

Ecological explanations for successful invasion of exotic plants

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Abstract The intentional introduction of exotic species can increase the level of local biodiversity, enrich people's material lives, and bring significant social and economic benefits that are also the symbols of human progress. However, along with the frequent intercourse among countries and regions, the frequency of uncontrolled cross-regional migration of species is increased and there is a lack of scientific management strategy for the intentional introduction of exotic species. Exotic species invasion, which is behind habitat fragmentation, has become the second largest threatening factor to the maintenance of the global-scale level of biological diversity. Exotic species invasion can destroy the structure of an ecosystem, disturb the economic life of a society, and do harm to human health. In this paper, the authors review some of the ecological explanations for issues such as “what causes or mechanisms have led to the successful invasion of exotic species”, including the “ideal weeds characteristics”, “biodiversity resistance hypothesis”, “enemies release hypothesis”, “evolution of increased competitive ability hypothesis”, “niche opportunity hypothesis”, and “novel weapon hypothesis”. The authors also analyze and evaluate the background and theoretical basis of the hypotheses, providing explanations for some phenomena, as well as the deficiencies of these explanations.

Keywords exotic plant, biological diversity, novel weapon hypothesis

1 Introduction

The Ecology of Invasions by Animals and Plants by British ecologist Charles S. Elton (1958) was the pioneer in the study of invasion ecology. In that book, it was for the first

time expounded how human activities had exotic animals, plants, and microbes introduced into the remotest regions of the earth. These biological invasions caused by human activities threaten ecosystems, economies, and human health, and have become issues of global concern (Gonzalez et al., 2008).

Bio-invasion can trace back to remote antiquity but little occurs under the natural condition without human intervention. Human beings introduce non-endemic species into new environments, consciously or unconsciously. This frequent cross-species, intercontinental migration is increasing the possibility of harmful bio-invasion. According to the data released by the Food and Agriculture Organization (FAO) of the United Nations, half the species of farm crops are introduced worldwide. For example, as the first diplomat in the history of China, Qian ZHANG was sent on a diplomatic mission to Western regions in Western Han Dynasty. He was the first to introduce grapes, carrots, pomegranate, alfalfa, etc., into the central plains region along the well-known “Silk-road”, and propelled Chinese civilization into a new chapter. In modern times, the successful cases of introduction of Holland's flowers, New Zealand kiwifruit, the Northeast wild soybean, etc, to the wide regions of China also demonstrate the benefits of exotic species through scientific introduction. The cross-regional exchanges not only increase local biodiversity and enrich local residents' material lives, but also bring significant social and economic benefits that are symbols of human progress. However, due to the lack of a comprehensive risk assessment system and serious consideration of this issue, the intentional introduction of exotic species often results in disaster as it seriously jeopardizes the country's ecological security. Biological invasion reduces the uniqueness of regional flora and fauna, breaking their geographical isolation and threatening local communities in terms of biodiversity, ecosystems, economy, and human security. Its impact is irreversible (Castello, 1995; Vitousek, 1997; White, 1997; Enserink, 1999; Mack, 2000; Pimentel, 2000). Take the case of

Solidago Canadensis in China, for example. This perennial herb, belonging to *Dicotyledoneae*, *Asterales*, *Compositae*, and *Solidago* L, originated from North America. In 1935, this species was introduced from Japan into the region of Shanghai and Nanjing as a garden flower and had been transformed into a weed by the 1980s. Right now it has spread to and is widely distributed along the railway lines of Shanghai City-Ningbo City, Shanghai City-Hangzhou City, Zhejiang province-Jiangxi province, and the area of Taizhou and Lishui in Zhejiang province. The situation has been at the third stage of invasion process according to the definition by Williamson et al. (1996). The invasion of *Solidago canadensis* has caused the death of local film-green shrubs and eroded cotton, corn, and soybean fields in east China, and has become a common weed in the environment. These are the most serious effects of foreign invasion. Most environmental hazards are caused by unconscious human activities due to the lack of awareness of the species. According to the survey result of the Nanjing Institute of Environmental Science, State Environmental Protection Administration, of 283 kinds of invasive species, there are 49.3% unconscious invasions and 39.6% conscious invasions.

As Elton mentioned, the harm of biological invasion can be seen mainly in three aspects. The first is the impact on the ecosystem: (a) exotic invasion species cause direct damage by changing the species' composition and the number of the local ecosystems or by changing the nutritional structure of the ecosystem; and (b) the competition between exotic and native species threatens the survival of native species and reduces the biodiversity of local ecosystems, even annihilating some local species in some cases (Baskin, 1998). The second is the impact on the economy. The research reports published by the International Union for Conservation of Nature (IUCN) on February 5, 2003 show that the economic loss from exotic invasion is over 400 billion dollars annually. Data collected from the United States, India, and South Africa in the United Nations report show that economic losses in those three countries due to exotic species invasions amounted to 150 billion US dollars, 130 billion US dollars, and more than 800 billion dollars, respectively. Li (2005), an academician of the Chinese Academy of Sciences, gave even more shocking data, showing that exotic species invasion in China caused annual losses of 119.8 billion Yuan, accounting for 1.36% of the gross domestic product. The third is the effect of the exotic organism invasion on human health and safety: apart from the impact on the ecological environment and economic production, it is a direct threat to human health and may form the source of new diseases. Some new infectious diseases have been directly brought in by travelers intentionally or unintentionally, and some have been indirectly introduced by exotic animals that were infected (McNeely, 2001). For instance, ragweed (originated from North America) was introduced into China 40 years ago; its pollen can cause

“epidemic hay fever”. The physical allergic asthma will result in sneezing, runny nose, and other symptoms. It can even cause death from other complications. It has now invaded into 15 provinces of China and has resulted in annual springtime subtilis fever epidemic, affecting people allergic to pollen.

China has imported a total of 283 kinds of invasive species, including 19 kinds of microorganisms, 18 kinds of aquatic plants, 170 kinds of terrestrial invertebrates, 3 kinds of amphibians and reptiles, 10 kinds of fish class, and 5 kinds of mammals (Li and Xie, 2002; Fig. 1).

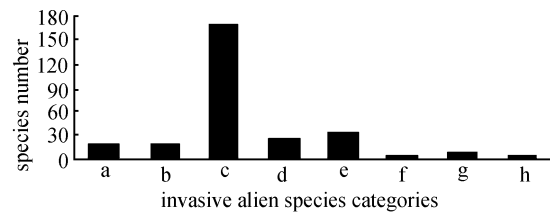


Fig. 1 Distribution group of all types of exotic invasive species in China (Li and Xie, 2002). a: microorganism; b: aquatic plant; c: terrestrial plant; d: aquatic invertebrate; e: terrestrial invertebrate; f: amphibian and reptile; g: fish; h: mammal.

With the “invasion of exotic organisms” and the public concern over the ecological environment, the problems of invasive exotic organisms have also become a hot topic for research. Retrieval of information from the latest literature (August 2008, Web of Science) over the past 10 years shows that the world’s 23 major ecology journals published a total of 973 articles on exotic invasion. The focus of all these is the question, “What causes or mechanisms have led to the successful invasion of exotic organisms?” To address this issue, scholars have put forward many possible explanations which are relatively influential hypotheses including (Table 1): “ideal weeds characteristics” (i.e., “Baker characteristics”), “biodiversity resistance hypothesis” (BRH), “enemies release hypothesis” (ERH), “evolution of increased competitive ability hypothesis” (EICA), “novel weapon hypothesis” (NWH), and “niche opportunity hypothesis” (NOH).

2 Ideal weeds characteristics

Baker (1965) proposed that the earliest spread of exotic invasive plant should have certain potential characteristics. He compared the characteristics of weeds and non-weeds, set out the weeds features, and meanwhile gave the definition of “ideal” weeds. During early times, the problem of what kind of exotic plant would become an invasive plant or what characteristics could distinguish the difference between the invasive plant and non-invasive plant had aroused widespread concern. One of the most influential theories consisted of the 12 life history characteristics of ideal weeds, which were put forward

Table 1 Major hypotheses for the success of exotic plants

hypothesis name	definition	references
ideal weeds characteristics	characters between weeds and non-weeds	Baker (1965)
biodiversity resistance hypothesis (BRH)	More diverse communities should be less susceptible to invasion by exotic species.	Elton (1958)
enemies release hypothesis (ERH)	Exotics are released from natural enemies that control their population growth.	Darwin (1859); Williams (1954)
evolution of increased competitive ability hypothesis (EICA)	Exotics experience rapid genetic changes linked to new selection pressure in the novel environment.	Hermes (1992); Blossey and Notzold (1995)
novel weapon hypothesis (NWH)	Exotics bring novel ways of biochemical interaction to recipient communities.	Rabotnov (1982); Willis (1994)
niche opportunity hypothesis (NOH)	Exotics are promoted among of resources, natural enemies, and the physical environment.	Shea & Cheeson (2002)

by Baker (1965), and thus were called the “Baker characteristics”. Baker put forward and defined the concept and characteristics of weeds on the basis of previous work and his own research work in abundance: “If, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man, without, of course, being deliberately cultivated plants”. Baker’s hypothesis of 12 “ideal characteristics of weeds”, characteristics of weeds or weed general characteristics, “Baker characteristics”, or “ideal” weed characteristics, was a sufficient condition for a plant to be a weed. Be consonant with all the 12 “ideal characteristics of weeds”, a plant would become a weed, but plants with a few characteristics of them could also become weeds.

Baker (1974) believed that species in line with more of the characteristics are more likely to become invasive species than the species with fewer characteristics. They could not have a successful invasion until exotic plants possess the capacity to grow rapidly in low population density. Compared with the sexual-reproduction-only plants, the plants that have the ability of vegetative reproduction own one more selective advantage: these plants are able to renew and open up a new habitat even if they are rare. If a plant completes sexual reproduction only through cross-pollination, then it would have a disadvantage in the competition with monoecious plants; monoecious plants with compatibility possess more selective advantages than those incompatible plants; plants with a variety of pollination systems have an extra selective advantage compared with the plants that have a specialized pollination system. The plants with multiple pollination systems may become the first outcrop angle in local external aggression. After invasive plants settle in the new habitat, the environment would suffer from multi-level selection pressure stress. Those that are resistant to drought, with short cycles and rapid growth of renewable capacity, and annual herbs have more selective advantages of invasion.

Plants improve their reproductive capacity through a variety of breeding ways. Under low-population-density

conditions, the vegetatively reproductive plants and adaptive plants can normally breed, but cross-pollination plants cannot (Baker, 1962, 1965). Herbivores would slow down the growth rate of plants and reduce the regeneration rate but increase the death rate. Some plants can escape from herbivores through physical or chemical means. If the plants have such a defense mechanism, they can reduce the risk of being food for animals. Plants would produce their own toxin to have allelopathic effects with non-weed plants and reduce the competition among species (Baker, 1965).

Daehler and Strong (1993), Pysek (1995), Mack (1996), Rejmanek (1996), Reichard and Hamilton (1997), Williamson (1999), Randall and Houshovsky (2000), and Kolar and Lodge (2001) supplemented the “Baker” features through revision. Pysek’s (1995) analysis of exotic species since 1942 suggested that whether exotic plants have a successful invasion has something to do with the height, life style, and competitiveness of the plants. Composites had a little higher possibility of successful invasion among the exotic invasive plants. Rejmanek (1996) found that the latitude of original places may predict the possibility of successful invasion by herbs. Reichard, and Reichard and Hamilton (1997) used discriminant analysis to study the relationship between woody plants and characteristics as follows: there is no need for pre-processing in the seed-sprouting period, and hermaphrodites and fruits can preserve a long time. Daehler’s (1993) data analysis suggested that agricultural weeds tended to be herbal, fast reproductive, and vegetative propagation plants, and invasions tended to be aquatic or semi-aquatic, herbal, lonely and clone trees. Kolar and Lodge compared different kinds of intruders and showed that the latter had some characters in common: the life history strategy of r-selection (pioneer habitats, short time to reproduce, high growth rate), and changing between r-selection and k-selection.

Sutherland (2004) proposed 10 characteristics differentiating weeds from non-weeds, native weeds from exotic weeds, by comparing 19 960 kinds of plants in the United

States, adding to and revising the Baker characteristics. Sutherland pointed out that Baker's characteristics can be supported by experimental data (such as the pollination, the short life cycle, closure growth, enemies and evils defense), but some of the characteristics cannot (such as vegetative reproduction, adaptive, wind pollination). Weeds and non-weeds can be distinguished by the characteristics of plants (i.e., life, life forms, habitats, defense mechanisms, and toxicity). In addition to life, other characteristics of the weeds are generally applied to local, exotic, and aggressive ones. Except for the high probability existing in the woody plants, invasive exotic species are rarely different from other weeds in history. Sutherland considered that if one plant has a successful invasion, then it would have much more strongly renewable capacity and vitality than non-weed plants. And the plants have such 10 kinds of characteristics: vegetatively reproductive, hermaphroditic or monoecious, self-compatible, wind-pollinated, tolerant of high levels, tolerant of low moisture regimes, annuals or biennials, perennial grasses or forbs, armed, and toxic. For example, weeds are mostly annuals and biennials and few are perennials. Compared with non-weeds, annuals and biennials are mostly toxic and they prefer dampness; few perennials are non-gramineae or shrubby, toxic, wetlands-growing, and shade-intolerant, and mostly are herbal, vine plants, and shrubs. There are more perennials, hermaphroditic, and cross-pollination shrubs in invasive weeds than in non-invasive weeds.

However, the Baker characteristics have not received wide approbates, and many scholars believe that they are incompletely correct. Holm (1978) thought that some of the world's exotic invasive weeds do not have these characteristics, while many non-invasive plants have some of the features.

Williamson (1996) did a correlation analysis between the extent of the "weed" invasion and the Baker characteristics. He thought that "there was no basis to do risk analysis with Baker characteristics". He believed that weeds and other plants had many different characteristics, and the Baker characteristics were wrong. A plant changes into a weed with the change of its characteristics as long as the environment changes.

To explore the life history characteristics of invasive species is of significance both theoretically and in application. It helps in understanding the biological invasion processes and mechanisms.

3 Biodiversity resistance hypothesis

Elton was a British ecologist who first defined and started research on the effect of exotic invasion on the structure of ecosystems, species composition, and biodiversity variation, and in 1958 he put forward the biodiversity resistance hypothesis (BRH) to explain exotic successful invasion. Elton (1958) suggested that the level of community

biodiversity plays a crucial role in the resistance of exotic invasion. Compared with the community composed of a few species, the community with rich species has a stronger resistibility to invasive species.

The BRH can explain well why so many exotic species fail to multiply in a new suitable environment, and elucidates the reason why exotic species cannot settle in a new habitat because of the strong influence from the local species. In addition, Elton also pointed out that islands (especially the small sea islands) were easily invaded due to the small number of local species and low levels of biodiversity.

The BRH has won some scholars' support, recognition, and a further explanation. The supporters proved and developed it both in theory and in experiment.

May and MacArthur (1972) verified the BRH over the relationship between environmental variability and the food size of niche. In their model, supposing that the food size is at a certain level and the plant community forms a stable structure through competition, the higher the level of ecosystem biodiversity and the stronger the competition of the plant communities, the more difficult the invasion of exotic species would be. The grass experiment Frank et al. (1991) did in the Yellowstone National Park achieved results that are consistent with the MacArthur model (1955): the stability of component types in a plant community strengthens with the diversity increase. Post and Pimm (1983) proposed the "Community assembly model", which showed that the increase in community diversity enhanced the community's ability to resist invasion. Law and Morton (1996) proposed the "Competition model" showing that the more species a community has, the more stable it is, and the stronger its ability to resist invasion. Dunkes (2002) proved the diversity of herb species would influence their susceptibility to the exotic species invasion in a microcosm experiment.

At the early stage, ecologists who were mainly engaged in the field of experimental observation supported the BRH. They observed that the invasion in species-poor ecosystems (such as archipelagoes) was more serious than that in species-rich ecosystems. Carlton (1979) intentionally introduced aquatic organisms in North America (mainly along the northern Gulf of Mexico and the Pacific Sea) to verify the BRH. Knops (1995) stated that exotic invasive plant species was negatively correlated with the plant community richness. Stohlgren (1999) found that the species-rich tropical regions had less exotic invasive species than the temperate zones of North and South America and Europe. In the glaciers deposited sand prairie northeast United States, experiments by Symstad (2000) showed that the ability of resisting invasions was enhanced with the increase in community diversity. Excluding the effect of non-biotic environmental factors, Naeem (2000) found the negative relationship between the level of native species diversity and the exotic plant *Crepis tectorum*. Higher resident diversity increased the environmental

selection pressure of plants and reduced the successful rate of *C. tectorum* invasion.

In a small-scale enclosed ecological observatory at Cedar Creek, Kennedy et al. (2002) did special research on the competition among species or within species of 13 kinds of exotic invasive plants (mainly European and Asian species) from 147 grasslands with different levels of plant species richness. They found that in the small experimental ranch with similar levels of species diversity, the increase in the number and types of species would enhance the region's anti-invasion capacity.

Lu and Ma (2005) surveyed the relationships between invasion patterns of croftonweed and native plant diversity at different times and space in southwest China, and the results show that higher native plant diversity also restrained croftonweed over the succession course of community.

However, the results of regional large-scale studies raised questions about the correctness of the BRH. Levine and D'Antonio (1999) thought that this hypothesis could just be clarified in a number of islands in the sea, or the region under artificial control, but their large-scale field investigations and research had not gained direct evidence for the relationship between the richness of biodiversity and the impedance of ecosystems. Although many models and field experiments showed that the increase in diversity could reduce the success rate of the invasion, these models were established on the basis of small-scale fields or excluding a variety of external factors so that the results of the study are different from the observation data in large-scale fields (Post and Pimm, 1983; Law and Morton, 1996). Levine et al. (2002) evaluated more than 150 researches on the hypothesis of biological invasion in the past 30 years, and their analyses showed that the structure and composition of plant diversity in the new environment through competitive inhibitive invasion was less than 5%.

In addition, researchers also found that some local species would not be able to impede invasion but would promote the invasion of exotic species. By the observation in the California coastal prairie, Maron and Connors (1996) provided evidence that invasion of *Bromus diandrus* could be facilitated by a native nitrogen-fixing shrub, bush lupine (*Lupinus arboreus*). Fix of nitrogen could fertilize the sandy soil, after the feeding *Lupinus arboreus* for insects, and cause a vacant niche where the exotic weed *Bromus diandrus* invaded into. Palmer and Maurer (1997) defined species such as *Lupinus arboreus* as "invasion promoters", and regions of high diversity had more "invasion promoters" so that they were easier to get invasion.

4 Enemies release hypothesis

Darwin (1859) initially described the enemies release hypothesis (ERH) as exotic species from the biosphere in

the natural enemies of the original constraints, to move to new habitats in the rapid proliferation of this phenomenon. In the ensuing 100 years, this became a hypothesis to explain the importance of foreign invasion theory and a research hot spot. Williams (1954), Elton (1958), Gillett (1962), and Keane and Crawly (2002) supplemented the contents of this hypothesis. The core is that when an exotic plant is introduced into new habitats, plants and other natural enemies of the predator are forced to reduce the choice, resulting in rapid growth of the number of new habitats and expansion of the spatial distribution. And it is covered by three main impact factors: natural enemies of plant populations are an important facilitator; natural enemies of native species have stronger selective inhibition than that of foreign species; and exotic plants can make use of natural enemies, enhancing the regulation of population density.

The study content of this hypothesis had two main aspects: one was to build up a large-scale mathematical model to analyze the impact of natural enemies on species in a particular area, and the other was to figure out the population behavior of species while in the absence of the main herbivores' natural enemies. Wolfe (2002) made use of the perennial plant *Silene latifolia* as a model system to test the accuracy of the ERH. *S. latifolia* was considered one of the most annoying farming weeds in America and Canada. Since its introduction in the 17th century from Europe, it had spread to most inland areas of North America. The research of 86 populations in both the United States and Europe shows that it presented greater significant impact of natural enemies in Europe, such as aphids, snails, and floral herbivores, especially seed predator and smut fungus. The extent of vulnerable plants in the United States was 17 times more than that in Europe. Wolfe thought that the successful invasion of *S. latifolia* into the mainland North America, at least in part, was to avoid predators or explained only by the low level of injury. Siemann and Rogers (2003), using a mathematical model system, suggested that another successful invasion of *Sapium sebiferum* from Asia to the south of the United States could also be well explained by the ERH.

At present, to prevent the introduction of natural enemies from their original habitats, biological control of invasive species has become an important means. In China, the introduction of *Aliernanthera philoxeroides* into the region of the southeast caused great harm in the water breeding, paddy field, and vegetable plot. Meanwhile, China's introduction of its natural enemies, *Agasicles hygrophila*, put *A. philoxeroides* under successful control (Zhang, 1997).

Throughout the literature, many ecologists hold suspicion on the ERH: on one hand, the lack of natural enemies was believed to be the best reason for the rapid spread of exotic plants; on the other hand, some research showed that the level of invasion was not decreased with the

introduction of the original natural enemies of invaders in the new habitats. Hierro and Callaway (2003) reported that all experiments of biological control of invasion species by the introduction of the original natural enemies in the new habitats ended in failure. The introduction of *A. hygrophila* and *Votiamalloy* (a moth) as natural enemies to control exotic species *A. philoxeroides* in Australia did not gain the desired results (Julien et al., 1992).

Maron and Vilà (2001) believed that in the research of the ERH, we must first establish a premise as to the extent of the impact of herbivores on the local number of plants. If herbivores do not affect much the number of local plant growth, then there is no reason that exotic plants will benefit from getting rid of natural enemies. Compared with non-perennial plants, seeds that rely on renewable one-year-old plants are vulnerable to grazing animal interference, resulting in lower seed production. This may be because exotic plants escape the invasion of special natural enemies and receive huge competitive advantage. By contrast, the perennial seeds or plants stored for a long period are affected by relatively small herbivores' interference for such reproduction.

Crawley (1989) excluded invertebrates in the experimental study of the natural enemies in the conclusions they reached and could not be sure of the decisive role of external enemies to plant invasion. The population number of some species dropped, while removing the natural enemies. Callaway et al. (1999) observed *Agapeta zoegana* in the wild, widely used in the biological control of *Centaurea maculosa*, which was considered one of the most destructive invasive plants in North America. The native species of *Festuca idahoensis* were planted together with *C. maculosa*. The former grew slowly when *A. zoegana* invaded the latter. In greenhouse experiments, *Festuca idahoensis* and *F. idahoensis* were seeded mixed or separately, accepting non-local herbivores (*Trichoplusia ni*) invasion at the same time. Pure sward to the interference was much smaller. Testing found that in order to be *Trichoplusia* attacks, the *C. maculosa* roots secreted more phenols; Callaway suggested grazing animals may enhance the *C. maculosa* effect on the surrounding plants. Keane and Crawley (2002) also found that the oligophagous enemies attack conversion to the host in the new habitat, the phenomenon of exotic species was more common, and invasive species in the new habitat will also be a new predator, thus the emergence of new enemies.

5 Evolution of increased competitive ability hypothesis

The authors of the evolution of increased competitive ability hypothesis (EICA) concluded that the main selective advantage of exotic invasive species comes from the adaptability to environmental change. Exotic

species invade into the new habitat where biological and non-biological environmental factors are completely different, adapt to the new environment, and make evolution of reaction quickly and effectively. EICA contains two meanings: One is that a tradeoff between the resources of growth and defense occurs. In new habitats, exotic plants lack natural enemies, so they can abandon some defense characters of natural enemies, and transfer the remaining biomass to create more characters of competitive advantage, such as size and fecundity (Hermes, 1992). The other is that exotic invasive species' adaptation to environment evolution includes behaviors, characters, and the changes of genomics (Siemann and Rogers, 2001; Callaway, 2004; Blumenthal and Hufbauer, 2007).

Crawley (1987) initially suggested that some of the invasion of exotic invasive species grow better than *in situ*, in his book *Colonization, Succession, and Stability*. Blossey and Notzold (1995) supported the EICA hypothesis and observed that *Lythrum salicaria* L. grew taller and the dry weight of biomass increased more quickly in North America than in the native region of Europe by comparing the difference between the individual characteristics of *L. salicaria* L. in both North America and Europe. They explained this phenomenon as *L. salicaria* L. escaping from the selection pressure of natural enemies. The energy would no longer be needed because the protection of the formation of the traits was used to improve the competitiveness of the species and the formation of the characters was a result of the evolution of species.

The study of Siemann and Rogers (2001) provided some evidence for the invasive species in the new habitat for adaptive evolution of genotype changes, and they put forward that the successful invasion may experience a complex genetic adjustment period. They took a 14-year observation of the introduction of *Sapium sebiferum* to North America from Asia, including measuring the diameter at breast height, analyzing total carbon and nitrogen of leaves, and assaying for tannin and calculating genotypes of basal area for each tree. They found that the adaptability evolution of invader *S. sebiferum* was the key to invasion process. At the early times of exotic species into the new habitats, plants evolve towards the direction of faster growth and more reproduction. With the increase in the number of exotic species, local herbivores begin preying on the rich resources of edible plants, and then plants begin to choose the direction of strengthening defense of evolution.

Blumenthal and Hufbauer (2007) compared the growth of plants from both native range and exotic range in each of 14 invasive species, *Abutilon theophrasti* Medik, India; *Aegilops cylindrical* Host, Turkey and Afghanistan; *Avena fatua* L., Afghanistan and Pakistan; *Bromus tectorum* L., Turkey; *Centaurea diffusa* Lam., Russia and Ukraine; *Centaurea maculosa* auct non Lam., Ukraine; *Desmodium tortuosum* (Sw.) DC., Brazil; *Echinochloa crus-galli* (L.)

Beauv., Afghanistan and Germany; *Elytrigia repens* (L.) Gould, Afghanistan and India; *Lespedeza cuneata* (Dum-Cours) G. Don., China and India; *Leucanthemum vulgare* Lam., Finland and Russia; *Linaria dalmatica* (L.) P. Mill., Macedonia and Novi-Begrade; *Poa annua* L., Afghanistan and India; and *Tragopogon dubius* Scop., Greece, at three levels of interspecific competition of local *Phalaris arundinacea* under the conditions of coexistence (no competition, two species were planted separately; low competition, two species were planted at the same time; and high competition, the invasive species were planted in the established population) in greenhouse that were set up to collect the growth situation among two-two species, and they found that the invasive plants were larger in the introduced range than that in the original range under no competitive conditions, whereas under a highly competitive condition the situation was inverse. They believed that genetic modification made invasive species penetrate to the interference of super-nutrition habitats more easily rather than the relatively primitive species community.

Callaway and Ridenour (2004) proposed that allelopathy enhanced the competitiveness of exotic species, and exotic species might evolve to the direction of more allelochemicals secretion. Such a direct competitive alternative choice substituted for the “growth and defense” balance, and made sublimation on the theory of EICA. Hull-Sanders et al. (2007) compared the *Solidago gigantea* chemical profile of 10 local stocks and 20 inter-American invasions from Europe. They thought EICA was on “growth and defense” transformation, and the plants lost part of the defense to natural enemies; the enemies of the defense still existed.

The main doubt of the challenger was that the invasive species showed greater size or better reproductive capacity in new habitats, but there were no direct data to prove that these traits of the species change to improve the competitiveness of natural enemies or their abilities to reduce the resistance; in addition, the specific shapes were not necessarily competitive advantage to the predators (Maron et al., 2004). Willis et al. (1999) compared the physiological characters of *L. salicaria* L. in Europe with those in North America, and they thought the EICA was not sufficient to explain the strong tendency of *L. salicaria* in the invasive habitats. The stem biomass and the relative growth rate (RGR) of *L. salicaria* were twice higher in the invasive range than that in the native range, but there was no significant change (that is, no significant difference in the phenol of leaves) in terms of resisting their natural herbivore enemies *Galerucella californiensis*.

6 Niche opportunity hypothesis

The niche opportunity hypothesis (NOH) was lately put forward by Shea and Chesson in 2002. Shea and Chesson

attempted to use the community ecology theory as a framework to explain biological invasion. They suggested the increase rate of exotic invaders in terms of interactions among resources, natural enemies, and the physical environment, all of which vary in time and space. How an exotic species responds to these factors determines its ability to invade. Niche opportunity was defined as a potential positive increase rate from low density in the given community for exotic species. Niche opportunity was combined with resource opportunity and natural enemy escape opportunity, or it was described as the relationships among resource, natural enemy, and physical environment, taking into account both time and space. The low niche opportunities resulted from high species diversity; thus, the invasion resistance ability of the community was strong.

Ecological niches through the analysis of changes over time and space of organisms, physical environment, and biological environment interaction relationship were defined. The coupling of physical factors (such as temperature and humidity) and biological factors (food resources, natural enemies, etc.) at a particular point in time and space formed a “niche space” (Shea and Chesson, 2002). The definition of species ecological niche was: the response and effect of each species of niche space (Chesson, 2000). Niche response was successful invasion of exotic species, which was based on population demographic variables to define, such as the survival rate and individual growth. One more important parameter was the result of the reaction, that was, per-capital rate of increase. Niche had multi-effect on the invasion of exotic species at the communities level, including resource consumption and other organisms competition for resources, the mutual interference, and the supply of natural enemies of space occupied, and so on. Communities within the local species and the response of the community decided to provide opportunities for foreign invaders, namely, whether the community to provide niche opportunities for the invaders.

The NOH comprehends the interaction among ERH, ROH, and the resource of the new habitat, natural enemies, and the physical environment. It indicates that the successful invaders are adaptors who can use multiple resource opportunities. Exotics are thought to gain advantages because they obtain a competitive advantage by escaping from specialist enemies and they have the ability to use fluctuant resources efficiently. Locals reduce their competitive ability as a result of the lack of the ability to use limited resources and the control of their natural enemies.

The NOH considers both the relationship between invasive species and the biological communities, and many factors such as the resources, natural enemies, and physical environment. But how to quantify and apply it to explain some ecological phenomena needs further study.

7 Novel weapon hypothesis

The presenter of the novel weapon hypothesis (NWH) thought that through a variety of ways, the invasion of the metabolic process releases some secondary chemical substances into the environment, by changing directly or indirectly the physical and chemical properties of soil habitats and soil microbial population structure to interfere with native species of normal growth and development process, and then the population level of competitive advantage (Mallik, 2000).

“Allelopathy” was originally proposed by a German scientist named Molish in 1937 who gave its meaning (Rice, 1974), i.e., biochemical interaction of all types of plant includes microbes, playing the role of inhibition and promotion. Later, it was modified by the American scientist Rice who defined it as: a plant releases chemical or biological substances by its own production to the environment which can impact another plant directly or indirectly through the poisoning effect (Rice, 1974). In order to strengthen the allelopathy of the effect of exchange, The International Institute of Allelopathy in 1994 founded the *Allelopathy Journal*. From the record of ISI Web of Science involving the literature sources of allelopathy, there are more than 10 kinds of journals belonging to the field of study of allelopathy. By August 25, 2008, SCI had a record with total relevant articles of about 2042, involving microorganisms, lower plants, higher plants, and the role of allelopathy in agriculture and forestry applications.

Under natural conditions, ragweeds (Wang, 1995; 1996) through evaporation, water leaching of the stems and leaves, and the material of root secretions have a significant allelopathy to the nearby plants and accompanying plants, which is also the main reason for their swift invasion. These kinds of sesquiterpenes isolated from the ethyl acetate extract of *Mikania micrantha* H. B. K. have a significant allelopathy to their commonly associated plant species, such as *Acacia mangium*, *Eucalyptus robusta*, and *Pinus massoniana* (Shao, 2005) in southern China. In the humid South Asia, the rainwater-dissolved liquid of the widely distributed *Chromolaena odorata* has an inhibition effect on germination of some plants, and its volatile oil has allelopathy to some vegetables, fungi, and insects (Ling, 2003). *Lantana camara* L., originated from the subtropical, is now widely distributed in tropical areas. Its whole or residual strains can secrete strong allelochemicals which lead to poisoning of animals and humans after they eat its leaves and fruit (Li and Xie, 2002). In southern China, the invasive plants *Wedelia chinensis* (Zeng, 1996), *Eupatorium adenophorum* (Yu, 2004), and *Eichhornia crassipes* (Sun, 1988) were also proved to play the role of allelopathy.

The known function pathways of allelopathy include changes in membrane permeability to inhibit plant nutrient absorption, inhibition of cell division and elongation of

ultra-structure, the impact of plant photosynthesis and respiration and the impact of the enzyme bioactivity and function, synthesis and metabolism of endogenous plant hormones, and protein synthesis. At the ecosystem level, allelopathy can have an important impact on the cycle of material and energy flows, the types of food chain systems, and biodiversity (Wang, 2007). What kinds of material play important roles in the pathway of allelopathy has become the focus of allelopathy study. In 1986, Rice classified the known allelopathy material with the function of inhibition into 15 major categories, and small phenolics, organic acids, and Terpenoids, among them, are common. So far, the identified allelopathy materials have been mostly small secondary metabolites of plants. At the molecular level, based on the function of genes or genome, the goal was to achieve the direct developmental utilization and control of the forefront study of allelopathy by biochemical synthesis or induction of allelopathy material. In a study of the invasive plant *Centaurea maculosa* from Europe to North America, which caused serious damage to the local ecological environment, Bais et al. (2002, 2003) found that (-)-catechol was a root secretion, produced during the germination and seedling growth stage of *C. maculosa* by combination of ecology, biogeography, plant physiology, biochemistry signal transduction and genomics research methods. After the successful invasion into North America, around the vicinity of the plants, the tolerance of (-)-catechol turned weaker. Meanwhile, it was also found that (-)-catechol could activate the root cell oxygen generation of local species of *Arabidopsis thaliana*, which caused Ca^{2+} ion signal transmission maladjustment and out of control of genome expression, finally leading to the death of root cells. *C. diffusa* was another kind of invasive weeds belonging to *centaurea*, which was studied by Vivanco et al. (2004). Its root could secrete a new natural product called 8-hydroxyquinoline. The pot culture trait showed the inhibition of the growth of North America experimental grassland was 30% more than that of the same species of European grassland, and the inhibition could be neutralized by adding activated carbon in soil. Both the studies of Bais and Vivanco provided evidence supporting the NWH hypothesis which was important and well accepted. Callaway et al. (2004) drew a conclusion after summarizing the studies of NWH hypothesis that proposed the “allelopathic advantage against resident species” (AARS) theory and pointed out that allelopathy was the core factor for the successful settling down of invasive plants.

In the research methods, plant allelochemicals extraction, isolation, and identification were the basis of allelopathy study. And the analysis of modern equipment, such as separation and purification for the gas chromatogram (GC), high performance liquid chromatography (HPLC) and for the structure identification of the gas chromatogram/mass spectrum (GC/MS), liquid chromatography/mass spectrum (LC/MS), nuclear magnetic

resonance (NMR), infra-red (IR), and ultraviolet (UV), plays an important role in the technology development. However, the analysis of modern equipment does not mean that people have eliminated the problem of understanding the inconsistencies in allelopathy research.

Based on the studies of previous scientists (Bais, 2002; Bais, 2003; Mitchell and Power, 2003; Reinhart, 2003) and our own laboratory experimental results, we conclude that the invasion of exotic plants at different stages has spatiotemporal differences between the species of allelochemicals production and their amount of environmental accumulation, while the number of allelochemicals in the development of invasive species, the competition and co-evolution with local species and co-evolution has a clear role in the regulatory effect, that is, "allelopathy has a connection with the amount of allelochemical accumulation in the environment", which is a supplement to the NWH hypothesis. In the study of allelopathy of *Solidago Canadensis* of nearby plants, we found that the low concentration of *S. Canadensis* root secretions in the environment could promote the growth of nearby plants. With the passage of time, the root secretions in the environment accumulated, and its concentration increase could result in inhibition of nearby plants.

8 Conclusions

Ecologists have made progress in the research into the mechanisms of exotic species invasion as discussed above. However, many problems still exist, such as the impact of the introduction frequency on the success of invasion, the role of random factors in the invasion process, how to integrate the results from different scales of study, how to manage and control exotic species in non-native ecosystems, and the influence of exotic species invasion on the biota formation in different bio-geological history regions. Factors related to exotic species invasion are complex and are very difficult to predict. It is also difficult to determine whether one or multi-factors control the process while a biological invasion occurs. Thus, we should not only consider the impact of multi-factors, but also pay attention to their combined effect. So far, to explain a successful invasion of exotic species, we need to use several theories or hypotheses for reference.

At present, there are several new trends in the research on exotic species invasion. The first is focusing on the mechanism of relationships and co-evolution among exotic plants, native species, and the environment; the second is exploring the reasons for successful invasion of exotic species under the background of other hot spots of ecological issues such as global warming, loss of biodiversity and bio-safety; the third is expanding the investigation measure in both aspects of macroscopic and microcosmic, and exposing questions from gene to biosphere level from various angles. Studying the

mechanism of successful invasion of exotic species can bring two benefits: it can help us understand the interaction among biology, non-biological factors and the environment and deepen our knowledge about nature; and it can provide us with more information about which species is the most threatening to plants in China, and what kind of measures should be taken to effectively prevent and scientifically manage its invasion.

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