

Review

Interaction between Nitrogen, Phosphorus, and Invasive Alien Plants

Youli Zhang^{1,2}, Zhanrui Leng³, Yueming Wu³, Hui Jia³, Chongling Yan⁴, Xinhong Wang⁴, Guangqian Ren³, Guirong Wu⁵ and Jian Li^{3,4,*}

- ¹ Agronomy College, Heilongjiang Bayi Agricultural University, Daqing 163319, China; zyl8181@byau.edu.cn
- ² National Coarse Cereals Engineering Research Center, Heilongjiang Bayi Agricultural University, Daqing 163319, China
- ³ Institute of Environment and Ecology, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China; bba@stmail.ujs.edu.cn (Z.L.); wym@stmail.ujs.edu.cn (Y.W.); 1000005403@ujs.edu.cn (H.J.); rgq@ujs.edu.cn (G.R.)
- ⁴ State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen 361102, China; ycl@xmu.edu.cn (C.Y.); xhwang@xmu.edu.cn (X.W.)
- ⁵ College of Food and Biological Engineering, Hezhou University, Hezhou 542899, China; 199300016@hzxy.edu.cn
- * Correspondence: 1000004601@ujs.edu.cn

Abstract: Plant invasion is significantly affected by environmental factors in the recipient habitats and affects the stability and sustainable development of society. The invasiveness of alien plants may be increased by anthropogenic-mediated disturbances, such as fluctuations in nutrients caused by excessive emissions of nitrogen (N) and phosphorus (P). To improve our understanding of the interactions between N and P fluctuations and invasive alien plants, the current report focuses on the biogeochemical behavior of N and P among invasive alien plants, native plants, and the soil within the plant–soil ecosystem. Our research, together with a synthesis of the literature, shows that fluctuations in N and P resources provide more opportunities and competitiveness for plant invasion. At the same time, the biogeochemical cycles of N and P are promoted because of their efficient and increased utilization and rate of release by invasive alien plants. However, there is no consensus on whether the N and P compositions of invasive species are different from those of the natives in their habitat. Quantitative studies that compare N and P contents in plant, litter, and soil between native plant communities and invaded communities on a global scale are an indispensable area of research focus for the future.

Keywords: plant invasion; eutrophication; biogeochemical cycle; nitrogen; phosphorus



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1. Introduction

Nitrogen (N) and phosphorus (P) are the most important nutrients for plant growth [1]. In plants, N mainly contributes to the biosynthesis of amino acids, proteins, and other macromolecular bioactive substances and is widely involved in various life activities [2]. Similarly, P plays a critical role in the construction of the nucleic acid structure and energy transformation in plants [3]. Maintaining the stability of the biogeochemical cycle of N and P is therefore of great significance to entire ecosystems. However, anthropogenic-mediated disturbances of N and P can have a major influence on the structure and functioning of ecosystems; for example, excessive emissions of N and P change the element compositions and stoichiometries in regional ecosystems and the relationships between species composition and ecological processes [4–6]. At the same time, invasive alien species (IAS) also pose a serious threaten to ecosystems, which may cause disturbances in biogenic element cycles, reduced biodiversity, ecosystem degradation, and even destruction of the original ecosystem [7]. As the second greatest threat to biodiversity after habitat fragmentation,

invasive alien plants are not dominant competitors in their natural systems but competitively exclude their new neighbors. For example, *Centaurea diffusa*, a Eurasian plant, has no impact on ^{32}P uptake by other Eurasian species. However, it significantly decreases the ^{32}P absorption of all North American grass species, due to its root activity and chemically mediated effects. On the other hand, no inhibitive effect was found on ^{32}P uptake of *C. diffusa* by North American grasses, while all Eurasian species showed a great negative influence on ^{32}P uptake by *C. diffusa* [8].

The composition of plant communities can be altered by the elemental compositions of their habitats [9]. Eutrophication is broadly considered a serious threat to biodiversity conservation and ecosystem functions. It is closely related to plant invasion and expansion. Thus, plant invasion may be triggered by the nutritional conditions in the recipient environment. Some researchers used molecular techniques to survey the phytogeography of two *Phragmites* spp., *Phragmites australis* and *Phragmites mauritianus*, and found that three haplotypes in these species are native, and both species have high genetic diversity. Meanwhile, there was no evidence of recent non-native haplotype invasion in the native region. Therefore, they suggested that the expansion of these two *Phragmites* species was most likely led by anthropogenic disturbance in the environment [10].

The competitive performance of invasive alien plants is often habitat dependent [11]. That is to say, resource availability in the habitat is a critical factor determining community susceptibility to alien plant invasion. It also determines the ability of alien plants to invade a particular habitat [12]. Among various factors, the coupling effect of N and P dictates the success of alien species invasion [13]. High N and P contents may promote invasion rather than being a consequence of invasion [14]. There is a positive and synergetic effect of N and P on the invasiveness of opportunistic alien species (Figure 1) [4].



Figure 1. Spread of *Alternanthera philoxeroides* Griseb in eutrophic wetland. Photos were taken in a eutrophic pool invaded by *A. philoxeroides* Griseb next to Huilong reservoir, Zhenjiang City, Jiangsu Province, China (119°45' E; 32°15' N) in 2018. These pictures show spread of *A. philoxeroides* Griseb over 3 months (9 July to 9 October 2018).

Therefore, instead of plant invasions influencing N and P enrichment (Table 1), N and P enrichment may exacerbate plant invasion. We suggest that linking abiotic factors, such as N and P concentration, is critical to identify how and why alien species successfully

expand and invade. This study synthesizes the available knowledge and information on the interaction processes and mechanisms between invasive alien plants and N and P in order to provide a better understanding of ecosystem functioning. In particular, this review establishes interaction mechanisms between invasive alien plants and nutrients (mainly N and P) in the context of ecosystem functioning.

Table 1. Interactions between invasive alien plants and N and P.

Interactions between Invasive Alien Plants and N and P			References
Effects of plant invasion on the N and P pool	N and P pool in invasive alien plants	Higher aboveground N and P accumulation than in native plants	[6,15–19]
		Larger N investment in photosynthetic production	[20–23]
		Decreased N allocation to defend structures	[20]
	N and P pool in invaded soil	Increased NH_4^+ content in soil	[24,25]
		Increased total N and P content in soil	[6,26,27]
		Promotion of N and P mineralization and acceleration of N and P cycles	[28–32]
Mechanisms of plant invasion promoted by N and P	High N and P tolerance hypothesis		[33]
	Growth rate hypothesis		[12,13,34–36]
	Biomass allocation hypothesis		[37,38]
	Enemy release hypothesis		[39–41]

2. Interaction Mechanism between N and P and Invasive Alien Plants

2.1. Influence of Invasive Alien Plants on N and P Pool in Soil and Plants

The success of invasion is mainly the result of the soil status or growing environment of invasive alien plants. Reports have suggested that differences in element compositions and stoichiometries in soils are mainly caused by the success of invasive species in invaded regions [42–47]. For example, Hu et al. (2019) reported similar results, showing that NH_4^+ concentration in soil invaded by *Chromolaena odorata* was 1.43 times that of native soil [24], and the NH_4^+ concentration of soil invaded by *Ageratina adenophora* was 1.56–2.10 times that of native soil [25]. Moreover, soil function may also show some alterations at an early stage of invasion [48]. The differences in soil properties and functioning may point toward the contributions of root exudates [49–51] and high productivity litter [26] and their associated spatial variability. For example, compared with the outside areas of the crown canopy of invasive alien plants, the physical and chemical properties of soil under the crown canopy of invasive species were found to be significantly different, although it was only a few meters away [6,52]. Similarly, various other conditions can be advantageous to invasive alien plants over native plants in the acquisition of resources. These include but are not limited to a higher photosynthetic rate, speedier growth rate, larger reproductive output, larger biomass, lower carbon-to-nutrient ratio in tissues, lower foliar construction cost, larger N investment in photosynthetic production, stronger capacity for nutrient absorption, and higher plasticity levels in the invasive alien plants [6]. All of these can cause alien plants to have greater advantages over native plants in resource acquisition because they can take advantage of nutrient pulses to acquire more resources and make better use of nutrients than native plants.

Compared with native species, the above factors may accelerate the global accumulation of nutrient elements (such as N and P) in the aboveground parts of invasive alien plants [6,15–19]. As reviewed elsewhere, the adaptation of invasive alien species to new environments can occur within a few generations, and there is also evidence suggesting that invasive alien plants can undergo rapid adaptive evolution [53,54]. For example, a study by Sun et al. (2021) found that invasive alien plants responded to soil nitrogen forms (nitrate

and ammonium), adapting or changing them and eventually feeding them back to the soil, microbes, and other components [39]. Moreover, in response to enemy release (the idea that invasive species are less impacted by enemies, such as herbivores, than native species because in a new geographic location, invasive species are freed from the parasites that kept their growth in check in their native environment), invasive species decrease N allocation to defense structures, such as cell walls, and enhance N allocation in photosynthetic tissues, leading to higher photosynthetic nitrogen-use efficiency (PNUE) [20]. Thus, invaders have a higher light-saturated photosynthetic rate (P_{max}) at a certain N concentration (N_m) in the invaded regions than in their native habitats [21]. For invasive species, increased P_{max} resulting from higher PNUE would also enhance the photosynthetic phosphorus-use efficiency (PPUE). High resource-use efficiency would be critical for the success of invasive species [22,23].

Resource-use efficiency is often dictated by underlying processes. For example, Sardans et al. (2017) conducted a meta-analysis and found a negative correlation of the Napierian logarithm response ratio between total N and Olsen P in invaded soils and the corresponding values in native plant soils. Concentrations of Olsen P and total N were 21%, and 19% higher, respectively, in the invaded soils than in their native competitor soils [6]. These results indicate that in the soil, biological processes mediated by invasive alien plants, rather than the geochemical processes are the critical factors that cause differences in soil characteristics. Similar research showed that N and P contents in the growth substrate will generally be increased by invasive species, and according to a meta-analysis, soil process rates, such as accelerated litter decomposition and mineralization, will also be enhanced [28–30].

The abovementioned research conclusions reflect more prominent performance-related trait values in non-native plants over native species, including growth rate, leaf-area allocation and shoot allocation, which are crucial driving factors in regulating the biogeochemical cycles of N and P [30–32]. The invasive species exhibiting these traits show that they have more strategic advantages for nutrient use over native plants [16,32,55], and these strategic advantages lead to the greatest enhancement in the N and P mineralization rates of soil [9]. Thus, invading plants transform pools and fluxes of N and P in the soil by accelerating N and P cycles in the ecosystem (Figure 2) [28–30]. This shows that the influence is multidirectional, and the impacts are heterogeneous, variable, and not unidirectional, even under particular environmental conditions [29]. Numerous studies have shown that global agriculture has changed dramatically in the last four decades [56,57]. More primitive lands (such as forests and grasslands) have been converted into agricultural land, and intensive agriculture is widely promoted. With the application of chemical fertilizers, higher amounts of N and P are artificially introduced into the soil and pollute the soil and water [58,59]. N and P pollution has a positive effect on the invasion of opportunistic alien plants, and a synergy exists. Thus, we can conclude that in addition to plant invasion influencing N and P enrichment, N and P enrichment influences plant invasion and determines how the ecosystem will function (Table 1) [4].

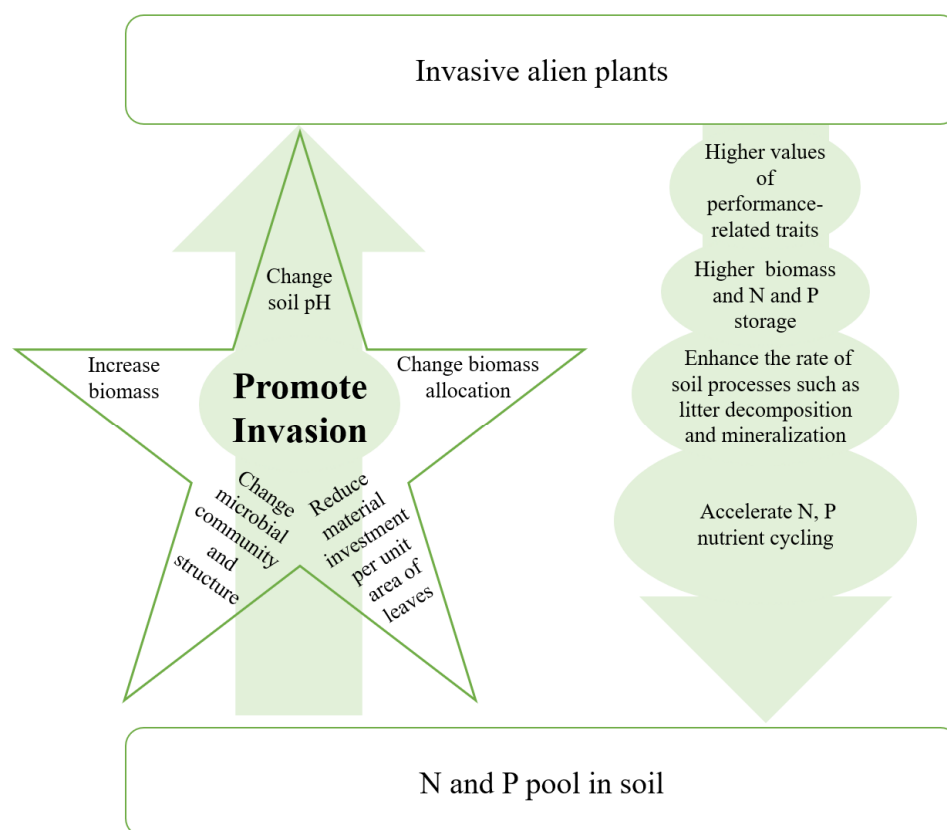


Figure 2. Interaction processes between invasive alien plants and N and P. Eco-mechanisms through which N and P promote plant invasion (left) and how plant invasion intensifies N and P enrichment (right) are shown.

2.2. The Influence of Nutrient Fluctuation Caused by N and P on the Invasiveness of Alien Plants

2.2.1. N and P Mediated Ecological Strategy and Interactions between Native and Invasive Alien Plants

There are differences in plant traits, ecological strategies, and responses to environmental nutrient conditions between invasive and native plants. For example, Dalle Fratte et al. (2019) conducted a study on plant traits in Northern Italy and showed that, due to increased soil N and P loadings in Southern Europe, plant communities are gradually shifting from “slow and conservative” to “fast and acquisitive” species, which may cause invasion by subtropical invasive alien plants and put a strain on biodiversity at the local scale [60]. Previous studies also indicate that invasive alien plants may have different N nutrition strategies compared with native plants. Invasive alien plants such as *Bidens pilosa*, *Microstegium vimineum*, and *Mikania micrantha* prefer to consume nitrate over ammonium [39,42,61]. This “preference” may contribute to its competition with native plants in some nitrate-rich habitats. By contrast, some invasive alien plants are reported to prefer ammonium. The African grass *Andropogon gayanus* was found to directly alter the understory structure of oligotrophic savannas in tropical Australia, which was attributed to the grass accelerating the ammoniation process and increasing soil ammonium availability to four times that of native plant soil, with a more than six times higher uptake rate of ammonium than native plants [62].

The availability of N and P and the N/P ratio profoundly impact interspecific competition in invaded habitats (Figures 1 and 2). High rates of nutrient deposition [51] facilitate non-native species dominance [34,63]. Therefore, nutrient deposition promotes the invasiveness of alien plants in the ecosystem [21]. Based on a quantification of relationships between successful plant invasion and soil conditions by a meta-analysis, Vilà et al. (2011)

found that the success of invasion was strongly related to higher soil N and P stocks [29]. Thus, compared to native plants, increased nutrient availability promotes the competitiveness of invasive species and further accelerates the success of invasion [64–67]. For example, in a study of eutrophic wetlands by Holdredge et al. the invasive alien *P. australis* showed great advantages in competing with native *P. americanus* [65]. Moreover, the N/P ratio also affects plant competitiveness. For example, in a low N/P ratio environment, native *Alopecurus* spp. showed great advantages due to high root biomass and length, whereas with a high N/P ratio, invasive *Agrostis* spp., with high root phosphatase activity, gained the advantage and suppressed *Alopecurus* [68]. Therefore, it is significant to clarify the growth patterns and competition dominance of invasive alien plants under various N and P concentrations in addition to considering their ratios [11].

2.2.2. Mechanisms of N and P Promote Alien Plant Invasion

The occurrence of invasion and the growth environment also determine the allocation of resources for the functioning and existence of plants. (1) In a highly N and P polluted environment (e.g., eutrophication), invasive alien plants were found to be more tolerant than most species [33], as they increase N allocation to photosynthetic activity and promote photosynthetic tissue growth. (2) As a response to the growth rate hypothesis, plants demand more rRNA and ribosomes for increased protein synthesis. This requires more phosphorus [13,35] to contribute to higher net primary productivity (NPP) [36], and plants exhibit an increase in overall biomass [12,34]. As shown by Broadbent et al. (2018), under high N conditions, the invasiveness of *Agrostis capillaris* was significantly increased, and a largely negative impact on native species growth was observed: the biomass of native plants was decreased by half, and total N content in tissues was decreased by up to 75% [27]. Hence, as the fluctuating resource hypothesis describes, those plant communities, which are more sensitive to N and P fluctuations, are more vulnerable to plant invasion [37,38,69]. (3) Additionally, as a response to environmental changes, invasion plant biomass allocation also dictates the changes in N and P levels [40], and this is known as plastic response to difference in resource availability. There are two different views on the nutrient allocation mechanism of invasive alien plants. In the “ratio” view, the plant allocates a proportion of total biomass to different structures at any point in time. In the “allometric” view, quantitative biomass allocation of a genotype is a fundamental aspect of the genotype’s “strategy” and the result of natural selection [41]. (4) Moreover, in environment with high resources, enemy release facilitates invasive alien plants over native plants [70,71]. These four aspects (high N and P tolerance hypothesis, growth rate hypothesis, biomass allocation hypothesis, and enemy release hypothesis) promote the growth and competitiveness of invasive alien plants and, therefore, dictate the success of invasion (Table 1) [39].

Although N is regarded as a nutrient that restricts primary productivity for some terrestrial ecosystems, increasing anthropogenic nutrient inputs [72] has already amplified the global N cycle approximately two-fold [73], and this speed could be increased further in the decades ahead [74]. Most studies in grassland [75] and terrestrial forest ecosystems [76] have reported that increasing atmospheric N deposition and eutrophication have caused the degradation of local communities, leading to accelerated plant invasion [38]. Where invasive alien plants successfully competed against native species that previously tolerated low N levels in the plant community, increased N deposition induced by human activities may serve as a critical power in driving plant invasion [77]. In addition, extensive research by our group on quantifying the relationship between plant invasion and N deposition and P stress in terrestrial ecosystems has shown that plant invasion and N deposition change the soil N-fixative bacteria (SNB) community structure by enhancing the ecological characteristics of soil microbial communities (such as *nifH* gene abundance), altering pH and other soil physicochemical properties and especially increasing the total number of SNB species. Bioavailability of N was increased in soil as a result of the combined effects of SNB and the acidification of deposited N and, thus, invasion by alien plants was accelerated [78,79]. Similarly, woody invasive alien plants may have higher resource

capture ability as well as higher relative growth rates from reduced material investment in leaves per unit area under N deposition [80]. In the competitive process between tested native and non-native species under N deposition, we found that there were negatively synergistic effects of N deposition and plant invasion on seed germination and growth of the tested native plants [81].

2.2.3. Strategies to Control Alien Plant Invasion

With ongoing deposition, N would cease to be a limiting nutrient for primary productivity; however, increased N bioavailability might result in a higher P requirement [77,82–84]. The accelerated growth of the tested invasive alien plants was found to be closely related to increased leaf P [77,85]. At the same time, this invasive species could selectively utilize insoluble P (Al-P) by enhancing root biomass in an environment with enriched N. A high N concentration in the soil might mean that the N demands are met for both invasive alien plants and native plants after P addition. However, with an even higher N and P demand than that of invasive species (such as *Solidago canadensis*), native species growth was promoted under N and P enrichment. More nutrients were allocated aboveground, and the growth of invasive alien plants was inhibited through shading. This is an argument in favor of the resource ratio hypothesis [86,87], which holds that plant distributions are determined by the availability of the resource that is most limiting, and resource demands vary among species, which in turn determines the competition effects. Altering the N and P ratio might be an alternative strategy to decrease invasive species competitiveness [85,86].

Successful alien plant invasion is principally due to their higher competitive dominance over native species [88]. Different nutrient components drive different invasive species, including the interspecies difference of invasive alien plants. In the coming decades, plant invasion could be more severe because of increased nutrient input from increasingly severe overfertilization and eutrophication. Hence, although an apparent conflict exists between preventing the dominance of invasive alien plants by decreasing nutrient inputs and increasing agricultural outputs by maintaining nutrients, this contributes to our understanding of how invasion mechanisms transform invaders' competitive dominance in soil with various nutrient compositions [89]. Moreover, greater understanding of the factors regulating the success of nutrient loading and restoration management might be an effective way to enhance the competitiveness and invasion resistance of native plants. For example, proper nutrition management, such as decreased N [11,51] and P [11,90,91] input, may contribute to the competitiveness of native species and resistance to invasive alien plants. Moreover, the content and form of N and P in the fertilizer can be purposefully adjusted according to the needs of the species to improve the resistance of native plants to invasive alien plants during artificial fertilization. The addition of carbon can stimulate microbial activity and lead to reduced N levels through microbial immobilization, and this is another way in which resources can be manipulated [86]. However, more field experiments are needed to explore and verify this hypothesis.

3. Conclusions and Prospects

Excessive emissions of N and P induced by human activity can reduce the resistance of native plants to invasive species. Once we understand their relationship more thoroughly, nutrient element management could serve as “chemotherapy” for invaded habitats contaminated with N and P, for instance, by artificially enhancing nutrient stresses (such as N and P) in ways that have negative influence on invasive instead of native species in a community. In most reports, there is mutual promotion between plant invasion and increased N and P. In other words, resource fluctuations resulting from N and P emissions provide more opportunities and competitiveness for the invasion of alien plants. At the same time, the biogeochemical cycles of N and P are promoted because of their efficient and higher utilization and release rates by invasive alien plants. However, there is no consensus on whether the elemental compositions of invasive species are different from those of natives. Quantitative research comparing the N and P contents of plant, litter, and

soil element contents between native plants and invaders in a global context is lacking. Thus, we should further investigate the role of N and P biogeochemical behavior in native and invasive species and the soil in plant–soil ecosystems.

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