known to regulate populations of wild bees and may be a factor contributing to bee decline [92,93]. In addition, specific micronutrients, especially Na and K, may be lacking in honey bee diets (which is similar to the diets of other bees), thereby forcing bees to search for a balanced diet [94]. The quality of the pollen diet has a known influence on the survival, physiology, and life-history traits of bees (of various taxa). These traits are all connected to fitness; therefore, pollen quality may influence bee foraging choices [95–104].

The TSR index will be used here to briefly discuss the feeding strategy of a pollen eater. As a model pollen eater, the mason bee *Osmia bicornis* Linnaeus 1758 (= *Osmia rufa* Linnaeus 1758; Hymenoptera, Megachilidae) will be used. *Osmia bicornis* larvae feed directly on unprocessed pollen provided by their mother to the nest [105,106]. Direct comparisons of the elemental composition of pollen with the composition of adult bodies and empty cocoons can identify stoichiometric mismatches and thus nutritional constraints, thereby providing the first hint for potential solutions that can be applied to overcome such limitations. Concentrations of nine elements (C, N, P, Ca, Mg, K, Na, Zn, and Cu) were measured in adult bee bodies, cocoons, and pollen eaten during bee development, and the elemental compositions of the bee bodies, cocoons, and pollen were compared. The TSRs were calculated separately for the bee bodies and cocoons to detect the elements that are scarce in pollen and therefore limiting to the development of the bee body and cocoon. Samples were not divided by sex. Detailed information on the materials and methods used as well as the study site are presented in Appendix S1.

The concept of “stoichiometric homeostasis” [1,9,34] predicts low changeability in the elemental composition of mature animals, particularly for the elements that are the most important physiologically and build molecules that are meaningful for fitness. Indeed, the elemental composition of bee bodies showed a low level of variability

Tab. 1 Elemental composition of *O. bicornis* bodies, cocoons, and pollen eaten during larval development.

		C	N	P	Ca	Mg	K	Na	Zn	Cu
		% d.m.						ppm d.m.		
Bee bodies (<i>N</i> = 13)										
Variability	Mean	48.56	13.15	0.52	0.02	0.08	1.70	211.65	70.28	12.83
	Min	47.15	11.98	0.33	0.01	0.07	1.21	138.17	64.21	9.01
	Max	50.12	15.34	0.66	0.04	0.11	2.48	283.51	78.24	19.53
	max/min	1.1	1.3	2.0	4.0	1.6	2.0	2.1	1.2	2.2
	SD	0.72	0.82	0.09	0.01	0.01	0.35	46.40	4.14	3.28
	CV	0.01	0.06	0.18	0.39	0.13	0.20	0.22	0.06	0.26
	Bee cocoons (<i>N</i> = 5)									
Variability	Mean	39.18	10.68	3.09	0.23	0.91	2.00	359.95	388.89	8.32
	Min	34.99	9.35	1.87	0.14	0.12	1.27	115.88	258.93	5.72
	Max	43.35	11.39	4.62	0.33	1.73	2.57	686.31	566.48	11.30
	max/min	1.2	1.2	2.5	2.4	14.4	2.0	5.9	2.2	2.0
	SD	3.15	0.87	1.08	0.08	0.75	0.48	215.97	111.65	2.32
	CV	0.08	0.08	0.35	0.35	0.82	0.24	0.60	0.29	0.28
	Bee-collected pollen (<i>N</i> = 8)									
Variability	Mean	47.08	4.13	0.46	0.09	0.10	0.66	78.01	63.03	14.00
	Min	44.79	3.79	0.22	0.07	0.08	0.46	56.48	33.93	10.89
	Max	50.18	5.07	0.71	0.13	0.13	0.82	119.56	92.46	18.23
	max/min	1.1	1.3	3.2	1.9	1.6	1.8	2.1	2.7	1.7
	SD	1.77	0.44	0.18	0.02	0.02	0.14	22.00	16.99	2.67
	CV	0.04	0.11	0.39	0.26	0.20	0.22	0.28	0.27	0.19

except for Ca and Cu (Tab. 1). The elemental composition of cocoons was highly variable except for N and Cu (Tab. 1).

The stoichiometric mismatches (i.e., constraints to growth), which were represented by the calculated TSR values, differed depending on the element and matter produced (either the bee body or cocoon). Na, K, and N were detected as potentially limiting for bee body production because the TSR values for these elements may exceed 4 (the effect is relatively strong for Na and K and relatively weak for N; Fig. 1; see Appendix S2 for details). The calculations are consistent with a recent study on salt foraging by another hymenopteran pollen eater, the honey bee. That study found that when a honey bee was given a choice of drinking pure water or water enriched with Na, K, Ca, Mg, N, and P, the honey bee preferred the Na- and K-enriched water, suggesting that honey bees forage for minerals that may be lacking in their floral diet (Na and K [94]). Cocoon production might be colimited by a scarcity of P, Zn, Mg, Na, K, Ca, and N (Fig. 1). However, some of these elements might have been deposited in the cocoon in high amounts because of a surplus in the food. A high variability of TSR values for cocoons is observed in all possibly limiting elements except for N. Because N scarcity in pollen may be limiting for the development of the bee body and bee cocoon (Fig. 1) and N concentrations in the bee cocoon present small variations relative to that of other elements (Tab. 1), N is hypothesized to represent an important element for cocoon production, showing conservative amount. In addition, N is an important component of proteins. Therefore, a trade-off may occur between the

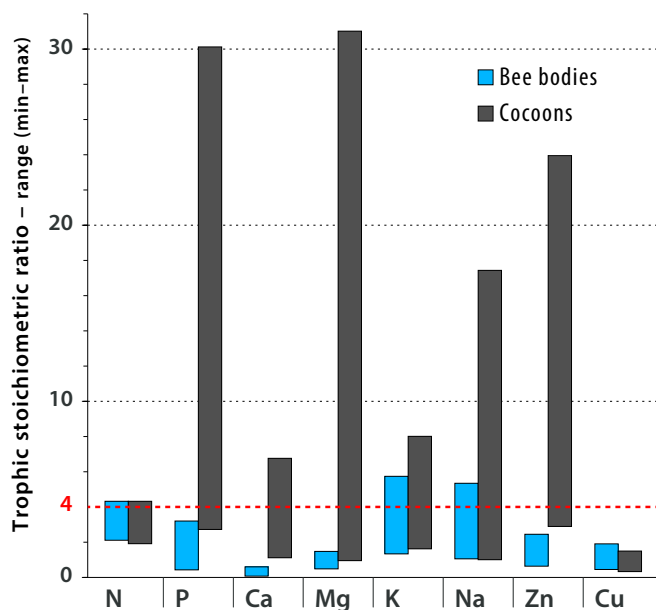


Fig. 1 Stoichiometric mismatches (TSRs) calculated separately for adult bees and their cocoons. The red line indicates the threshold value of TSR = 4, i.e., the threshold of the stoichiometric mismatch. The bars denote possible variations in the mismatches and shows the range of minimal–maximal calculated TSR values. See Appendix S2 for details. K and Na may be the most limiting elements for bee bodies, and P, Mg, Zn, and Na may be the most limiting for cocoon production.

deposition of N from the pollen to the bee body and cocoon. Hence, N-rich pollen might be favored by the bees. High variability of the TSR values for P, Mg, Na, and Zn suggest that (i) conflicts occur between the body and the cocoon in the deposition of these elements, which indicates that these elements might be invested primarily in body building and secondarily in cocoon development, with both investments improving fitness; or (ii) surplus amounts of these elements are deposited in the cocoon for storage and not for improving fitness. Of these elements, the scarcity of K and Na in pollen may be limiting for the development of bee bodies (Fig. 1), suggesting that a trade-off between K and Na occurs between their allocation into the bee body or the cocoon. Therefore, when collecting pollen for larvae, females may favor species rich in K and Na. In cocoons, P, Ca, Mg, and Zn show high concentrations that are highly variable (Tab. 1), which suggests that these three elements are incorporated into cocoons when available in pollen in adequate concentrations. Whether the deposition of any of these elements in the cocoon influences the role of the cocoon in bee fitness is not known. The calcification of other insects cocoons has been suggested to represent an adaptive modification that allows for the building of a strong cocoon while using a smaller amount of amino acids [107]. Because amino acids are N-rich, the origin of such mechanisms might be caused by a trade-off between the deposition

of N in the bee body and deposition in the cocoon. It is important to acknowledge a colimiting effect posed on growth and development by the scarcity of several elements in food, and not just the most limiting element [3,15,58]. Supplementing the diet of developing *Bombyx mori* larva with a set of elements (N, K, Ca, and Cu [108] and N, P, K, and Ca [109]) has been shown to result in better larva development and the production of heavier cocoons than was observed in specimens fed a diet that was not supplemented with elements or only partially supplemented (using only chosen elements in various combinations). Similarly, the growth and development of *O. bicornis* may be colimited by a scarcity in the pollen of elements that have been indicated as possibly limiting in this study (N, K, and Na – limiting for the bee body and cocoon; P, Ca, Mg, and Zn may be limiting for cocoon but their function is not known, and these elements might be stored in cocoons without improving the bee fitness).

The availability of certain elements in the food of *O. bicornis* may result in limitations on the growth and development of its body and the production of the cocoon. Therefore, the amount of possibly limiting elements should be maximized during pollen collection by the adult bee female for its progeny. The possibility of gathering the necessary amounts of elements depends on the availability of the elements in the pollen offered by particular plant species that can be reached by foraging bees. Thus, the taxonomical variability of pollen stoichiometry and the need to collect stoichiometrically balanced pollen should influence plant–bee interactions. The taxonomical variability of pollen elemental compositions can be studied by investigating the literature. Therefore, 26 studies that detailed the pollen of various plant species collected worldwide were used to investigate variations in the composition of 11 elements in pollen (Tab. 2; see Appendix S3 for details). The concentration of Na showed the highest variability among the elements. The scarcity of Na in pollen may limit the development of *O. bicornis* (Fig. 1); thus, species of pollen that are rich in this element should be favored by the bee. The variability in the concentration of another potentially limiting element, K, was also high (Tab. 2, Appendix S3). Therefore, favored plant species may also be selected by *O. bicornis* based on the K concentration in the pollen.

The feeding strategy of a pollen eater is inconsistent with that of other herbivorous insects because of the exceptional nutritional richness of pollen. Nevertheless, pollen

Tab. 2 Variability in the concentration (ppm d.m.) of various elements in pollen based on literature data, with various taxa and various populations of the same pollen taxon considered.

	N (N = 77)	P (N = 191)	S (N = 132)	K (N = 233)	Na (N = 197)	Mg (N = 239)	Ca (N = 241)	Fe (N = 254)	Zn (N = 200)	Cu (N = 180)	Mn (N = 154)
Mean	21285.41	3637.37	2830.94	7479.40	786.98	1454.22	2120.36	343.59	71.24	13.13	48.24
Min	3600.00	234.40	962.03	1300.00	4.95	121.53	200.39	6.00	16.00	1.74	5.00
Max	97000.00	11600.00	6092.83	75459.72	16782.53	5833.32	17634.32	9559.00	795.00	59.00	685.10
max/min	26.9	49.5	6.3	58.0	3390.4	48.00	88.00	1593.2	49.7	33.9	137.0
SD	20821.41	2623.83	929.77	6338.25	2021.55	912.23	1911.14	914.46	77.60	10.28	71.78
CV	0.98	0.72	0.33	0.85	2.57	0.63	0.90	2.66	1.09	0.78	1.49

For each study, the mean measured concentration of an element for a single taxon was considered (species, family, or polyfloral pollen) per genotype and collection site. Hand-collected pollen and honey bee-collected pollen pellets were evaluated. The results were reported in 26 studies from worldwide locations. See Appendix S3 for details. N – number of mean values used for the calculations. The three minerals, Na, Fe, and Mn, showed the highest variability in concentration (shaded cells). All of the element concentrations except for S are highly variable and show approximately 30–3000-fold differences between the minimal and maximal concentrations reported for a single element.

is not well balanced stoichiometrically, and its elemental composition is highly variable among taxa thus also among seasons and habitats. This variation might affect the feeding strategy, reproduction patterns, and mortality risk of pollen eaters. Optimizing the composition of collected pollen species (maximizing the amounts of the most limiting elements and minimizing the costs of food collection) may represent a strategy employed by bees to overcome stoichiometric mismatches. Bees favor certain species of pollen, and the floral preference might be related to the nutritional quality of the pollen [98–101,110–121]. These preferences do not appear to be related to the total protein content of the pollen [101,115,117,118]. Schmidt [117] demonstrated that honey bees significantly prefer multifloral pollen to single-species pollen. It has been shown for *O. bicornis* that potentially detrimental corollaries of foraging on suboptimal resources may be mitigated by mixing low- and high-quality matter [122]. Because the pollen of various plant species tends to vary widely in its stoichiometry, mixing certain proportions of different species should stoichiometrically balance the bee diet. Therefore, ecological stoichiometry may shape the interactions of pollen eaters with their host plants. The framework of ecological stoichiometry allows for the generation of testable hypotheses concerning plant – herbivorous insect interactions and may be used in the future to study the interactions related to nutritional colimitations on herbivore growth, development, and fitness.

Concluding remarks

The energy budget of organisms constitute the basis for generalizations in ecosystem ecology and evolutionary theory, including hypotheses on plant–herbivore interactions. The problem of maintaining stoichiometric balance appears to be equally important. The framework of ecological stoichiometry acknowledges that an organism’s performance is partly determined by the consistency between the stoichiometry of the resources and the stoichiometry of the organism. Mismatches between the chemical composition of a consumer’s tissues and that of its resources negatively affect the life-history traits (growth rates, body size, reproduction strategies, survival, etc.). The proportions of elements in food and tissues may represent a currency of choice in life-history optimization studies.

Mulder et al. [75] highlighted the need for generalizations without oversimplification to identify traits that underlie species responses and ecological processes, including consumer–resource interactions. Sterner and Hessen [4] argued that understanding herbivores as adaptive systems that maximize the yield relative to the food consumed represents such a generalization, thereby enabling researchers to predict ecological interactions. The development of ecological stoichiometry over the last 15 years has shown the reliability and dependability of this framework in explaining underlying ecological processes and interactions (for reviews see [1,9,28,30–35]. Leal et al. [123] recently advocated for the integration of ecological stoichiometry studies with other frameworks. The example of the TSR index as an indicator

of elemental mismatches between plant-eating insects and their food showed that the use of ecological stoichiometry might provide new and valuable data on plant–insect interactions. Thus, the dependence of life-history traits on food stoichiometry should be considered when discussing the expression and evolution of these traits and their effects on plant – herbivorous insect interactions. The TSR may serve as a convenient tool that facilitates identifying and comparing the fitness-limiting effects imposed on herbivores by the elemental composition of their hosts.

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Supplementary material

The following supplementary material for this article is available at <http://pbsociety.org.pl/journals/index.php/aa/rt/suppFiles/aa.1710/0>:

Appendix S1 Materials and methods used.

Appendix S2 Minimal and maximal values of the calculated TSRs.

Appendix S3 Concentrations of elements in pollen, as reported in the literature.

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Interakcje roślin z owadami mogą być kształtowane przez stechiometrię ekologiczną

Streszczenie

Głównym czynnikiem, którego wpływ na organizmy uwzględnia się w ekologii ekosystemów i ekologii ewolucyjnej jest bilans energetyczny. Wskutek tego badacze skupiają się na energetycznych korzyściach i kosztach adaptacji, wydajności przyswajania i inwestycji energii oraz ograniczeniach budżetu energetycznego. Jednak równie ważny jest problem bilansu stechiometrycznego i rozbieżności pomiędzy składem budulca tworzącego tkanki konsumenta oraz jego pokarmu. Ta rozbieżność kształtuje cechy historii życiowych organizmów (np. tempo wzrostu, wielkość ciała czy strategię reprodukcji) oraz wpływa na interakcje roślin z roślinożercami. W związku z tym stechiometria (proporcje pierwiastków) tkanek konsumenta i jego pokarmu może służyć jako narzędzie badawcze podczas studiowania mechanizmów kształtujących interakcje roślin z owadami roślinożernymi. W części przeglądowej niniejszej pracy przedstawione są ramy programu badawczego stechiometrii ekologicznej, w kontekście oddziaływań roślina–owad w ekosystemach lądowych. Zaproponowany jest wskaźnik *trophic stoichiometric ratio* (TSR) – narzędzie użyteczne do wykrywania pierwiastków stężonych w pożywieniu w zbyt małych ilościach względem potrzeb konsumenta, potencjalnie limitujących wzrost i rozwój roślinożercy, tym samym kształtując zależności między roślinami, a roślinożercami. Rozwijając idee przedstawione w części przeglądowej, zaprezentowano, na przykładzie murarki ogrodowej (*Osmia bicornis* – pszczoła samotna, pyłkożerca), jak zastosowanie programu stechiometrii ekologicznej do badania interakcji roślina–owad, może owocować interesującymi hipotezami i ważkimi wyjaśnieniami. Wzrost i rozwój murarki może być kolimitowany przez niedobór K, Na oraz N w pożywieniu (pyłku roślinnym), natomiast produkcja kokonu może być kolimitowana przez niedobór P, Mg, K, Na, Zn, Ca oraz N. Skład pierwiastkowy pyłku odznacza się wysoką zmiennością taksonomiczną. Konieczność stechiometrycznego zbilansowania diety może kształtować strategie zdobywania pokarmu i reprodukcji oraz wpływać na śmiertelność i dostosowanie pyłkożercy, kształtując interakcje owada z roślinami. Zależność cech historii życiowych od stechiometrii pożywienia powinna być brana pod uwagę podczas badania ewolucji historii życiowych oraz interakcji roślin z owadami. Wskaźnik TSR może służyć jako poręczne, a zarazem skuteczne narzędzie podczas takich badań.