Comparison of the herbivore defense and competitive ability of ancestral and modern genotypes of an invasive plant, *Lespedeza cuneata*

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The evolution of increased competitive ability (EICA) hypothesis provides a compelling explanation for the success of invasive species. It contends that because alien plants have escaped their coevolved natural enemies, selection pressures favor a diversion of resources from herbivore defense to traits that confer increased competitive ability. Here, we provide evidence for EICA in the noxious grassland invader *Lespedeza cuneata*, by comparing the ancestral genotype introduced to North America in 1930 with modern-day invasive (North American) and native (Japanese) genotypes. We found that the invasive genotype was a better competitor than either the native or the ancestral genotype. Further, the invasive genotype exhibited greater induced resistance but lower constitutive resistance than the ancestral and native genotypes. Our results suggest that selection has played a pivotal role in shaping this invasive plant species into a more aggressive, but less constitutively defended competitor.

The rapid population growth and high densities reached by invasive species provides scientists with many opportunities to investigate the mechanisms that regulate the abundance and distribution of organisms. Such research is a conservation priority since invasive species cause significant environmental and economic damage, and pinpointing the mechanisms that allow invasive species to achieve community dominance facilitates planning their eradication (Wilcove et al. 1998). One possible mechanism that has been invoked, but has proven difficult to test rigorously, is that invasive species evolve increased competitive ability in their introduced range, allowing them to outcompete native species and achieve community dominance. This ‘evolution of increased competitive ability’ (EICA) hypothesis (Blossey and Nötzold 1995) contends that in their introduced range, invasive species lack co-evolved enemies (Mitchell and Power 2003). As a result, natural selection favors genotypes that invest more resources in competitive traits at the expense of herbivore defense, leading to invasive genotypes that are more poorly defended against enemy attack, but are stronger competitors (Blossey and Nötzold 1995) than conspecifics from the native range.

Plants have two main strategies to resist herbivory. They may employ constitutive defenses, which are expressed continuously, or induced defense systems, which are stimulated only after attack from an herbivore (Karban and Baldwin 1997). Induced defenses have been demonstrated in over 100 plant species, and are thought to have evolved as a cost-saving measure, allowing plants to elevate defensive responses when herbivores are present, thus forgoing defensive costs when herbivores are absent (Karban and Baldwin 1997, Agrawal and Rutter 1998). EICA predicts that plants in the introduced range should exhibit reduced constitutive resistance, but it is unclear how escape from coevolved herbivores may affect induced resistance. Eigenbrode et al. (2008) suggest that a lack of interactions with herbivores will reduce selection pressures for induced defenses and lead to greater variability in induced defenses, rather than stronger induction. Alternatively, we hypothesize that invasive species in their new range should rely on more cost-effective induced resistance. Because invasive plants are infrequently attacked by herbivores they will likely be selected to invest fewer resources in constitutive defenses. A coinciding drop in induced defenses would leave the plant completely vulnerable to herbivore attack. Those genotypes with both lower constitutive and induced defenses would likely be selected against because they would experience extremely low fitness in the face of herbivore attack.

and invasive genotypes may reflect genetic variation across the native range rather than differences that have evolved since introduction. Indeed, in a common garden experiment, van Kleunen and Schmid 2003 found that the variation in performance among plants from different populations within the native range exceeded the difference in performance between the native and the invasive plants. In addition, this comparison of genotypes ignores the possibility that evolutionary change has also occurred in the native range. Because environments have changed considerably over the past century, current native genotypes may not accurately represent genotypes originally introduced into the invaded range.

Here, we take advantage of a unique opportunity to compare invasive genotypes of *Lespedeza cuneata* (Fabacea, Chinese bush clover) with ancestral genotypes from the original introduction. *Lespedeza cuneata* is a noxious grassland invader that depresses native biodiversity, alters grassland ecosystem function, and has negative economic impacts on agricultural grasslands (Eddy and Moore 1998). This plant species is native to Asia, and was introduced to North America from Japan in the 1920s as a hay and forage crop. Seeds have been maintained in collection by the Genetic Resource Information Network (GRIN) of the US Dept of Agriculture since 1930, providing us with the ability to compare genotypes before and after 76 years of evolution.

We compared the competitive ability and type of defenses against herbivores among genotypes from the native range, the invaded range (North America, specifically Illinois), and the ancestral introduction (seeds collected in North America in 1930) in a series of controlled greenhouse and growth chamber experiments. We refer to these genotypes as ‘native’, ‘invasive’ and ‘ancestral’, respectively. In North America, *L. cuneata* receives less than 2% herbivory due to insects, and no other obvious enemy damage, and is thus likely to have been ‘released’ from herbivory (Schutenhofer and Knight 2007). Yet, it remains to be determined whether EICA has contributed to *L. cuneata’s* successful invasion of North America.

Though recent interpretations of the EICA hypothesis (Keane and Crawley 2002, Müller-Schärer et al. 2004) suggest that escape from specialist herbivores is of paramount importance to the success of introduced species, several studies indicate that escape from generalist herbivores may also play an important role in the success of invasive species (Maron and Vilá 2001). In particular, with respect to changes in herbivore defense in invasive species, a recent study of the invasive species *Solidago gigantea* (Hull-Sanders et al. 2007) showed that while defenses against specialist herbivores were retained, defenses against generalist herbivores were reduced. Similarly, defenses against generalist herbivores in the invasive species *Sapium sebiferum* were also reduced in the introduced genotypes (Siemann and Rogers 2003). Here, we tested predictions from the EICA hypothesis that genotypes from the invasive range would exhibit increased competitive ability and reduced constitutive resistance against a generalist herbivore compared to the native and ancestral genotypes, and that the invasive genotypes would have higher inducible defenses than its native and ancestral conspecifics.

**Material and methods**

**Study species**

*Lespedeza cuneata*  
The perennial legume *Lespedeza cuneata* is a shrubby plant that can reach a height of up to 2 m. It reproduces by seed and through adventitious root buds (Kalburtji et al. 2001). Little is known of the herbivore community in the native range, but species of the genus *Lespedeza* are associated with at least 65 species of arthropods in their native range (Zheng et al. 2006). Although there is considerable variation in herbivore defense levels, this species is generally well defended against herbivory by high levels of tannins in the leaves and stems (Windham et al. 1988). These tannins have also been shown to inhibit the growth of other plants (Kalburtji et al. 2001). Furthermore, a variety of other chemicals have been isolated from leaves of *L. cuneata* that might play a role in defense, such as isoflavonone, isoflavone, sterol, triterpenoid, flavonol, flavonol glycosides and flavone C-glycosides (Deng et al. 2007, Kwon and Bae 2009).

*Lespedeza cuneata* was first introduced to the United States from Japan in 1896 by the North Carolina Agriculture Experiment Station (Ohlenbusch et al. 2001). However, it was not used as a soil stabilizer and forage and hay crop until after its second introduction in 1924 to the Arlington Experiment Farm in Virginia (Eddy and Moore 1998). Three different cultivars of *L. cuneata*, selected for finer stems with greater branching, have been released throughout the southern United States: Arlington, released in 1939, Sera, released in 1959, and Interstate, released in 1969 (Guernsey 1970). *Lespedeza cuneata* was first introduced to Illinois and surrounding states in the 1930s when it was planted on roadsides and strip-mines (Ohlenbusch et al. 2001). While the original introduction of *L. cuneata* was the Arlington cultivar, the *L. cuneata* present in the state today is likely a mixture of the descendents of the three cultivars, all of which are descendents of the original Japanese plants.

We compared the competitive abilities and herbivore defenses of three *L. cuneata* genotypes: ancestral, native and invasive. Both the ancestral genotype and the native genotype were acquired from GRIN of the US Dept of Agriculture’s Agriculture Research Service. In 1930, six years after its introduction, *L. cuneata* seeds were collected from near the Arlington Experiment Farm and maintained in collection by GRIN (USDA 2006). This genotype is referred to as the ancestral genotype. Seeds of six lines, which were collected from different populations in Japan at different times and maintained in collection by GRIN, were mixed together and are referred to as the native genotype. In 2005, seeds were collected from 20 plants located near the Southern Illinois University Edwardsville in Edwardsville, Illinois and are referred to as the invasive genotype. We used 6–20 randomly selected lines of each genotype to minimize the chance of spurious results due to the traits of single lines. This methodology limits our ability to make generalizations across the invasive range, but
allows to test if the predictions of the EICA hypothesis are valid in some cases.

Differences in environmental conditions could affect the maternal resources of the seeds of each genotype. In particular, seeds of the native and ancestral genotypes were collected from plants grown in a greenhouse, whereas those of the invasive genotype were collected from field plants. Seeds with more maternal resources may have a growth and thus a competitive advantage over those with fewer resources. Although maternal environmental effects can be transmitted in a variety of ways, one obvious indicator of maternal resources is seed mass (Roach and Wulff 1987). We weighed 25 seeds of each genotype to assess the degree of maternal resources is seed mass between the genotypes with preplanned comparisons between individual pairs of genotypes (pdff tdiff options of the LSMEANS statement).

*Helicoverpa zea* (Lepidoptera: Noctuidae)

Eggs of *Helicoverpa zea*, or the corn earworm, were obtained from the North Carolina State Insectary (North Carolina State Univ., Raleigh, NC). Following hatching, larvae were grown in containers on artificial diet for seven days prior to being placed on the plants. *Helicoverpa zea* is a generalist herbivore that is known to attack every field and vegetable crop in North Carolina, and is one of the principal herbivores of *L. cuneata* in North America (Buntin 1991). It is unknown if *L. cuneata* supports any specialist herbivore in its native range.

**Plant competition assay**

*B. cuneata* seeds were scarified with emory paper and sown into seed trays. After two weeks, seedlings were transplanted into 10 cm pots (393 cm$^3$). Ten replicates of each genotype were grown with each of the genotypes (three focal genotypes $\times$ three competitor genotypes $\times$ 10 replicates $= 90$ experimental units). Plants were arranged randomly in the greenhouse. One plant in each pot was considered a focal plant (i.e. the plant of interest), while the other was considered a competitor plant (i.e. a treatment). Though the EICA hypothesis specifically refers to interspecific competition, we chose to assess the intraspecific competitive abilities of the three genotypes to avoid arbitrarily selecting a single competitor species. For example, in a recent study of the competitive ability of the invasive species *Lepidium draba*, one competitor species was harmed by competition with the invasive, while a second was not impacted (McKenney et al. 2007). Ideally, competitive ability would be assessed under field conditions with multiple competitor species. However, in our case, this type of study would risk introduction of new genetic material (i.e. Japanese DNA) into the established invasive population.

Plants were grown in a greenhouse with supplemental lighting at 24°C during the day and 21°C at night. Watering and fertilizing were kept to a minimum to ensure that the plants were forced to compete for soil resources, but were not so stressed by competition that any died. After five months, the aboveground biomass was harvested, dried and weighed.

**Herbivore defense assay**

To quantify the relative investment in plant defenses, we assessed constitutive and inducible resistance using bioassays with *H. zea*. Seed germination was accomplished as in the competition study, except trays of seeds were placed in a growth chamber to eliminate potential damage from any herbivores residing in the greenhouse. Growth chambers were set at 25°C during the day and 21°C at night with a 16 h day. Plants were fertilized weekly. After three weeks, 54 seedlings of each of the three genotypes (ancestral, native and invasive) were transplanted into individual 10 cm pots (393 cm$^3$). Four weeks later, 45 plants of each genotype were subjected to herbivory by *H. zea* caterpillars. To achieve variation in the amount of initial damage that plants received, we enclosed zero, one, two or three young (second or third instar) caterpillars with plants in plastic bags.

After three days, we removed the caterpillars and visually estimated the degree of herbivory per plant. We counted the number of leaves on each plant and estimated the number of leaves receiving 25%, 50%, 75% or 100% damage. Using these data, we then estimated the total damage on each plant as a percent of the initial number of leaves. After one week, one leaf (three leaflets) was removed from each plant and placed in a petri dish with one newly hatched *H. zea* caterpillar. After three days, the caterpillars were removed, euthanized and weighed to the nearest mg on a microbalance. Constitutive resistance levels were assessed by measuring the growth of caterpillars on plants that had not received any herbivore damage (i.e. they received zero caterpillars), while inducibility levels were assessed by measuring the growth of caterpillars on plants that have received some herbivory damage. Caterpillars were assumed to grow more slowly on well defended plants and more quickly on poorly defended plants (Van Zandt 2007).

**Statistical analysis**

Statistical analyses were performed using SAS ver. 9.0 (SAS Inst.). Final plant biomass data were log transformed prior to analysis to normalize the residuals. We used an analysis of variance (PROC GLM) with preplanned comparisons between individual pairs of genotypes (pdff tdiff option of the LSMEANS statement) to determine the effect of competitor plant, focal plant and their interaction on final plant biomass.

We conducted an analysis of covariance (PROC GLM) to examine the relationship between caterpillar biomass and percent plant damage of each genotype. We used the biomass of caterpillars growing on plants that did not receive any herbivory damage (as indicated by the intercept of the slopes) as an estimate of constitutive defenses, and the slope of the relationship to indicate inducibility (after Van Zandt 2007). Plants displayed different ranges of herbivore damage. The native plants had an even distribution up to 25% damage with two outliers receiving $>$40% damage, the invasive up to 30% damage with one outlier receiving $>$40% damage, and the ancestral up to 23% damage with two outliers receiving $>$40% damage. In order to compare the same range of damage for each genotype, plants that received more than 23% damage were removed from the analysis (two
ancestral plants, three native plants and seven invasive plants). Preplanned contrasts were conducted (CONTRAST statement) to compare both the slopes and the intercepts of individual pairs of the genotypes. Separate regressions (PROC REG) of the relationship between damage and caterpillar mass were conducted for each of the three genotypes to determine the slopes of the lines.

**Results**

As predicted by the EICA hypothesis, we found that the invasive genotype outcompeted the ancestral and native genotypes (Fig. 1, Table 1). Specifically, aboveground biomass of the invasive genotype was greater than both the native and ancestral genotype and was unaffected by the identity of the competitor, whereas both the native and ancestral genotypes had reduced aboveground biomass when they were paired with the invasive genotype relative to other competitors.

Seeds of the invasive genotype (1.63 ± 0.06 mg (mean ± SE)) were marginally, but not significantly smaller than seeds of the native genotype (1.79 ± 0.06 mg) (t = 1.88; p = 0.0631; DF = 2), and were smaller than seeds of the ancestral genotype (1.88 ± 0.06 mg) (t = 2.97; p = 0.004; DF = 2). There was no difference in the seed mass of the ancestral and native genotypes (t = 1.09; p = 0.281; DF = 2).

The caterpillars grown on the undamaged invasive genotype were larger than caterpillars growing on the undamaged ancestral and native genotypes (invasive vs native F = 5.58; p = 0.0196; DF = 1); invasive vs ancestral F = 14.54; p = 0.0002; DF = 1), indicating that both ancestral and native *L. cuneata* genotypes had stronger constitutive resistance than the invasive genotype (Fig. 2b, Table 2). Further, only the invasive genotype exhibited induced resistance against herbivores (Fig. 2a, Table 2), as indicated by a significant negative relationship between the degree of herbivore damage and caterpillar body mass. The impact of herbivory on the degree of induced resistance in the invasive genotypes was significantly different from both the native (F = 5.48; p = 0.0207; DF = 1) and the ancestral (F = 3.96; p = 0.0486; DF = 1) genotypes.

**Discussion**

This study is the first to use ancestral genotypes from the introduction of an invasive species to test the EICA hypothesis. Our results for *Lespedeza cuneata* showed that the established invasive genotype (North American) was a better competitor than both its ancestral (1930s) and its native (Japanese) counterparts, and that this increased competitive ability coincided with a less costly herbivore defense strategy. However, the

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Table 1. Analysis of variance of the effect of genotype (ancestral, native or invasive), competitor genotype (ancestral, native or invasive), and their interaction on the aboveground biomass of *Lespedeza cuneata*.

- asterisks indicate statistical significance: *p < 0.05; **p < 0.01; ***p < 0.001.
- each competing pair of plants included a treatment plant (the competitor) and a plant of interest (the focal plant).

Figure 1. Aboveground biomass of invasive, native and ancestral *L. cuneata* (y-axis) when grown in competition with a second invasive, native, or ancestral individual (x-axis). Each line represents the mass of the three different genotypes when grown in the three competitor treatments. ANOVA showed a significant interaction between the identity of the focal plant and that of the competitor plant (Table 1). Bars indicate SE.

Figure 2. Relationship between the mass of *H. zea* caterpillars grown on invasive, native and ancestral *L. cuneata* plants and the degree of herbivore damage the plants had previously experienced. The slope of the line represents the degree of inducibility of defenses, as indicated by a reduction in caterpillar mass with increasing levels of damage. The level of constitutive resistance is determined by assessing the size of the caterpillars on the undamaged plants (i.e. the y-intercept); larger sized caterpillars indicate lower levels of constitutive resistance in plants.
limited number of genotypes included in this study limits
the broad application of the results. The inclusion of more
populations from both the invasive and native range would
help to verify whether this is a general pattern for L. cuneata
in North America or a result peculiar to these particular
populations. The rate of evolutionary change in competitive
ability and defense strategy suggested by our results for
L. cuneata is very fast relative to what has, until recently,
been considered typical rates of evolution (Losos et al. 1997,
Reznick et al. 1997, Kinnison et al. 1998). Few studies have
access to ancestral genotypes, which can provide excellent insight
into the evolutionary process (see also Ellner et al. 1999,
Hairston et al. 1999).

To date, there has been mixed support for the EICA
hypothesis; some studies have found evidence of EICA
(Siemann and Rogers 2003, Wolfe et al. 2004, Joshi and
Vrieling 2005, Stastny et al. 2005, Johnson et al. 2007,
et al. 2008) and some have not (Bossdorf et al. 2005, Franks
et al. 2008a). Many early studies did not simultaneously
consider competitive ability and herbivore defense, and/or
did not directly measure competitive ability but focused on
growth rate. In addition, most studies did not consider both
constitutive and induced resistance defenses or did not distingui
sh between these two strategies. Our study highlights
the importance of considering the complexity of herbivore
defenses when examining plant responses to herbivory in the
case of plant invasion. Depending on how the study was
conducted, observed plant responses may be due to constitui
tive resistance or the fact that they have been induced. There
fore, studies that show elevated plant defenses of introduced
species may seem to be inconsistent with EICA, but may in
fact be consistent with its predictions due to the impact of
inducible defenses. Alternatively, the lack of support for
EICA in some studies may reflect an inability of some alien
species to evolve increased competitive ability either due
to an inadequate time period for evolution, weak selection
pressure, or a lack of genetic variation for traits related to
competitive ability that may be especially likely for alien
species established from a few founder individuals. Finally, the
mixed support for the EICA hypothesis might suggest that
other mechanisms besides EICA are important explanations
for the invasiveness of alien plant species.

The finding that invasive genotypes of many invasive spe
cies grow faster and attain a larger size than their native coun
terparts (Leger and Rice 2003, Siemann and Rogers 2003,
2005) has been interpreted as strong support for the EICA
hypothesis. However, it is unclear if this shift to a ‘weeder’
lifestyle is more than coincidental with increased competiti
ve ability (McKenney et al. 2007). Indeed, a recent survey
of the competitive abilities of 14 invasive species found that
the invasive genotypes were generally larger than the native
genotypes only in the absence of competition (Blumenthal and
Hubauer 2007). Because the defining characteristic of an
invasive species is its ability to dominate native habitats and
replace native species, the evolution of increased com
petitive ability might best be examined by comparing the
effects of the native and invasive genotypes on the growth
and survivorship of other plants (Vilà et al. 2003). Exotic
species that have not become invasive may also demonstrate
a shift to rapid, weedy growth patterns. Yet, these species do
not harm the native plant community. Alternatively, a plant
may have extremely detrimental effects on surrounding indi
viduals without displaying faster growth or larger size. This
might be the case for allelopathic plant species or for those
that modify habitats (i.e., soil salinity: El-Ghareeb 1991, or
nitrogen availability: Holmes and Growling 1997).

Here, we have shown that the invasive genotype of L. cuneata
had a detrimental effect on the native and ancestral genotypes
(Fig. 1). As the invasive genotype, which was the best com
petitor, did not have the highest seed mass, genetic differences
in competitive ability rather than differences in maternal resources
most likely explain our experimental results. As members of
the same species, these genotypes likely occupy very similar
niches and the reduced growth of the ancestral genotype when
paired with the invasive genotype is likely due to resource
competition. Though the invasive genotype is not any larger,
it is unaffected by the presence of conspecific competitors.
However, it had a large effect on the biomass of its competitors,
and it is this harm to other plants that is the hallmark of an
invasive species. It is unclear if this same trend would be seen
in competition against interspecific competitors.

We found that the invasive genotype of L. cuneata shifted
from a constitutive to an inducible defense strategy, a pattern
also observed in Alliaria petiolata (Cipollini et al. 2005), one
of the only other studies to have considered both induced
and constitutive defenses in invasive plants. Well-defended,
introduced species like L. cuneata and A. petiolata may be
only rarely attacked by resident herbivores, potentially reduc
ing the necessity for costly constitutive defenses. At the same
time, induced defenses are extremely effective against non
adapted generalists, but may be less effective and possibly
even detrimental when employed against specialists, which
may coopt the costly defensive compounds, thus protecting
themselves from predators and parasites (Kahl et al. 2000,
Baldwin et al. 2001). In the absence of any specialists, as is
the case for both L. cuneata and A. petiolata, there is likely no
additional cost associated with relying on induced defenses.

In addition to being more effective against generalist her
bivores, a theoretical study by Bergelson et al. (2001) sug
gested that herbivores evolve tolerance to induced defenses
much more slowly than to constitutive defenses. Species that
have the genetic variation to alter their investment in consti
tutive and induced defenses, such that they rely on induced
rather than constitutive defenses may be more likely to
become invasive in a new range because the native herbivore
population will be less likely to rapidly evolve tolerance to
their defensive compounds.

Table 2. Analysis of covariance (ANCOVA) of the effect of genotype and
percent plant damage on the individual body mass of Helicoverpa zea
(Noctuidae) caterpillars.

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Asterisks indicate statistical significance: *p < 0.05; ***p < 0.001.
After introduction to a new continent, invasive species typically go through a lag phase, in which they remain present in the new environment, but do not dominate communities and displace native species. This lag phase may represent the early stages of exponential population growth and/or the time necessary for plants to adapt to new environmental conditions (Lee 2002). For many exotic species, the dispersal vector that originally introduced the species to its new range still exists and continuously introduces new genetic material into the population. The increase in genetic variation may allow for more rapid evolution by natural selection and an increased threat of invasiveness. While our results must be interpreted with caution, this research suggests that significant evolution has occurred in this alien plant species, and that evolutionary adaptation may indeed contribute to the lag phase. The unfortunate conservation implication is that introduced species that appear to have little or no damaging effects on native ecosystems may in fact become more aggressive invaders in the future.

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