植物-植食性动物相互关系研究进展

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摘 要 植物光合作用固定下来的能量沿食物链首先流向相邻营养级的植食性动物。植物-植食性动物相互关系是自然界中最普遍、最重要的一种种间关系, 是食物网理论的基础与核心。该文从植食性动物对植物个体、种群和群落特征的影响, 以及植物在个体、种群和群落3个水平上对植食性动物的防御机制与策略两方面, 综述了当前植物-植食性动物相互关系的研究进展。植食性动物的采食, 可以显著改变植物个体或种群的生长、繁殖和存活率, 植物种群的变化则进一步反馈于植物群落组成和多样性特征。相应地, 植物在个体、种群和群落水平形成了一系列的防御机制, 其中在个体和种群水平以化学与物理防御为主, 而群落水平则是通过影响动物的行为或天敌而实现的。该文对相关领域的重要假说和理论进行了介绍、比较。最后, 该文提出了植物-植食性动物相互关系研究的未来发展趋势。随着全球变化和人类活动对自然系统干扰的加剧, 在不同的时空尺度上探索这些干扰如何影响动植物关系, 以及这些影响如何反馈于生态系统的结构、功能和稳定性, 不但有重要的理论意义, 也将为未来制定合理的生态系统管理政策提供实际支撑。

关键词 植食性动物; 植物-植食性动物互作; 植物多样性; 植物防御

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Research progresses of plant-herbivore interactions

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Abstract

Plant-herbivore interaction is one of the most common and important interspecific relationships in nature, which is the core and foundation of the food web theory. In this paper, we review the effects of herbivores on the characteristics of plant individuals, populations and communities, as well as the defense strategies and mechanisms of plants against herbivores at the levels of individuals, populations and communities. Herbivory can significantly change the growth, reproduction and survival rates of plant individuals and populations, which can in turn affect the composition and diversity of plant communities. In order to defend against herbivory, plants have evolved a series of defense mechanisms at the individual, population and community levels. At the individual and population levels, plants avoid herbivory mainly by chemical and physical defense. At the community level, however, plant defenses are achieved mainly by their influences on the behaviors of herbivores. This paper then introduces and compares important hypotheses and theories in related fields. Finally, we point out major existing research issues and identify possible future research directions. Given that natural systems are experiencing strong disturbances from human activities and climate changes, exploring how these disturbances affect plant-animal interactions, and how these changes in plant-animal interactions feedback on the structure, function and stability of the ecosystems, will not only have important theoretical significance, but also help us to formulate successful ecosystem management policy in the future.

Key words herbivore; plant-herbivore interaction; plant diversity; plant defense

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物种之间的相互关系是维持食物网结构与生物多样性的基础。自然界中被植物光合作用固定下来的能量, 沿食物链首先流向相邻营养级的植食性动物。植食性动物可以显著改变植物种群的多度和分布, 调节植物群落物种组成与多样性, 进而对生态系统的功能和稳定性产生深远影响。与此同时, 在长期的进化过程中, 植物也形成了一系列物理与化学防御策略, 以降低植食性动物对自身的伤害程度。因此, 植物-植食性动物相互关系是自然界中最普遍、最重要的一种种间互作, 也是食物网及其众多衍生理论的核心组成部分。20世纪60年代, 美国生态学家Hairston等(1960)提出的“绿色世界假说”(green world hypothesis, 也称HSS假说), 揭示了捕食者对食草动物和植物的下行调控作用。该假说认为, 自然界中植物的繁盛是因为肉食动物对植食性动物的捕食限制了后者的种群多度, 从而间接有利于植物生长。尽管“绿色世界假说”强调的是捕食者的生态效应, 但其中的植物-植食性动物相互关系是介导这一生态效应的核心环节。

以“绿色世界假说”为起点, 植物-植食性动物相互关系的研究在其后几十年中得到蓬勃发展, 并拓展出众多重要的研究分支。这些研究分支可分为3个方面: 1)植食性动物对植物种群或群落特征的影响; 2)植物如何在种群或群落水平上对植食性动物的采食进行防御; 3)植物-植食性动物的协同进化。这些研究领域在日后继续发展、分化, 并形成一系列重要的理论和假说。至今, 植物-植食性动物互作关系已经成为群落生态学的核心研究领域。本文简要介绍前两个方面的研究进展, 并总结当前研究的不足, 最后对未来研究方向进行展望。

1 植食性动物对植物的影响

植食性动物可以通过营养性或非营养性作用对植物产生影响。营养性作用即直接采食作用, 这是植食性动物对植物最主要、最广泛的作用方式。非营养性作用, 是指除了直接采食作用外, 植食性动物对植物施加的间接影响。这一作用方式常见于脊椎植食性动物, 尤其是大型脊椎植食性动物。非营养作用包括动物的践踏、挖掘、倒卧、磨蹭, 或者其在打斗、玩耍、求偶、领地标记过程中对植物产

生的效应。典型案例是大象通过践踏、磨蹭等行为对非洲干草原树木的损毁(Pringle, 2008)。尽管植食性动物对植物的非营养性作用十分普遍且重要, 但由于在野外条件下很难区分动物对植物的营养和非营养性作用, 两者常常是交互地对植物产生影响, 因此单独研究非营养性作用并不常见(Goheen *et al.*, 2010; Pringle *et al.*, 2011; Li *et al.*, 2018)。植食性动物对植物影响的研究可以分为两个阶段: 早期的研究大多关注植物种群水平的响应; 近年来, 随着人们对植物多样性对生态系统功能调节作用认识的加深, 植食性动物对植物群落特征的影响成为研究重点。

1.1 种群水平

植食性动物通常会影响到植物种群的生长与繁殖性能, 如生物量、开花量、种子产量等, 从而改变植物种群的多度和分布范围。通常认为, 非脊椎植食性动物(如昆虫)对植物种群的影响弱于脊椎植食性动物(Crawley, 1989a; Myers & Sarfraz, 2017)。

1.1.1 种群性能

1.1.1.1 开花量 植食性昆虫对植物的采食, 通常会损害花芽和花蕾组织, 延缓其萌发时间, 减少植物花朵的产量(Hendrix, 1988; Karban & Strauss 1993; Liu *et al.*, 2011; Lemoine *et al.*, 2017)。很多植食性昆虫会对高等植物的花朵或花蕾进行采食。例如, 在松柏科植物中, 云杉卷叶蛾(*Choristoneura occidentalis*)采食会导致植物在生长季(5–8月)损失接近40%的大孢子叶球(Boa-Antwi, 2009)。在被子植物中, 昆虫采食导致的植物的花产量下降幅度在10%–100%之间浮动。通过对英国橡树(*Quercus robur*)种群花产量为期6年的监测, Crawley (1985)发现犬儒瘿蜂(*Andricus quercuscalicis*)的采食会导致橡树26%–47%的花死亡, 但对其他一些植物物种的花致死率高达100%。同样, 在北美大陆, 昆虫的去除会导致三齿蒿(*Artemisia tridentata*)的花序生长率提高22%, 花产量增加325%(Takahashi & Huntly, 2010)。脊椎动物对植物花影响的研究大多关注大型植食性动物的作用, 其对植物花产量的影响因动物的密度与植物物种而异(Sabo, 2019)。在北美堪萨斯的高草草原, 野牛(*Bos bison*)采食导致斑鸠菊属植物 *Vernonia baldwinii* 的花产量增加了2倍, 而家牛(*Bos taurus*)的采食则对其没有影响。野牛和家牛对 *Baptisia*

*bracteata*的花产量则均无显著影响(Damhoureyeh & Hartnett, 1997; Elson & Hartnett, 2017)。在阿根廷的巴塔哥尼亚草原,放牧家畜会导致大多数草本植物的开花时间滞后,花期缩短,并使植物提前进入结实期,而且这些效应会随着放牧强度的变化而波动(Tadey, 2020)。植食性动物对花朵的采食或损害,还可以间接影响植物-传粉者之间的互作关系,进而对植物种群生长和繁殖产生影响,这方面的作用十分重要,正在引起越来越多的关注(Mothershead & Marquis, 2000; Lucas-Barbosa *et al.*, 2011; Lucas-Barbosa, 2016; Moreira *et al.*, 2019)。

1.1.1.2 结实量 植食动物对植物种子或果实的影响程度通常因动物类群与生态系统类型而异(Crawley, 2013)。例如,植食性昆虫采食导致松柏科植物果实产量减少20%左右(Mattson, 1986; Frank & Jenkins, 1987; Mosseler *et al.*, 1992; Crawley, 2013; Rosenberg *et al.*, 2015),但是这一比例要远低于由鸟类或哺乳动物所导致的果实减产率(Janzen, 1971; Smith & Reichman, 1984; Gautier-Hion *et al.*, 1985; Estrada & Fleming, 2012; Lai *et al.*, 2014; Carpenter *et al.*, 2018)。在巴西的热带雨林中,可食埃塔棕(*Euterpe edulis*)的种子约有40%被脊椎动物所采食,其中鼠类和野猪(*Sus scrofa*)等动物占主导地位(Galetti *et al.*, 2015)。Lecomte等(2017)比较了麋鹿(*Cervus elaphus*)、鼠类和昆虫对地中海岩蔷薇(*Cistus ladanifer*)种子产量的影响,发现鹿的采食损坏了42.3%的繁殖组织,而昆虫导致的种子损失同样高达40%,相反,鼠类采食导致的种子损失率仅为6%。一些研究则发现昆虫对植物种子产量的影响很大。例如,食根性的蛴螬属幼虫*Hepialus californicus*的去除没有影响植物的繁殖输出,但是对食叶性昆虫的去除则导致种子产量增加了31% (Maron, 1998)。日本丽金龟(*Popillia japonica*)的采食会导致月见草(*Oenothera biennis*)的种子产量增加,但降低了种子的单粒质量(Lemoine *et al.*, 2017)。

1.1.1.3 幼苗的建成、生长与存活率 软体动物与植食性脊椎动物常常被认为是植物幼苗的主要采食者(Crawley, 1983; Jones & Jones, 1984; Edwards & Crawley, 1999; Villar *et al.*, 2019)。在欧洲的温带草地,软体动物的采食会导致树木幼苗的生物量损失高达75%,而鼠类甚至会将幼苗全部啃食,昆虫对树木幼苗的影响则不明显。这些植食性动物对树木

幼苗的影响在春季较弱,在秋季较强(Hulme, 1994)。在墨西哥南部热带雨林为期5年的实验发现,中型和大型植食性脊椎动物去除会导致树木幼苗密度上升23%,而植食性动物全部去除则导致树木幼苗密度上升61% (Camargo-Sanabria *et al.*, 2015)。相反,在美国中西部的温带森林中,Johnson等(2015)发现2年的植食性脊椎动物去除处理并没有对糖槭(*Acer saccharum*)、红花槭(*Acer rubrum*)、*Quercus alba*和*Quercus rubra*等植物幼苗的生长和存活率产生明显的影响。总的来说,植食性昆虫对植物幼苗的影响比脊椎动物的影响普遍,但是其作用程度较弱(Crawley, 1983)。

1.1.2 种群多度和分布

植食性动物对植物种群生长与繁殖性能,如生长率、开花量、种子产量等的影响,会最终反馈到种群多度和分布的变化上。早期的研究大多侧重于比较植食性非脊椎和脊椎动物对植物种群多度和分布影响的差异,或者关注单一植食性动物类群对不同植物种群的影响(Crawley, 1989b; Hulme, 1994; Damhoureyeh & Hartnett, 1997; Gómez, 2005; Russell *et al.*, 2010)。脊椎动物由于其体型大,食物消耗多,对植物多度的影响通常大于植食性昆虫。例如,在墨西哥南部的热带雨林,植食性脊椎动物的去除会显著提高其两种喜食植物——*Brosimum alicastrum*和*Ampelocera hottlei*的种群多度(Camargo-Sanabria *et al.*, 2015)。随着人类活动对不同生态系统的干扰增加,一些研究还关注人类活动和生境类型会如何调节植食性动物对植物种群的影响。例如,Maron和Crone (2006)在对30个野外研究进行meta分析后发现,植食性动物对植物种群多度和生长的影响取决于生态系统类型和人类活动的强度。草地生态系统中植食性动物对植物种群的影响通常要高于林地生态系统,因为前者的植食性动物密度通常高于后者。在人类干扰强烈的生境,植食性动物对植物种群的影响要强于干扰较少的生境。干扰生境中常常以生长快速的一年生植物为主,其对动物采食的防御较弱。全球气候变化也能够影响植物-植食性动物互作关系(Maron & Vilà, 2001; Bale *et al.*, 2002; Karuppaiah & Sujayanad, 2012)。例如,气候干旱加剧了非洲干草原大型食草动物对小灌木*Hibiscus meyeri*种群密度的负面影响,这是因为环境胁迫使得植物无法分配更多资源去在动物采食后进行补偿

生长(Louthan *et al.*, 2013)。植食性动物对生物入侵的影响是另一个研究热点。在美国宾夕法尼亚州的温带森林, 白尾鹿(*Odocoileus virginianus*)的采食导致了柔枝莠竹(*Microstegium vimineum*)和葱芥(*Alliaria petiolata*)等入侵植物的快速扩张(Eschtruth & Battles, 2009)。

1.2 群落水平

植食性动物对不同植物种群的选择性采食, 会导致植物物种之间竞争关系的失衡, 从而改变植物群落多样性和物种组成, 而群落结构的改变则进一步影响了植物群落的生产力。早期的研究多集中于植食性脊椎或非脊椎动物影响植物多样性的机制, 而随着地上-地下互作生态学的兴起(van der Putten *et al.*, 2001; Bardgett & Wardle, 2003; Wardle *et al.*, 2004; de Deyn & van der Putten, 2005), 一些研究开始关注地上-地下植食性动物相互作用及其发生机制, 以及这些互作对植物群落结构与功能的可能影响(van Ruijven *et al.*, 2005; Huang *et al.*, 2012; Johnson *et al.*, 2012; Borgström *et al.*, 2017)。

1.2.1 多样性

自20世纪90年代起, 生物多样性-生态系统功能关系逐渐成为生态学的研究热点。在动植物关系领域, 研究者也开始关注植食性动物对植物群落多样性的影响。植食性动物主要通过影响优势种植物与其他物种的竞争关系, 种群更新, 植物繁殖体的扩散等机制对植物群落多样性产生作用。植食性动物采食通常可以增加植物多样性(Collins *et al.*, 1998; Liu *et al.*, 2015), 但也有研究发现动物采食对植物多样性的影响是负面或者中性的(Bakker *et al.*, 2006; Allan & Crawley, 2011; Borer *et al.*, 2014; Koerner *et al.*, 2018; Villar *et al.*, 2019)。

植食性动物对植物多样性的影响主要由动物食性、动物群落组成、生境资源状况等多种因素决定。动物的食性很大程度决定着其对植物多样性的影响。例如, 专性植食动物尤其是优势植物物种的专性植食动物往往对植物多样性的维持具有重要贡献, 而广食性物种则通常不利于植物多样性的维持(Olff & Ritchie, 1999)。体型较小的动物, 如植食性昆虫等, 通常喜食质量(如氮含量)较高的植物种类, 具有较强的采食选择性, 因而其对植物多样性的影响是负面的。体型较大的动物, 如有蹄类动物或者放牧家畜, 在采食过程中更重视食物数量而不是质

量, 大多喜食优势物种, 因而通常可以提高植物多样性(Borer *et al.*, 2014; Liu *et al.*, 2015; Wang *et al.*, 2019)。在多种食草动物共同作用的情况下, 如果动物的食性差异较大, 动物对不同植物物种的采食平衡了采食压力, 产生互补效应, 则有利于维持群落植物多样性。例如, 在我国东北松嫩平原, 绵羊喜食杂类草, 而蝗虫喜食禾草, 两者对草地植物的采食平衡了植物的种间竞争关系, 维持了植物多样性(Zhong *et al.*, 2014)。同样, 当家畜多样性增加时, 其采食互补效应也会有利于草地植物多样性的维持(Liu *et al.*, 2015; Zhu *et al.*, 2015; Martin *et al.*, 2019; Wang *et al.*, 2019)。相反, 如果动物食性相似, 其对某一植物物种或者类群的采食压力会叠加, 产生加和效应, 不利于植物群落多样性的提高(Olff & Ritchie, 1999; van der Plas *et al.*, 2016)。此外, 生境的植物生产力状况也是调节植食性动物影响植物多样性的重要因子。生产力较高的生境中, 植食性动物的采食通常会增加植物多样性(Bakker *et al.*, 2006; Eldridge *et al.*, 2018)。

1.2.2 生产力

植食性动物对植物群落生产力的影响与动物的类群、密度和生境的资源状况密切相关。脊椎动物因为其较高的能量需求, 其采食常常会对植物生产力产生较强的负面影响。而非脊椎动物, 尤其是昆虫, 只有当其密度较高(如种群爆发)时, 才会在较短时间内对植物群落生物量产生显著影响(Belovsky & Slade, 2000; Zhong *et al.*, 2014)。此外, 较高的食草动物密度, 通常会降低植物群落生产力(Li *et al.*, 2011)。例如, 草地生态系统中重度或过度的家畜放牧会导致植物地上地下生物量锐减, 导致植被退化、荒漠化和沙漠化。适度或者较低的动物密度, 则对植物生产力没有影响, 一些情况下还可以促进植物生物量的积累(Liu *et al.*, 2015)。土壤肥力也可以调节食草动物对植物生产力的影响。在土壤肥沃的生境中, 动物采食对植物生物量的影响较弱, 因为植物可以进行较好的补偿生长, 弥补了动物采食导致的生物量损失(Bakker *et al.*, 2006; Pringle *et al.*, 2007; Zhu *et al.*, 2019)。值得注意的是, 植食性动物对植物的影响途径是十分复杂的。动物采食活动一方面会对植物生长产生不利影响, 但另一方面其通过粪尿排泄, 改变枯落物数量和质量、土壤微生物活性, 改变植物与其他动物的互作关系

等间接途径,从而间接有利于植物生长(Goheen *et al.*, 2010; Pringle *et al.*, 2011; Zhong *et al.*, 2017; Li *et al.*, 2018)。植食性动物对植物生产力的影响,是其直接采食作用和众多间接影响途径的净效应。

地上-地下生物互作对植物多样性和生产力的影响得到越来越多的关注。地上-地下植食性动物可以通过诱导植物的生理化学反应,或者通过其他生物组分如天敌、寄生生物等途径进行相互作用,而这些相互作用会反过来改变植物地上、地下生物量积累,分配以及植物群落多样性(Brown & Gange, 1989; van Ruijven *et al.*, 2005; Coupe *et al.*, 2009; Huang *et al.*, 2012)。例如,在欧洲草地生态系统,地上植食性昆虫的单独采食并没有显著影响植物生物量,但是地上-地下植食性昆虫同时存在时,则导致植物生物量下降了11%;此外,地上昆虫的存在提高了植物群落均匀度,但是地下昆虫则对植物多样性没有显著影响(Borgström *et al.*, 2017)。

2 植物对植食性动物的防御

在植物-植食性动物互作中,植物在长期进化过程中形成了一系列防御机制来抵御动物的采食,包括在个体、种群和群落水平上。不同植食动物对植物化学与物理防御的应对往往存在差异,这些差异可能与两者协同进化历程有关。

2.1 个体和种群水平

植物在个体和种群水平上对植食性动物的防御策略可以分为物理和化学防御两个方面。物理防御即通过改变形态结构抵抗动物采食的防御方式(Sanson *et al.*, 2001; Ibanez *et al.*, 2013)。例如,植物通过改变叶脉结构、叶片厚度、叶片表面茸毛以及植物的表皮等来抵御植食性昆虫的采食(王小菲等, 2015)。当要抵抗更大型的植食性动物时,植物会进化出更强有力的物理防御特征,例如刺结构。植物产生刺结构是需要消耗能量的,植物会根据特定生境的动物采食压力而调整其对物理防御资源的投入程度。通常而言,在植食性动物密度较高的地方,植物带刺结构更为常见(Belovsky *et al.*, 1991)。而动物对植物组织的长期频繁采食,也会诱导植物产生更多的刺结构(Milewski *et al.*, 1991)。植物的刺结构还可以通过一些微妙的机制去防御动物采食。例如,一些植物的刺上生长着特定的微生物或病原体,在其扎进动物皮肤时,也把病原体带给动物,从而对

后者产生更大的伤害,形成更显著的防御效应(Halpern *et al.*, 2007)。

相比物理防御,植物的化学防御策略是当前更为热门的研究领域。20世纪50年代,研究者在一些植物中首次发现次生代谢物,并认为这些化合物可能是植物用于防御植食性动物或病原体的攻击而产生的(Dethier, 1954; Fraenkel, 1959; Whittaker & Feeny, 1971),这些工作被认为是植物防御理论研究的开端。此后, Karban和Baldwin (1997)以及Karbon和Myers (2003)发现一些植物被植食性动物攻击后,可以产生挥发性的化学物质(如茉莉酸类),这些物质通过空气的传播而在同种或者不同物种植物之间进行交流,“提醒”邻居植物产生防御反应。例如,在美国加利福尼亚的荒漠生态系统中,昆虫的采食会导致三齿蒿产生挥发性气味,导致相隔60 cm外的邻居植物被昆虫采食的概率显著降低(Karbon *et al.*, 2006; Heil & Karban, 2010)。目前,植物挥发性化学物质在诱导植物防御反应中的作用及其在农业生物防控中的应用,已经成为植物-植食性动物关系的一个热点研究领域(Stamp, 2003; Karban, 2011; Wasternack & Hause, 2013; Schuman & Baldwin, 2016; Turlings & Erb, 2018)。

基于大量的实验性研究,过去几十年间在植物防御机制领域中涌现出大量的新理论和新假说。这些理论和假说均因塑造了相应的预测和假设,并在各自的领域中得到一定的支持。其中,影响力较大的假说有4个,分别是最佳防御假说(optimal defense hypothesis)、生长速率假说(growth rate hypothesis)、碳-养分平衡假说(carbon-nutrient balance hypothesis)和生长-分化平衡假说(growth-differentiation balance hypothesis)(表1)。

在个体和种群水平上解释植物-植食性动物关系变化的重要理论还包括植物胁迫假说(plant stress hypothesis)(White, 1974, 1984, 2009)和植物生长势假说(plant vigor hypothesis)(Price, 1991)。前者认为植物在受到胁迫时,其组织中(尤其韧皮部中)的氮含量会上升,从而导致这些植物上的植食性昆虫种类和数量增多(White, 1984)。后者则认为,植食性动物更倾向于采食生长旺盛的植物新枝嫩芽,这可能与这些新鲜组织中养分含量更高有关。植物胁迫假说和植物生长势假说并不是两个完全对立的理论,其描述了植物不同生长或生理阶段对植食性动物的

表1 植物个体或种群防御机制及假说
Table 1 Plant defense mechanisms at individual and population levels

假说 Hypothesis	解释 Explanation	文献 Reference
最佳防御假说 Optimal defense hypothesis	这一假说阐明了植物的防御需求如何驱动次生代谢产物的进化, 并通过付出防御成本使得植物的适合度达到最大化。该假说的核心思想是: 生物在进化与防御资源分配过程中, 会使后代个体获得最大的适合度。 This hypothesis addresses how defensive needs of a plant contribute to the evolution of secondary metabolites, with costs of defense paid to maximize plant fitness. The basic hypothesis states that, "Organisms evolve and allocate defenses in a way that maximizes individual inclusive fitness".	Feeny, 1975, 1976; Kooyers <i>et al.</i> , 2017
生长速率假说 Growth rate hypothesis	该假说探讨了环境中资源获得性、植物生长率与植物防御水平之间的关系。当环境资源供给低时, 植物常常具有较低的生长速率, 而防御水平则较高; 反之亦然。 It addresses genotypic variation in plant defenses, via resources shaping inherent growth rate and, subsequently, the constraints on defense against herbivores; among plant species, as maximal growth rate (at optimal resources) decreases, the constitutive level of defense increases.	Coley <i>et al.</i> , 1985; Endara & Coley, 2011
碳-养分平衡假说 Carbon-nutrient balance hypothesis	这是一个关于环境中碳和营养的供应如何影响植物防御表现型表达的模型。基本的假设是, 如果植物获取的碳:营养比例控制了资源在不同植物功能之间的分配, 那么该植物与防御相关的表型表达将受到影响。 This is a model of how the supply of carbon and nutrients in the environment influence the phenotypic expression of defense by plants. Basically, the hypothesis is that if the carbon:nutrient ratio acquired by a plant controls allocation of resources to plant functions, then the phenotypic expression of that plant's genetic potential for defenses will be affected.	Bryant <i>et al.</i> , 1983; Tuomi <i>et al.</i> , 1988; Hamilton <i>et al.</i> , 2001
生长-分化平衡假说 Growth-differentiation balance hypothesis	该假说提供了一个框架, 用于预测植物在一系列环境条件下如何把资源均衡分配给分化相关和生长相关的过程。在该假说中, 生长相关的过程是指根、茎和叶等器官的产生, 以及任何需要大量细胞分裂和伸长的过程; 分化则指的是与现有细胞结构或功能增强相关的过程。 It provides a framework for predicting how plants will balance allocation between differentiation-related processes and growth-related processes over a range of environmental conditions. Growth refers to the production of roots, stems, and leaves, or any process that requires substantial cell division and elongation. Differentiation refers to enhancement of the structure or function of existing cells.	Herms & Mattson, 1992; Barton & Koricheva, 2010

防御与吸引机制, 这一过程都由植物养分含量的变化所介导(White, 2009)。

2.2 群落水平

植物群落组成, 尤其是一些特定邻居植物的存在, 可以改变植食性动物对寄主植物的采食。Tahvanainen和Root (1972)最早发现非寄主邻居植物会降低寄主植物被动物采食风险的现象, 即联合抗性假说 (associational resistance hypothesis)(Root, 1973)。相反地, 当邻居植物是植食性动物的喜食物种时, 与其为邻则会提高自身被动物采食的风险, 即联合易感性假说(associational susceptibility hypothesis)(Parker & Root, 1981; Thomas, 1986; White & Whitham, 2000)。过去几十年, 以上两个假说在植食性脊椎动物(McNaughton, 1978; Hjalten *et al.*, 1993; Callaway *et al.*, 2005; Wang *et al.*, 2010a, 2010b; Zhong *et al.*, 2014)和非脊椎动物(Hambck *et al.*, 2000; Hahn & Orrock, 2016; Coverdale *et al.*, 2018)中均被广泛证实, 尽管联合易感性假说的普遍性似乎略少于联合抗性假说(Barbosa *et al.*, 2009; Underwood *et al.*, 2014)。

联合抗性和联合易感性的形成机制有非生物和生物两方面。非生物机制包括土壤理化性质、小气候状况的变化等(Barbosa *et al.*, 2009; 曾凡勇和孙

志强, 2014)。例如, 邻居植物会导致微生物境中温度、光照和湿度等条件的改变, 从而间接影响昆虫的产卵、生长和发育, 并改变其对寄主植物的取食。此外, 小气候还可以通过改变天敌的搜寻、捕食等行为, 间接影响植食性昆虫的种群数量及其对植物的伤害程度。生物机制主要是指邻居植物对植食性昆虫取食、存活、繁殖及其天敌等的直接作用效应。例如, 邻居植物可以通过简单的视觉或者通过产生挥发物而增加植食性动物对寄主的搜寻难度, 从而降低寄主植物被侵害的可能性(Coll & Bottrell, 1994; Hambck *et al.*, 2000; Zhong *et al.*, 2014)。或者, 邻居植物通过提供适宜的生境或食物吸引天敌, 进而间接降低植食性种群多度, 导致“联合抗性”的发生(Harmon *et al.*, 2000)。

在过去30年, 随着生物多样性的丧失及其对生态系统功能和服务维持重要性的认识, 人们开始逐渐关注植物多样性在防控病虫害发生中的重要作用。Pimentel (1961)首次报道病虫害在人工林中要比在多样性高的自然森林系统中严重的现象。随后, 无论在草地还是森林生态系统, 均有越来越多的实验证据支持了生物多样性是抑制和降低病虫害爆发的重要因素的观点(Unsicker *et al.*, 2006; Borer *et al.*, 2014; Moreira *et al.*, 2016; Guo *et al.*, 2019)。但是,

也有一些研究发现,随着植物物种多样性增加,植食性昆虫种类和数量随之增加并提高了其对植物的危害水平(Mulder, 1999; Otway *et al.*, 2005; Scherber *et al.*, 2006; Schuldt *et al.*, 2010; Guo *et al.*, 2019)。Jactel和Brockerhoff (2007)在对全球119个森林生态系统的研究结果进行meta分析后发现,树种多样性的增加能有效减少林间昆虫数量。在由不同树种所组成的群落中,寡食性昆虫的数量明显较少,而杂食性昆虫数量存在一定的变化。他们认为天然林树种的组成比寄主树种丰富度更为重要。

针对植物多样性-病虫害发生关系,人们提出了一系列理论对其进行解释。其中最具代表性的是资源浓度假说(resource concentration hypothesis)、资源稀释假说(resource dilution hypothesis)、资源特化假说(resource specialization hypothesis)、资源数量假说 (more individuals hypothesis) 和天敌假说 (enemies hypothesis)等(表2)。

3 展望

植物-植食性动物相互关系是自然界存在最广泛,也是最重要的一种种间相互作用形式。植物-植食性动物互作是食物网理论的基础,其强度变化对生态系统结构、功能和稳定性都有重要影响。早期研究大多集中在个体或种群水平上,而近年来随着群落生态学的发展,尤其是生物多样性研究的兴起,

研究者更多在群落水平上开展研究。传统的植物-植食性动物相互关系研究关注两个方面的效应,即植食性动物采食对植物个体、种群与群落的影响,以及植物在个体、种群和群落水平对动物采食的防御机制。这两方面的研究在近年来都获得快速发展,各自形成了一系列重要的假说和理论,并使得植物-植食性动物相互关系成为生态学研究的核心领域。

尽管如此,当前仍有众多问题限制着人们对植物-植食性动物相互作用的认识。首先,植食性动物对植物多样性影响的研究大多关注地上动物的作用,对地下动物,尤其是地上-地下植食性动物互作对植物多样性影响的关注较少(Huang *et al.*, 2012; Borgström *et al.*, 2017); 很多研究仅关注特定的动物类群,例如脊椎(如放牧家畜)与非脊椎动物(如昆虫)对植物种群和群落的作用,而在自然界中脊椎与非脊椎动物常常是共存并一起作用于植物的(Zhong *et al.*, 2014),因而对于两类动物如何协同影响植物种群与群落特征将是未来的研究重点。其次,在植物对植食性动物防御机制方面,在种群水平上,尽管大量研究关注植物的化学和物理防御,但对两者如何协同抵御植食动物的采食尚不清楚(王小菲等, 2015); 在群落水平,植物多样性,尤其是物种丰富度对植食性动物的防御效应是当前的研究热点(Jactel & Brockerhoff, 2007; Guo *et al.*, 2019),但人们对植物群落的其他特征,例如均匀度、功能多样

表2 植物多样性防御植食性昆虫的重要假说

Table 2 Ecological theories for the effects of plant diversity on herbivorous insects and the mechanisms underpinning such effects

假说 Hypothesis	解释 Explanation	文献 Reference
资源浓度假说 Resource concentration hypothesis	植食性昆虫更倾向于在寄主植物密度相对较高的生境中聚集或爆发。因此,较高的植物多样性通过稀释寄主植物的相对多度,降低昆虫多度。 Herbivores frequently forage in a density-dependent manner, and therefore increasing plant species or genotype number while keeping plant density constant reduces the probability of finding a preferred host plant species (or genotype), ultimately leading to lower herbivore abundance and damage on individual plants.	Root, 1973
资源稀释假说 Resource dilution hypothesis	与上述假说相反,该假说认为较高的植物多样性稀释了寄主植物的相对密度,使得更多的植食性动物集中在较少的植物个体中,加剧了对植物个体的采食程度。 As the density of plant items (species or genotypes) decreases (i.e. dilution), herbivores concentrate on the few available items and thus cause more damage in species-rich than in species-poor communities.	Otway <i>et al.</i> , 2005; Sholes, 2008
资源特化假说 Resource specialization hypothesis	较高的植物多样性可以提供更多的资源种类和生态位,从而支持了更高的植食性动物多样性。 Increased plant diversity provides a greater diversity of resources which favors an increase in consumer species richness due to an accumulation of consumers specializing on different resources.	Keddy, 1984; Hurlbert, 2004
资源数量假说 More individuals hypothesis	较高的植物多样性通过提高植物生产力,进而促进植食性动物的多度和多样性的上升。 High plant diversity increases plant productivity, such that an increase in the resource base positively influences consumer abundance, and that this in turn leads to an abundance-driven accumulation of consumer species.	Srivastava & Lawton, 1998
天敌假说 Enemies hypothesis	较高的植物多样性通过更多的食物和生境资源而有利于天敌多样性和多度的增加,后者的增加反过来降低了植食性动物的种群多度。 An indirect mechanism for plant diversity effects on herbivores as it holds that increasing plant diversity results in a greater availability of refuges and alternative resources, that this favors a greater abundance and diversity of predators and parasitoids, and that increased enemy recruitment ultimately leads to stronger enemy top-down effects on herbivore populations.	Elton, 1958; Russell, 1989

性、物种组成, 以及微气候等对植食性动物的影响仍所知甚少。最后, 跨大尺度的区域环境及地理样带上的研究也可能对植物-植食性动物相互作用关系的形成机制提供独特的视角和途径。例如, 随着大范围地理区域植物生产力的变化, 植食性动物对植物群落多样性和物种组成的影响也随之变化 (Bakker *et al.*, 2006; Koerner *et al.*, 2018)。在植物防御方面, 由于热带地区与温带和寒带地区相比, 常常具有较高的植食性动物多样性和多度 (Carmona *et al.*, 2011), 这些地区的植物是否经历较高的动物采食压力 (Moles *et al.*, 2011), 进而投入较大的能量进行物理与化学防御 (Pearse & Hipp, 2012), 也是植物防御研究中的一个热点问题。我国幅员辽阔, 且南北气候差异较大, 动植物资源丰富, 这为国内开展相关研究提供了有利的资源和条件, 然而目前国内大尺度植物-植食性动物相互作用格局的研究很少, 这些都将是下一步研究的重点。

综上, 植物-植食性动物相互关系是生态学的核心研究领域, 尽管其在一些研究分支已经取得了长足的进展, 但是许多现象背后的机制尚未完全清楚, 依然需要开展更多的实验性和理论性研究去解决这些问题。随着全球变化和人类活动对自然系统干扰的加剧, 在不同的时空尺度上探索这些干扰如何影响动植物关系, 以及这些影响如何反馈于生态系统的结构、功能和稳定性, 不但有重要的理论意义, 也必将为我们未来制订合理的生态系统管理政策提供实际依据。

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