

Chapter 12

Eco-evolutionary Dynamics of Above- and Belowground Herbivores and Invasive Plants



Wei Huang, Evan Siemann, and Jianqing Ding

12.1 Introduction

Herbivory is a major determinant of plant growth, reproduction, and defense. Ecological changes in abundance and composition of herbivores may alter plant phenotypic traits but also serve as an important selective agent triggering adaptive evolution in these traits, which in turn may alter interactions with surrounding organisms, in particular herbivores that exerted the selective pressure (Utsumi 2011; Ohgushi 2016). These interdependent ecological and evolutionary processes are often viewed as “eco-evolutionary dynamics” and have been documented in many different systems aboveground, but little attention has been paid to belowground (Fussmann et al. 2007; Pelletier et al. 2009; Hendry 2016). Moreover, above- and belowground herbivores can indirectly interact with each other via the shared host plant, resulting in a wide range of impacts on plant phenotypic traits depending on whether their combined impacts are independent, synergistic, or offsetting (Kaplan et al. 2008b; Erwin et al. 2014; Mundim et al. 2017). Thus, it is imperative to include above- and belowground herbivores in eco-evolutionary dynamics of plant and herbivore interactions in order to extrapolate how ecological changes in herbivores drive plant trait evolution and how evolution of plant traits influences

W. Huang

Key Laboratory of Aquatic Plant and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, Hubei, China

Institute of Plant Sciences, University of Bern, Bern, Switzerland

e-mail: huangwei0519@wbcas.cn

E. Siemann

Department of Biosciences, Rice University, Houston, TX, USA

e-mail: siemann@rice.edu

J. Ding (✉)

School of Life Sciences, Henan University, Kaifeng, Henan, China

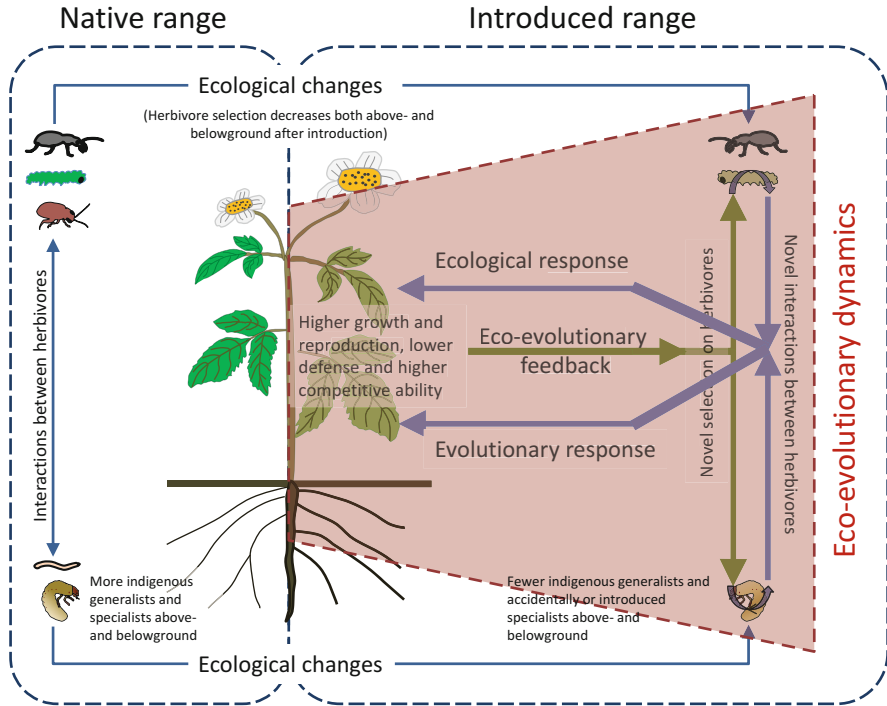


Fig. 12.1 The eco-evolutionary dynamics of above- and belowground interactions in invasive plants. Invasive plants often experience lower above- and belowground herbivore loads in the introduced range than in the native range. This ecological variation in herbivore pressure may drive evolutionary changes in plant traits, for example, increasing growth and reproduction and decreasing chemical defenses. Simultaneously, evolutionary changes in invasive plants may influence ecological interactions between above- and belowground herbivores

ecological processes in plant–herbivore interactions (van der Putten et al. 2009; van Geem et al. 2013).

Invasive plants are excellent candidates for examining the interplay between ecological and evolutionary processes in the context of above- and belowground interactions (Fig. 12.1) (van der Putten et al. 2009; Harvey et al. 2010; Vestergård et al. 2015). Firstly, invasive plants are often released from their coevolved above- and belowground specialist herbivores and may experience attack from a different group of generalists in the introduced range (Elton 1958; Maron and Vilà 2001; Keane and Crawley 2002; but see Chun et al. 2010). The variations in abundance and composition of herbivores in the introduced range may change selective pressure of herbivory on invasive plants. Secondly, these ecological variations in herbivore pressure may drive evolutionary changes in plant traits. Specifically, lower herbivore loads in the introduced range may select for increased competitive ability of invasive plants by evolutionary shifts in allocation from defense against herbivores to growth and/or reproduction (Blumenthal and Hufbauer 2007; Feng et al. 2009; Huang et al.

2010; but see Felker-Quinn et al. 2013). Lastly, evolutionary changes in invasive plants may influence ecological interactions, when the interactions with above- and belowground herbivores in the introduced range are modified by these genetic changes in plant defense and growth traits (Pearse and Altermatt 2013; Tanner et al. 2013; Bezemer et al. 2014). Thus, studies on the response of invasive and native populations of invasive plant species to above- and belowground herbivores may provide new insight into the interplay of ecological and evolutionary processes in altering the interactions among aboveground herbivores, belowground herbivores, and plants.

In this chapter, we review existing knowledge about eco-evolutionary dynamics of aboveground herbivores, belowground herbivores, and invasive plants. We aim to (1) provide an overview of the variation in herbivore communities associated with invasive plants in both above- and belowground compartments, (2) identify how above- and belowground herbivores drive selection on growth and defense traits of invasive plants, and (3) discuss whether genetic differences in growth and defense between native and invasive populations affect above- and belowground communities differently. In addition, we present a case study to illustrate interactions and feedbacks in eco-evolutionary dynamics.

12.2 Variations in Above- and Belowground Herbivores Between Introduced and Native Ranges

Herbivores can drastically influence plant growth, reproduction, abundance, and distribution. The Enemy Release Hypothesis (ERH) postulates that exotic plants will gain a competitive advantage over native plants through a plastic phenotypic (ecological) response to escaping suppression by coevolved natural enemies (Elton 1958; Maron and Vilà 2001; Keane and Crawley 2002). Although invasive plants commonly escape their co-evolved specialists, they may also be attacked by generalist natural enemies in the introduced range (Maron and Vilà 2001; Bezemer et al. 2014). The Biotic Resistance Hypothesis (BRH) emphasizes the importance of generalists in limiting invasions and posits that some exotic plants will be constrained by generalists because they can recognize, exploit, and suppress exotic plants in the introduced range (Parker and Hay 2005).

In addition to varying by diet breadth, herbivores attacking invasive plants vary in feeding guild, such as chewing vs. sucking feeders, foliar vs. seed feeders as well as gall formers and miners. Many studies have found herbivore community composition differs between invasive plants and related resident plants. For example, Ando et al. (2010) showed that herbivore species richness on invasive *Solidago altissima* and the native congener *S. virgaurea* were similar in the introduced range, but *S. altissima* plants were predominantly attacked by sucking feeders, while *S. virgaurea* plants were mainly attacked by foliar chewers and miners. In a manipulative common garden experiment, Burghardt and Tallamy (2013) found

that the impact of plant origin (native vs. invasive plants) on abundance of herbivores differed among herbivore feeding guilds. Plant origin had a stronger effect on abundance of chewing feeders than sucking feeders, while xylem feeder abundance was unaffected by plant origin.

To date, studies on the variations in herbivores between introduced and native ranges of invasive plants have mainly focused on aboveground enemies. Belowground enemies have received little attention, despite the fact that belowground enemies are pervasive in most terrestrial ecosystems and play critical roles in mediating the abundance and spread of plants and plant-associated organisms (van Dam 2009; van der Putten et al. 2009; Johnson and Rasmann 2015). In a biogeographical field survey, Cripps et al. (2006) showed that invasive plant *Lepidium draba* is attacked by root chewers and galls in the native range, but no root herbivores feed on *L. draba* in the introduced range, indicating *L. draba* completely escaped from suppression by belowground herbivores. Although direct evidence of escaping belowground herbivores is scarce, classical biological control provides clear information that belowground herbivores may be a major driver of plant invasions (Blossey 1993; Gerber et al. 2007; Huang et al. 2011). A review by Blossey and Hunt-Joshi (2003) showed that a total of 49 belowground herbivores have been released to control 19 invasive plants and more than half of them suppress their host plants.

Taken together, previous studies clearly demonstrate that above- and belowground herbivore communities differ between native and introduced ranges in their composition, abundance, and species richness (Maron and Vilà 2001; Blossey and Hunt-Joshi 2003; Cripps et al. 2006). Therefore, plant invasions offer an excellent opportunity to investigate eco-evolutionary dynamics in both above- and belowground compartments and future studies examining the role of natural enemies in plant invasions should benefit from combined above- and belowground perspectives.

12.3 Evolution of Plant Defense and Changes in Plant–Herbivore Interactions During Plant Invasions

12.3.1 Impact of Aboveground Herbivores

12.3.1.1 Trade-Off Between Plant Growth and Defense

Herbivores feed on almost all parts of plants, including leaves, stems, roots, flowers, fruits, and seeds. Thus, herbivory is considered an important selective agent in the evolution of many plant traits, such as growth, reproduction, and defense (Agrawal et al. 2012; Züst et al. 2012; Huber et al. 2016a). As a result, release from co-evolved natural enemies may not only lead to ecological benefits for invasive plants, but also drive evolution in a suite of traits of invasive plants (Bossdorf et al. 2005; Lin et al. 2015b; Uesugi and Kessler 2016). As an extension of the ERH, the Evolution of

Increased Competitive Ability hypothesis (EICA) posits that invasive plants that escape from specialist herbivores may increase their competitive ability through an evolutionary shift in resource allocation away from defense against herbivores toward traits conferring increased competitive ability, such as growth and reproduction (Blossey and Nötzold 1995).

Many studies have tested the predictions of EICA hypothesis, but found mixed results (Bossdorf et al. 2005; Chun et al. 2010; Felker-Quinn et al. 2013). Some studies supported the EICA hypothesis and found a trade-off between plant growth and defense (Joshi and Tielbörger 2012; Huang and Ding 2016). However, other studies did not support the EICA hypothesis and showed that invasive plants had either greater performance or lower defense (Meyer et al. 2005; Caño et al. 2009). The mixed results may be due to overlooking the abundance and composition of herbivores in the introduced range (Müller-Schärer et al. 2004; Orians and Ward 2010; Prior et al. 2015). Invasive plants often escape specialists, but may encounter generalists in the introduced range. Furthermore, invasive plants may reestablish associations with coevolved specialists or generalists due to accidental or intended introductions by human activities. Thus, herbivores in the introduced range, regardless of origins, may also have the potential to affect the evolutionary direction and magnitude of plant defense and growth.

12.3.1.2 Plant Resistance

Resistance is a defensive trait that protects a plant from herbivores by reducing the performance and/or preference of the herbivores. Specialist and generalist herbivores can exert opposite selection pressures on plant resistance (van der Meijden 1996; Lankau 2007; Ali and Agrawal 2012). The Shifting Defense Hypothesis (SDH) argued that invasive plants should maintain or increase their less-costly, toxic defense compounds (qualitative defenses) to defend against generalists and decrease their more-costly, digestibility-reducing compounds (quantitative defenses) which are more important in defense against specialists (Müller-Schärer et al. 2004). A meta-analysis and some empirical studies supported SDH (Joshi and Vrieling 2005; Doorduyn and Vrieling 2011). However, invasive plants may reacquire their resistance against herbivores, including specialists and generalists, when they are introduced from native ranges, or when herbivores from introduced range could adapt to the invasive plants (Siemann et al. 2006; Fukano and Yahara 2012; Sakata et al. 2014).

Plant resistance to herbivory is not only expressed constitutively, but can also be induced upon herbivore attack (Karban and Myers 1989; Agrawal 2005; Kant et al. 2015). This induced resistance may be a cost-saving defense strategy, because plants can increase resistance when herbivores are present, while shifting resources from defense to growth and reproduction when herbivores are absent (Agrawal and Karban 1999; Cipollini and Heil 2010; Karban 2011). Many studies have demonstrated trade-offs between constitutive and induced resistance and trade-offs between defense and growth (Kempel et al. 2011). It is, therefore, reasonable to expect that

invasive populations that are rarely attacked by herbivores in the introduced range should have higher induced resistance and lower constitutive resistance than their native conspecifics. This shift in defense strategies may favor invasive plants in competition with native plants. Although previous studies have demonstrated changes in induced resistance of invasive plants (Cipollini et al. 2005; Eigenbrode et al. 2008; Wang et al. 2012), theory that predicts evolutionary directions and consequences is still in its infancy. Thus, we need more detailed comparisons between native and invasive populations to fully evaluate how induced resistance changes during plant invasion.

Furthermore, some plants utilize indirect defenses [e.g., extrafloral nectar (EFNs) and volatile organic compounds (VOCs)] to attract predators or parasitoids of herbivores for reducing damage levels (Arimura et al. 2005; Heil 2008; Kessler and Heil 2011). To date, these indirect defenses have been demonstrated in many plant species under both laboratory and field conditions (Poelman et al. 2011; Mathur et al. 2013; Huang et al. 2015). In contrast to the evolution of direct defenses which are affected mainly by herbivores alone, the evolution of indirect defenses may be determined by herbivores and their natural enemies simultaneously (Poelman and Kessler 2016). Novel herbivore communities or differences in the predator and parasitoid communities in the introduced range may each influence selection on indirect defense, resulting in indirect defense being more sensitive to the changes in interaction network structure than is direct defense (Carrillo et al. 2012a; Wang et al. 2013). Based on limited available information and mixed results in plant invasion, it is still unclear how selection by herbivores affects indirect defense of invasive plants. Furthermore, changes in indirect defense compounds in the introduced range may also be the result of other selection pressures since VOCs and EFNs are also affected by many other biotic factors, such as plant neighbor identity and pollinators (Heil and Karban 2010; Heil 2011; Karban et al. 2014).

12.3.1.3 Plant Tolerance

In addition to resisting herbivore attack, plants also tolerate damage by herbivores. Tolerance is the ability to prevent or attenuate the negative impacts of herbivores through compensatory growth (Strauss and Agrawal 1999; Agrawal 2011; Fornoni 2011). The high growth rate of plants from invasive populations may lead to higher tolerance since plant growth rate is often positively correlated with tolerance to herbivory (Agrawal 2011). Also, negative correlations between herbivore resistance and tolerance have been detected in many agricultural and wild plant species (Núñez-Farfán et al. 2007); as a result invasive plants with lower resistance may have higher tolerance (Wang et al. 2011). Furthermore, invasive plants are still attacked by some herbivores in the introduced range that could favor a strategy of increased tolerance (Fornoni 2011). A growing body of research has indeed found that invasive populations maintained or increased tolerance compared to conspecific native populations after artificial damage, specialist or generalist herbivory, or in field conditions (Bossdorf et al. 2004; Huang et al. 2010; Gard et al. 2013; Huang

and Ding 2016). However, a few studies have found lower tolerance in invasive populations (Oduor et al. 2011; Lin et al. 2015b). Testing the traits underlying such differences in tolerance will reveal a better understanding of the role of herbivore tolerance in plant invasions.

12.3.2 Impact of Belowground Herbivores

Up to now, investigation of the impact of herbivores on the evolutionary trajectories of invasive plants has mostly focused on aboveground interactions and plant traits. There is comparatively little known about whether and how belowground herbivores affect root traits such as growth and belowground defense strategies of invasive plants. It is likely belowground herbivores would affect plant traits because they also have the potential to affect plant growth and defense (Pierre et al. 2012; Erwin et al. 2013; Huber et al. 2016a), and many invasive plants are released from suppression by belowground herbivores (Blossey and Hunt-Joshi 2003; Cripps et al. 2006; Knochel et al. 2010).

12.3.2.1 Plant Growth

Among plant root traits, root branching and specific root length (root length to mass ratio) are two important indicators of environmental changes, such as temperature, precipitation, and fertilization (Ostonen et al. 2007; Arredondo and Johnson 2011; Postma et al. 2014). Greater branching and higher specific root length may lead plants to absorb soil water and nutrients more efficiently, but may also render plants more vulnerable to belowground herbivores. Recently, Dawson and Schrama (2016) predicted that invasive plants should evolve to have greater branching and higher specific root length when released from their belowground enemies because such variations in root traits could increase their competitive ability through more resource uptake. So far, however, no empirical study has tested this hypothesis. In contrast, root biomass has been extensively studied and many studies have demonstrated that plants from the introduced range invest relatively fewer resources to belowground than to aboveground, leading to invasive populations that have lower root-to-shoot ratio than native populations (Huang et al. 2012b; Liao et al. 2013; Lin et al. 2015a).

12.3.2.2 Plant Defense

Plants are known to defend against belowground herbivores through increasing root toxins after attack, releasing volatile chemicals to attract the enemies of belowground herbivores, and/or compensatory growth (Rasmann and Agrawal 2008; van Dam 2009; Huber et al. 2016b). For plant root defense, in the study that put forward

the EICA hypothesis, Blossey and Nötzold (1995) tested the performance of root feeding larvae of the weevil *Hylobius transversovittatus*, on potted plants of *Lythrum salicaria* from introduced and native ranges. They found that larval weight and survival were significantly higher on invasive plants than on native conspecifics, indicating that *L. salicaria* may have evolved lower resistance to belowground herbivores in the introduced range. For plant root tolerance, Huang et al. (2012b) demonstrated that there was no significant difference in root tolerance between native and invasive populations of Chinese tallow tree after root herbivory. However, to date, research on invasive plant root growth and defense is so limited that it is unlikely to predict how root growth and defense of invasive plants evolve under new selections. Thus, it is imperative to include different root traits and defensive strategies into studies of invasive plants in order to extrapolate the evolutionary trajectories of root growth and defensive strategies during the process of invasion.

12.3.3 Impact of Above- and Belowground Herbivore Interactions

Above- and belowground herbivores are linked through induced responses of the shared host plant. First, above- and belowground herbivores can interact through plant direct resistance which can influence herbivore growth and/or foraging behavior (Erb et al. 2009; Robert et al. 2012). Second, interactions between above- and belowground herbivores can be mediated by plant indirect resistance [e.g., herbivore induced plant volatiles (HIPVs)] which can attract the natural enemies of herbivores (Rasmann and Turlings 2007; Soler et al. 2007). Finally, plant tolerance also has potential to affect above- and belowground herbivores interactions via shifting allocation of primary metabolites between above- and belowground structures (Kaplan et al. 2008a; Johnson et al. 2009). Thus, it is reasonable to predict that variation in selection on plant defense strategies may not only depend on the abundance and identity of herbivores but also on the interactions among herbivores. Genetic variation in plant defense may lead to different plant genotypes showing different physiological responses to above- and belowground herbivores that in turn alter the outcome of their interactions (Hol et al. 2004; Wurst et al. 2008; Kafle et al. 2014). Furthermore, the outcome of above- and belowground interactions with different plant genotypes likely depends on the feeding guild, modes of feeding, and diet breadth of herbivores with interactions potentially varying among specific combinations of herbivores (Johnson et al. 2012; Singh et al. 2014).

Under these conditions, invasive plants are likely to confront new combinations of both above- and belowground herbivores in terms of the taxa present as well as the feeding guilds, especially when some guilds are lacking in the introduced range. Thus, changes in above- and belowground herbivore interactions may also play a critical role in driving adaptive evolution of defense strategies for invasive plants. However, to date, most studies examining the role of herbivores in the evolution of

defense during plant invasion focused on herbivore release and/or gain and treated above- and belowground herbivores separately (if they included belowground herbivores). Furthermore, our current understanding of how genetic variation in invasive plant defenses affects above- and belowground herbivores is quite limited. As a consequence, we know little about feedbacks resulting from eco-evolutionary dynamics. Thus, investigating the difference in above- and belowground herbivore interactions between native and introduced ranges and feedback of genetic variation in defense to above- and belowground herbivores would be two important steps to understanding evolutionary trajectories of invasive plant defenses and corresponding ecological consequences.

12.4 Case Studies: Above- and Belowground Herbivore Interactions in *Triadica sebifera*

Triadica sebifera (synonyms include *Sapium sebiferum*) is a rapidly growing Euphorb tree (Zhang and Lin 1994). It is native to China and has become a severe invader in the southeastern United States (Siemann and Rogers 2003a; Pattison and Mack 2008). In China, *T. sebifera* is attacked by a diversity of specialist and generalist herbivores from both above- and belowground compartments (Zheng et al. 2005; Huang et al. 2014). However, only a few foliar chewing generalists (no sucking feeders or seed predators) and no root herbivores are detected in the USA (Siemann and Rogers 2003b, c), indicating *T. sebifera* experiences low above- and belowground herbivore loads after invasion. A recent apparently accidental introduction of a specialist leaf miner and roller from Asia has expanded the feeding modes of herbivores attacking *T. sebifera* (Davis et al. 2013). Recent studies on *Triadica sebifera* showed that *T. sebifera* generally had lower resistance to both above- and belowground herbivores, higher tolerance to aboveground herbivores, and comparable tolerance to belowground herbivores after invasion (Table 12.1). Furthermore, con- and heterospecific above- and belowground herbivore interactions were more intense on invasive populations than on native ones (Table 12.1). These results suggest that invasive plants evolve different growth and defense strategies to above- and belowground herbivores after invasion and feedback of these changes to herbivores interactions is stronger after invasion (see below for details).

12.4.1 Aboveground Herbivores

In a 14-year common garden experiment in North America, Siemann and Rogers (2001) found that invasive populations of *T. sebifera* had greater basal area and produced more seeds, but had lower foliar tannins than native populations. These

Table 12.1 Summary of reports on above–belowground herbivores interactions and plant responses to herbivory in invasive plant *Triadica sebifera*

	No-herbivory		Aboveground herbivory		Belowground herbivory		Both herbivory	
			Generalist	Specialist	Specialist	Specialist	Conspecifics (above facilitate below, below inhibit above)	Heterospecifics (reciprocal inhibition)
Insect performance			- or ↑	↑	↑	↑	Above -, below ↑	Above ↓, Below ↓
Plant growth	↑		↑	↑	↑	-	-	
Direct resistance	↓		- or ↓	↓	↓	↓	Leaf, -, root ↓	Root ↑, leaf ↑
Indirect resistance	↓, - or ↑		-	↑	↑			
Tolerance			↑	↑	↑	-		
References	Siemann and Rogers (2001), Carrillo et al. (2012a, b), Wang et al. (2013), Siemann et al. (2017)	Siemann and Rogers (2003b, c), Rogers and Siemann (2005), Huang et al. (2010, 2012a), Carrillo et al. (2012b, 2014) Wang et al. (2013)	Zou et al. (2008b), Huang et al. (2010, 2012b), Wang et al. (2011, 2013)	Huang et al. (2012b, 2014), Li et al. (2016)	Huang et al. (2012b, 2014)	Li et al. (2016)		

For insects, ↓, - and ↑ indicate insect performance decreased, no changed or increased on invasive populations, relative to native populations, respectively. For plants, ↓, - and ↑ indicate the growth, resistance, or tolerance of invasive populations was lower; had no significant change; or was higher than native populations, respectively

results were consistent with the EICA hypothesis and provided clear evidence that release from herbivores facilitates evolutionary changes in resource allocation between growth, reproduction, and defense. In another introduced site in Hawaii, Siemann and Rogers (2003b) found that a generalist beetle from the native range caused greater damage on plants from invasive populations. Similarly, caged North American generalist grasshoppers (Siemann and Rogers 2003c) and Asian specialist beetles (Zou et al. 2008b) caused more damage to plants from invasive populations when given a choice between plants from invasive or native populations. Overall, these studies indicate that *T. sebifera* decreases resistance to aboveground herbivores after invasion. However, the greater performance of plants from invasive populations than native populations in common gardens in North America, Hawaii, and Asia in which aboveground herbivores were suppressed suggests that the link from herbivore damage to plant performance may not be simple (Siemann et al. 2017).

In contrast to resistance, invasive *T. sebifera* exhibits higher tolerance to aboveground herbivory than native conspecifics when plants are exposed to simulated defoliation (Rogers and Siemann 2005), generalist herbivores (Rogers and Siemann 2005; Huang et al. 2012a; Carrillo et al. 2014), specialist herbivores (Zou et al. 2008b; Wang et al. 2011; Huang et al. 2012a), and natural herbivore communities (Zou et al. 2008a, b). Huang et al. (2010) examined the resistance and tolerance of *T. sebifera* from introduced and native ranges to specialist and generalist caterpillars. Bioassays and chemical analyses demonstrated that invasive populations had lower resistance to specialist caterpillars than native populations, but similar resistance to the generalist caterpillar. Furthermore, a common garden experiment showed that invasive populations had higher herbivore tolerance than native ones, especially for generalists (Huang et al. 2010). Taken together, changes in composition (specialist vs. generalist) and abundance (lower generalist loads) of aboveground herbivores have the potential to drive *T. sebifera* to evolve lower resistance and higher tolerance to herbivory.

In addition, *T. sebifera* produces EFN in glands at the base and underside margins of leaves that potentially act as an indirect defense through attracting arthropod predators and parasitoids of herbivores. Several studies have investigated EFN production of *T. sebifera* populations from introduced and native ranges, but results were mixed. For example, invasive populations had less (Carrillo et al. 2012a), similar, (Carrillo et al. 2012b) or more constitutive EFN production (Wang et al. 2013) than native populations in different studies. These contrasting results may result from different methodology used because EFNs are affected by environmental conditions and plant physiological status (Heil 2008; Izaguirre et al. 2013; Jones and Koptur 2015). Although EFN production can be induced by aboveground herbivory, studies showed that *T. sebifera* EFN production did not differ between native and invasive populations after simulated leaf herbivory (Rogers et al. 2003; Carrillo et al. 2012a) or generalist caterpillar damage (Carrillo et al. 2012b). Wang et al. (2013) investigated the impact of generalist and specialist herbivory on EFNs and found similar responses to generalist herbivory, while specialist caterpillars elicited more EFNs on plants from native populations than from invasive populations. These

studies indicated that changes in aboveground herbivores between introduced and native ranges may be also able to exert selection pressure on indirect resistance. Plants may retain constitutive and induced EFN in the introduced range to efficiently defend against generalists through attracting organisms in the higher trophic levels, while induced indirect resistance to specialist herbivores is attenuated because of lack of specialists.

12.4.2 Belowground Herbivores

Despite the fact that belowground herbivores strongly affect *T. sebifera* in the native range (Zheng et al. 2005), the role of belowground herbivores in driving the evolution of *T. sebifera* traits has received less attention. To date, such studies mainly focused on the response of *T. sebifera* to potential biological control agents or simulated root herbivory. For example, Huang et al. (2012b) and Li et al. (2016) found that larvae of a specialist flea beetle developed better on roots of plants from invasive populations than native populations. Chemical analyses showed that the invasive populations had lower root tannins than native populations, which may underlie the observed changes in larval performance between invasive and native populations (Huang et al. 2014). These results indicate that invasive *T. sebifera* decreases the investment of resources in belowground resistance, displaying the same evolutionary pattern as aboveground resistance. However, in contrast to increasing tolerance to aboveground herbivores, invasive populations had comparable compensatory growth to native populations after feeding by larvae of specialist flea beetle or simulated root damage (Huang et al. 2012b; Carrillo and Siemann 2016). These studies suggest that invasive plants, such as *T. sebifera*, have evolved lower belowground resistance and maintained their tolerance to belowground herbivores, thus supporting the EICA hypothesis predictions that invasive plants invest less resource into defense.

12.4.3 Above- and Belowground Herbivore Interactions

Aboveground herbivores may influence the induced response elicited by belowground herbivores, and vice versa, resulting in plant responses to single above- or belowground herbivores differing from their responses to multiple herbivores (Erb et al. 2008; Kaplan et al. 2008b; Huang et al. 2013, 2017; Soler et al. 2013). The specialist flea beetle, *Bikasha collaris*, is a common herbivore attacking *T. sebifera* in the native range (Huang et al. 2011). The flea beetle has aboveground adult and belowground larval life stages that cause serious damage to leaves and roots, respectively. In a recent study, Huang et al. (2014) found that both larvae and adults performed better on plants from invasive populations than from native populations, suggesting invasive *T. sebifera* decreased resistance to herbivores in both above- and

belowground compartments. However, adult feeding significantly decreased root tannins and increased larval survival, and these effects were stronger on invasive populations than on native populations. In contrast, larval feeding significantly increased leaf tannins and decreased adult survival, but plant origin and larvae feeding had no interactive effect. Apart from conspecific species, *T. sebifera* is also attacked by heterospecific above- and belowground herbivores in the native range. Li et al. (2016) examined the interaction between aboveground specialist leaf-rolling weevil *Heterapoderopsis bicallosicollis* and/or belowground *B. collaris* larvae on *T. sebifera* from introduced and native ranges. In contrast to conspecific species, the weevil and beetle inhibited each other. In addition, such reciprocal negative feedback between weevil and beetle species was stronger in invasive populations than in native populations. Overall, these studies show that the contrasting patterns of asymmetric feedback (facilitation and inhibition) in conspecific species and reciprocal negative feedback in heterospecific species are stronger in invasive populations. However, how changed selective pressure drives observed resistance strategies of invasive *T. sebifera* is still unknown.

Above- and belowground herbivore interactions also affect invasive plant tolerance. Huang et al. (2012b) examined plant tolerance to *B. collaris* adult and larval herbivory and found that invasive populations had higher tolerance to adult herbivory than native populations, while tolerance to larval herbivory was comparable. But when both adults and larvae were present, tolerance was still not different between invasive and native populations as there was no significant difference in biomass between invasive and native populations. In a recent study using simulated above- and belowground herbivory, Carrillo and Siemann (2016) also found there was no difference in tolerance to combined above- and belowground damage between invasive and native populations. These studies indicate that the presence of belowground herbivores strongly affects plant tolerance to aboveground herbivores, but this effect only occurs in invasive populations.

Changes in resistance and tolerance may in turn influence invasive plant resource investment into growth. In a study using *B. collaris* adults and larvae, Huang et al. (2012b) found adults and larvae each significantly decreased plant biomass. But adults more strongly affected aboveground biomass, while larvae more strongly affected belowground biomass. Furthermore, when plants were exposed to both herbivore stages, plants had lower biomass than predicted by the independent effects of each herbivore, suggesting simultaneous above- and belowground herbivory had a non-additive effect on plant growth.

Taken together, by examining the combined effects of above- and belowground herbivores on growth and defense of invasive plant and evaluating the feedbacks of invasive plant to above- and belowground herbivores simultaneously, these studies on *T. sebifera* and its herbivores exhibited eco-evolutionary dynamics of above- and belowground plant-herbivore interactions in biological invasion. These results suggest that selection pressure imposed by both above- and belowground herbivores is different from selection pressure imposed by either above- or belowground herbivores alone, especially for invasive plant resistance and tolerance. Compared with plants from native populations, plants from invasive populations had lower

resistance to above- and belowground herbivory by generalists or specialists, but higher tolerance to aboveground herbivory only. This in turn leads to invasive populations that have greater total and aboveground biomass, but comparable belowground biomass. These results indicate invasive plants may adopt an “above-ground first” strategy, allocating more resources aboveground in response to selection for increased competitive ability, which increases aboveground tolerance to herbivory (Huang et al. 2012a, b). Furthermore, evolution of invasive plant growth and defense affects aboveground, belowground herbivores, and their interactions. Invasive plants intensify the herbivores interactions, regardless of asymmetric feedback in conspecific species or reciprocal negative feedback in heterospecific species. These intensified feedbacks may considerably change the population dynamics and community compositions of herbivores in the introduced range.

12.5 Conclusions

The effect of combined above- and belowground herbivores on eco-evolutionary dynamics of invasive plants is largely different from the effect of each single herbivore (Fig. 12.1). Therefore, without integration of herbivores in both above- and belowground compartments, it is hard to make accurate predictions of how variation in herbivores contributes to the success of invasive plants. Furthermore, changes in growth and defense of invasive plants have profound impacts on above- and belowground herbivores, not only affecting herbivores in each compartment but also their interactions (Fig. 12.1). Thus, without evaluation of the impacts of invasive plants on herbivores in both above- and belowground compartments, it is impossible to have full understanding of how invasive plants affect population dynamics and community composition of herbivores in the introduced range. Together, future studies should focus on the impacts of and feedbacks to herbivores during plant invasions from both above- and belowground perspectives.

Our chapter also emphasizes that invasive plants may be excellent models to explore fundamental ecological and evolutionary questions regarding multispecies plant–herbivore interactions. This reflects, in part, that invasive plants experience different herbivore pressure in the introduced range compared to their native range and such changes in herbivore pressure may drive evolution of invasive plants in the new range. Invasive plants may change defense and growth strategies in both the above- and belowground compartments. The novel defense and growth strategies may be adaptive for invasive plants when they suffer lower above- and belowground herbivory in the introduced range compared with the native range. The resources saved from lower defense may be used to increase plant growth and reproduction and facilitate further invasion. Furthermore, novel defense and growth strategies may alter the outcome of above- and belowground herbivore interactions in the introduced range, for instance, strengthening or weakening the facilitation or inhibition between herbivores. As a result, changed interactions between herbivores may directly influence organisms that are closely associated with above- or belowground

herbivores in higher trophic levels. Alternatively, it may also indirectly affect competition between invasive plants and resident plants through host shifts of herbivores between invasive and resident plants. Thus, the interactions and feedbacks of above- and belowground herbivores may play an important role in plant invasions and determine the magnitude of negative impacts on resident communities.

Furthermore, studies on interactions of above- and belowground herbivores on invasive plants also have practical implications for management of invasive species (Huang et al. 2012b; Vestergård et al. 2015; Li et al. 2016). Biological control by releasing host-specific herbivores of invasive plants has long been recognized as an efficient and sustainable method of managing invasive plants, but the success rate is not high (van Driesche et al. 2010). Simultaneously releasing both above- and belowground host-specific herbivores or a single herbivore with above- and belowground life stages may make control more efficient, because herbivores attacking in one plant compartment could modify plant defense (e.g., tolerance) in another compartment (Huang et al. 2012b; Carrillo and Siemann 2016).

The current state of research also has important implications for the impacts of herbivores on plant evolution of both above- and belowground traits. The selection pressure of herbivores may not only affect plant parts where herbivores feed, but also in distant parts that are not sites of herbivore feeding through resource allocation trade-offs or plant systemic induced responses (Erb et al. 2008; Kaplan et al. 2008a; Huang et al. 2012b; Biere and Goverse 2016). Therefore, aboveground herbivores may not only be able to shape plant evolutionary trajectories of aboveground traits but also traits of roots, and vice versa. Furthermore, selection pressure of herbivory in above- and belowground compartments may be not constant, varying temporally and spatially (Siemann and Rogers 2003b; Agrawal et al. 2006; Huber et al. 2016b). Thus, temporal and spatial variability of above- and belowground herbivores may yield different patterns of eco-evolutionary dynamics of herbivores and plants. For example, native resident generalists may accumulate over time on invasive plants and co-evolved specialists may be introduced for biological control of some invasive plants (Siemann et al. 2006; Bezemer et al. 2014; Gruntman et al. 2017). Thus, experiments at multiple temporal and spatial scales may help to better understand the ecological and evolutionary processes of invasive plants both above- and belowground.

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