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Interactions between plants and herbivores: A review of plant defense

Bin Gong [a], Guangfu Zhang [a,b,*]

[a] Jiangsu Key Laboratory of Biodiversity and Biotechnology, School of Life Sciences, Nanjing Normal University, Nanjing 210023, China
[b] State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS), Nanjing 210008, China

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ABSTRACT

Ecologists have long ignored or underestimated the importance of plant–herbivore interactions owing to the diversities of herbivores, plant defensive strategies and ecological systems. In this review, we briefly discussed the categories of herbivores. Then we reviewed the major types of plant defenses against herbivores. Selective forces of herbivore pressures have led to the evolution of various defensive mechanisms in plants, which can be classified into (i) resistance traits that reduce the amount of damage received, including physical, chemical, and biotic traits; (ii) tolerance mechanisms that decrease the impact of herbivore damage, and (iii) escape strategies that reduce the probability of plants to be found by herbivores. These strategies have been studied at different levels from molecular genetics and genomics, to chemistry and physiology, to community and ecosystem ecology. We summarized the development of the methodology for studying plant defenses against herbivores. Particularly, 24 of those hypotheses and models, which are influential in the international community concerning the relationship between plants and herbivores, including the defensive mimicry hypothesis, the compensatory continuum hypothesis, the slow-growth-high-mortality hypothesis, etc, were introduced and grouped into four categories according to plant defense strategies in the present review. Finally, we also reviewed the research progress of plant–herbivore interactions in China, and discussed the perspectives of studies on plant–herbivore interactions.

1. Introduction

The interactions between plants and herbivores are among the most important ecological interactions in nature [1]. As primary producers, almost all plants inevitably avoid being eaten by herbivores [2]. Thus, these relationships will affect nutrient cycles and energy flows of food chains [3]. It is reported that these herbivores consume over 15% of the whole plant biomass produced annually in temperate and tropical ecosystems. Accordingly, this makes herbivory the major conduit by which energy enters food chains [1,4].

More than three-quarters of animals are herbivores in nature, which play a significant role in shaping ecosystem structure and function [5,6]. Herbivores have a strong effect on their distributions and abundances by consuming plants [7,8]. They also exert a strong selective pressure on plant population by increasing its mortality and depleting biomass which can be used for plant growth and reproduction [9]. On the contrary, such habitat conditions as community type, plant density and light intensity, will result in spatial variation of plant-eating insects. Therefore, the interactions between plants and herbivores not only affect the structure and dynamics of plant populations, but also affect community composition and diversity, as well as ecosystem through food web and nutrient cycles [10].

When attacked by herbivores, plants can take various defensive measures, which are essential in the research field of interactions between plants and herbivores. Firstly, plant defense has played a critical role in the long-term co-evolution of plants and herbivores. For this reason, understanding the evolution and ecology of plant defenses is nearly equivalent to understanding the origin and function of extant ecosystems [1]. Secondly, the plant defense research deals with multiple subdisciplines and different scales, for example, from genetics and genomic to chemistry and physiology, to community ecology, ecosystem sciences and global patterns of herbivory and defense [1]. Another reason for studying plant defense against herbivores is that every year herbivory causes world economies to lose billions of dollars of revenue related to agriculture, horticulture and forestry [11]. Therefore, the study of plant defense is particularly necessary. It is quite common to carry out studies about plant defense characteristics, defense mechanisms and other respects abroad; however, there are very few related researches at home.

In this review, we briefly discussed the categories of herbivores. Then we reviewed the major types of plant defenses against herbivores from an ecological point of view, classified them into three categories including resistance traits, tolerance mechanisms and escape strategies. We also summarized the development of the

* Corresponding author. Jiangsu Key Laboratory of Biodiversity and Biotechnology, School of Life Sciences, Nanjing Normal University, Nanjing 210023, China. Tel: +86-25-13915978931; fax: +86-25-85891839.
E-mail address: zhangguangfu@njnu.edu.cn (G. Zhang).

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methodology for studying plant defenses against herbivores. Numerous theoretical models and hypotheses, which are influential in the international community concerning the relationship between plants and herbivores, were introduced in the present review. They can be grouped into four categories according to plant defense strategies; meanwhile most of them were reviewed within each category. Finally, we also reviewed the research progress of plant–herbivore interactions in China, and then discussed the perspectives of studies on plant–herbivore interactions to provide a theoretical basis for our future research.

2. Categories of herbivores

2.1. According to zoological classification criteria

According to zoological classification criteria, herbivores can be divided into herbivorous vertebrates and invertebrates. Most part of the former is generally herbivorous mammals (mainly ungulates), which is widely recognized as an important factor in maintaining the biodiversity of grasslands [12–14]. Meanwhile the latter mainly consists of Arthropoda (including herbivorous insects and crustaceans) and Mollusca (usually Gastropoda, such as snails, slugs, etc.). Initially many authors reported important relationships between mammalians and plants. By contrast, little attention was paid to the role of invertebrate herbivores in shaping plant community and population dynamics. However, such studies becoming a great part of ecology have been well documented in the literature in the past decades. Many studies have demonstrated that invertebrate herbivores have an important effect on secondary succession of plant communities [15–20].

Most mammals and mollusks feed on plant seedlings while insects do great damage to adult plants in the field. Interaction between plants and insects from different forest ecosystems has been widely carried out. Because of their different mouthparts, leaf damages by insects include chewing, skeletonizing, insect galling, mining, rolling, and sucking [21]. Plants and insects comprise most part of the organisms on Earth, and their interactions have profound implications not only for both ecological and evolutionary processes [22–24], but also for ecosystem nutrient cycling and energy flow [22,25]. Currently, researches on interactions between mollusks and plants are not as many as those relationships between insects and plants, but most studies on mollusk herbivory have suggested that mollusks, consuming little biomass, do enhance seedling mortality of subdominant herbs [14,26]. Generally mollusks are likely to feed on seedlings instead of adult plants, causing a great influence on plant individuals which is disproportionate to the biomass removed [27,28]. For example, a mollusk can kill a whole seedling with the removal of one bite of the hypocotyl while a similar bite to a mature leaf would have a negligible effect on the survival of the plant [29]. Therefore mollusks have a great impact on community composition of herb layer [30,31], especially for seedlings since their establishment is the crucial point in a species' life cycle [31–33].

Lodge [34] once pointed out that aquatic herbivores had little effect on the aquatic plants. However, studies hereafter have shown that aquatic herbivores have a strong impact on aquatic plant biomass [35] and species composition [36]. As common aquatic herbivores, some snails (from Gastropoda) and crustaceans (from Crustacea), like crayfishes, are distributed widely in the field. Nowadays, most of them have been applied as generalist herbivores during bioassay experiment to elucidate the relationship between aquatic herbivores and plants [8,37–39].

2.2. According to herbivores' preference for plant species

According to herbivores' preference for plant species, herbivores can be divided into generalists and specialists (including oligophagous and monophagous). Most herbivorous mammals and mollusks usually belong to generalist consumers while most plant-eating insects belong to specialist consumers [39]. For example, crayfishes (from crustacean) are often used as generalist herbivores in experiments (Fig. 1). Generalist herbivores refer to animals that can feed on most plants, and will not give up feeding on some certain plant species because of their special feeding preferences. Plant defenses and natural enemies are widely believed to be the main reasons why specialist herbivores only rely on one food source [3].

In view of the fact that generalists and specialists have different dependence and effect on plants [40], there are two viewpoints: some scholars believe that generalist consumers have greater effects on plant fitness and community composition [8,39,41,42]. On the contrary, other scholars hold that specialist consumers cause more damage to plants because they have superiority to generalists in food-searching and food utilization, food location and detoxifying, with fewer chance of being exposed to natural enemies [43]. Such disparity may be attributed to the different research content which is

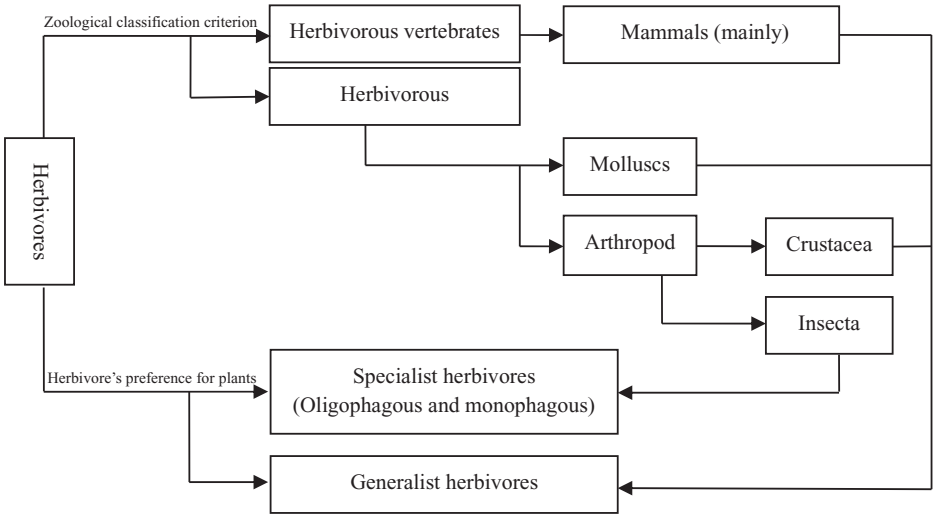

Fig. 1. Categories of herbivores.