7

INVASIVE SPECIES

Chapter Outline

An invasive **non-native species** is of concern because it can devastate an ecosystem's structure and function and can cause environmental and economic harm. During invasion **native species** are often outcompeted from their own habitat and even decimated. Invasion of non-native species is considered to be the second greatest cause of serious species decline and extinction only after habitat destruction. Non-native species are also known as aliens, exotics, introduced species, nonindigenous species, immigrants, and exogenous.

A non-native species does not necessarily have to be invasive, but a small proportion of non-native species (about 10%) usually become invasive. A species is called **invasive** if it establishes a rapidly growing population and proliferates in an ecosystem where it was previously not present.

Non-native species are continuously being introduced for different reasons to an ecosystem where they have not lived before. Some are introduced deliberately for horticultural, agricultural, and recreational purposes. In fact, agriculture is based on the practice of introducing non-native crops and livestock into new habitats. This includes non-native species that are introduced for land reclamation and soil conservation (see **Case Studies 7.1 and 7.2** on pages 165 and 169, respectively). Other non-native species (such as rats, mice, dogs, cats, and goats) are brought accidentally or intentionally during expanded human settlements. These introduced species are all notorious in decimating local species. Increased international travel and trade has also resulted in accidental introduction of many species. Today, the increase in international trade is probably the main cause for the unprecedented rate of introduction of non-native species worldwide. One effective transportation of aquatic species worldwide is the release of ballast water from cargo ships. The use of seawater as ballast in cargo ships began in the 1880s. Today, the scale of the transported ballast water is enormous. Big cargo ships can carry more than 60 million liters of ballast water, and more than 45,000 cargo ships move up to 12 billion tons of ballast water around the world each year.

The economical impact of invasive species is enormous and is on the rise. Direct annual economic loss from invasive species is about $1.4 trillion worldwide and $200 billion in the United States. Florida alone spends about $50 million each year just to control invasive plants. Some species are particularly troublesome; for instance, the zebra mussel (*Dreissena polymorpha*) is responsible for fouling vessel hulls and clogging industrial pipelines with an annual control cost of $140 million for the United States and Canada. The invasion of the star thistle (*Centaurea solstitialis*) in the Sacramento Valley, California, has caused annual economical loss of $56 million as a result of a decline in the water supply. It is estimated that the invasion of the salt cedar (*Tamarix* sp.) in the United States has an annual cost of up to $180 million in lost water supplies. In the United States at least 4,500 non-native species are now established, of which 675 species cause severe economic harm. The adverse economic effects of invasive species include direct damage to native commercial species, adverse effects on ecosystem services, and cost of control measures. The total economic impact of invasive species is probably underestimated because this does not include the cost of total eradication or restoration of affected ecosystems. Also, potential cost of species extinction, which could include loss of economic opportunities from native species, is not included. Invasive species have also disrupted critical ecological functions in many ecosystems, and in turn this affects potential economic output provided by these ecosystems. Invasion can also interfere with aesthetic values by creating excessive shade or blocked vision by tall growing non-native vegetation. This in turn can reduce recreational or other values of the ecosystem. Another example of the negative aesthetic impact of invasive species is loud noise from non-native coqui frogs (*Eleutherodactylus coqui*) in Hawaii.

Invasive species pose a challenge for ecosystem restoration. First, control methods are needed to halt and eventually eradicate invasive species, and this must be followed by restoration of native ecosystems. Second, restoration of degraded ecosystems can be implemented to constrain invasion of non-native species. Examples of these strategies (control, eradication, restoration) are provided in this chapter.

7.1 Process of Invasion

Invasion is a complex process that includes several steps, starting with translocation and introduction of a non-native species to a site outside its native range (**Figure 7.1**). The introduction to a new site is followed by a slow initial spread (lag growth) of the non-native species. The lag growth could involve acclimatization of the non-native species. Absence of appropriate symbiotic organisms—such as pollinators, nitrogen-fixing bacteria, or mycorrhizal fungi—can often be a limiting factor for initial population growth. Invasive species are often generalist

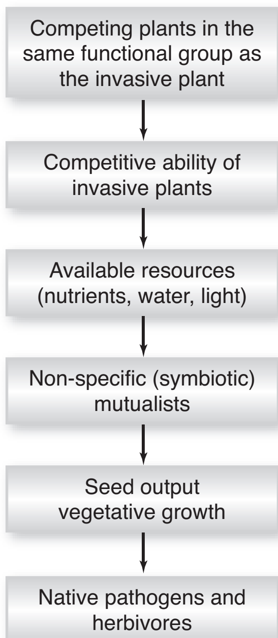

Figure 7.1 Causal relationship between factors and processes may affect invasion of non-native species into plant communities. (Reproduced from *Invasive Alien Species: A New Synthesis (SCOPE 63)*, edited by Harold A. Mooney, Richard N. Mack, Jeffrey A. McNeely, Laurie E. Neville, Peter Johan Schei, and Jeffery K. Waage, copyright SCOPE, Island Press, 2005.)

in their symbiotic relationship and can therefore partner with local symbiotic organisms. Colonization of appropriate pollinators and increased vectors of seed dispersal by local animals of course facilitate further population expansion in the new range. The formation of a population of non-native species that maintains itself (i.e., is not dependent on immigration) is termed naturalization. The establishment of **naturalized** populations is followed by the formation of dense monopopulation and rapid population expansion through invasion. This typically involves competition between native and non-native species. Invasive plant species can outcompete native vegetation, which could result in local extinction of native plants. Eventually, the invasive population may stabilize when it reaches its physiological–geographical boundaries.

Why do invasive species proliferate in their adventive range? The main mechanism behind invasion involves release from natural enemies from their native habitat including predators, herbivores, and pathogens. This has also been called the "release from natural enemies hypothesis." The success of invasive non-native species might depend on the extent of release from pathogens. In support of this hypothesis, plant species brought from Europe to North America have much less fungal and viral infections in their naturalized range than in their native range. Although invasive species have escaped from pathogens in their home range, they typically accumulate fewer pathogens in their adventive range. **Invasiveness** of non-native plants is therefore a function of both escape from enemies in their native range and low pathogen load in their adventive range. Invasiveness of ecosystems is usually measured as the proportion of non-native species to native species in an ecosystem.

Traits of non-native species that promote invasiveness include rapid growth, early maturation, self-pollination, large seed production, effective good (seed) dispersal ability, high seed germination rates, and ability to survive under a wide range of environmental conditions. Strong competitive ability is probably the most important feature of invasive species. The extent of invasion is a function of both the aggressiveness of the non-native species and the vulnerability or invasiveness of the ecosystem in question. Invasiveness of ecosystem depends on degradation factors of such as habitat fragmentation, habitat conversion, eutrophication, and generally increased frequency of natural and/or anthropogenic disturbances.

Ecosystems vary in their susceptibility to invasion. A few ecosystems show abiotic resistance to invasion due to unsuitable environmental conditions. These include exceptionally dry or cold environments found in deserts, tropical dry forests, and arctic ecosystems. On the other hand, islands, lakes, and rivers are particularly susceptible for invasion. Rivers and lakes provide suitable conditions for many species and islands may have high proportion of endemic species.

Ecosystems can also show biotic resistance for invasion. Biotic resistance is expressed as high competitiveness of native species and high resilience of the native community. Biodiversity is another determining factor of biotic resistance that can influence the invasiveness of non-native species. Communities harboring low species richness are usually vulnerable to invasions, especially if no or few species exist in the same functional group as the invasive species. Reducing the number of species in any ecosystem will, therefore, increase the likelihood of invasion.

The magnitude of invasion is determined by the competitiveness of the invading species and rate of invasion. Several factors can influence the rate of plant invasion. The number of introduction points (foci) into the new range and the number of invasive individuals is probably the greatest determining factor of invasion rate. Continuous invasion of the non-native species depends on availability and size of appropriate habitat adjacent to the introduction point.

The rate of invasion is often astounding. A good example of this is the well-documented invasion of the European starling (*Sturnus vulgaris*) into North America. The initial introduction of this bird took place in 1890 when about 120 starlings were released in New York's Central Park during a Shakespearian festival. Starlings are omnivorous, aggressive, and tenacious, which probably makes them successful invaders. They spread quickly to many urban areas and formed large colonies. Today, the European starling is found across America from Mexico to Alaska. The total population size is estimated to be at least 100 million individuals. Some of the largest populations contain a few million individuals.

Starlings often outcompete native bird species for their habitats and are ferocious in food competition. Attempts to eradicate starlings or halt their invasion have so far been unsuccessful. Another example of an aggressive invasive species is the introduction of fire ants (*Solenopsis invicta*) in the southern United States. Fire ants typically outcompete native ants where they invade. Fire ants were accidentally introduced in the 1930s from South America to the port in Mobile, Alabama. They have invaded the southeast United States and are found from North Carolina to Texas.

7.2 Effects of Invasion on Ecosystems

Invasion of non-native species into native communities can affect species composition, especially if a dominant monopopulation is formed. The ecosystem functioning is consequently changed. The impact of the invasion is best demonstrated by examples from islands and peninsulas that harbor high proportions of **endemic** species, but the principle also applies to land-locked ecosystems.

Invasion of non-native species has particularly affected ecosystems on islands and peninsulas. Particularly hard hit in the United States are Hawaii and Florida, where many ecosystems are now dominated by non-native species. For instance, on Hawaii about 80% of plants are non-native and 14% are invasive. Approximately 12% of the native flora of Hawaii is now extinct since European settlement. On Hawaii, about 25% of insects, 40% of birds, and almost all freshwater fishes are invasive. Similarly, in Florida invasive species comprise high proportions of the flora and fauna.

Another good example of the damage of invasive non-native plants on an island ecosystem is that of miconia (*Miconia calvescens*) in French Polynesia. This species not only has changed the structure of forests by dominating the forest canopy but also eliminates native understory species. Miconia is native to the tropical rain forests of Central America, where its natural habitat is typically small clearings in the forest. It colonizes rapidly such clearings that are caused by natural disturbances in the tropical forest. This plant was introduced as an ornamental plant to Tahiti in 1937. Since then it has invaded rapidly and formed dense, monospecific stands, currently covering more than 70% of the island. The thick canopy of miconia prevents the growth of an otherwise diverse understory community.

Introduction of non-native animals can intensify grazing pressure, which consequently affects plant communities. Grazing by non-native animals can have devastating effects on island ecosystems. Grazing degrades vegetation, causes extinctions, and facilitates invasion of non-native plants. For instance, goats were introduced to the tiny island of St. Helena, in the Atlantic Ocean in 1513. These goats have not only changed plant communities but also are responsible for the extinction of more than 50 endemic plants on the island.

Invasive non-native species not only modify structure of plant communities but also affect ecosystem functioning. Invasion of non-native plants can alter the soil chemistry. For example, invasion of the non-native legume *Myrica faya* in Hawaii has increased N inputs 500% to the ecosystem. This high input of N into the native ecosystem has consequently lead to drastic changes in the community composition. Invasive species can induce soil erosion with devastating consequences. The invasion of miconia on Tahiti has increased soil erosion on the island. Miconia has a very shallow root system, which does not anchor the soil on steep hills that are typical for the island. Because of the shallow roots of miconia landslides have increased drastically on Tahiti. Invasive plants can also alter fire regime either by suppressing or increasing frequency of natural fire. Several non-native grass species introduced to Hawaii have increased by 300% the extent of fire in woodlands. Another example is the invasion of cheatgrass (*Bromus tectorum*) into western North America where it dominates more than 40 million hectares and has increased fire frequency by more than 1,000%. Furthermore, grazing pressure by introduced animals has resulted in an alternative ecosystem dominated by pyrogenic grasses. Invasive plants can alter soil's hydrology by increasing drastically evapotranspiration. This can eventually lead to salinization of soils that has adverse effects on the ecosystem. The invasion of the star thistle (*Centaurea solstitialis*) and salt cedar (*Tamarix ramosissima*) in the United States has adversely affected hydrology of local areas.

Invasion can have a direct effect on the genetic make-up (genome) of resident native populations. Hybridization can now be more easily detected by using molecular techniques. Hybridization between native and non-native species is common (see discussion in Chapter 12). This results in changed genetic diversity of the resident population. For example, the native Pecos pupfish (*Cyprinodon pecosensis*) in Texas has hybridized with the invasive sheepshead minnow

(*Cyprinodon variegatus*) to the extent that the original genotype of Pecos pupfish is probably extinct. Hybridization of non-native and native species has even resulted in new invasive species. The American cordgrass (*Spartina foliosa*) formed an aggressive hybrid with the native cordgrass in England (*S. anglica*) that is now invading salt marshes in Europe and the United States.

Invasive non-native species can have devastating effects on native communities by inducing diseases. For instance, in Hawaii non-native birds from Asia are host to avian pox and avian malaria. The diseases are transmitted to native birds and have brought some endemic bird species to the brink of extinction. Another example of such an interaction is the introduced Asian chestnut blight fungus (*Cryphonectria parasitica*) that has virtually devastated every native chestnut tree (*Castanea dentata*) in the eastern United States (**Figure 7.2**). The chestnut used to be the dominant tree of the forest canopy ranging from Georgia to Maine. The chestnut blight was first observed in New York City in 1904 on plants imported from Asia. The spread of this fungal disease was phenomenal, and in less than half a century it spread over more than 91 million hectares of the eastern United States. Consequently, the chestnut was almost brought to extinction. Today, the American chestnut is very rare and is only found in a few isolated places. The fungus had devastating effects on the entire forest ecosystem.

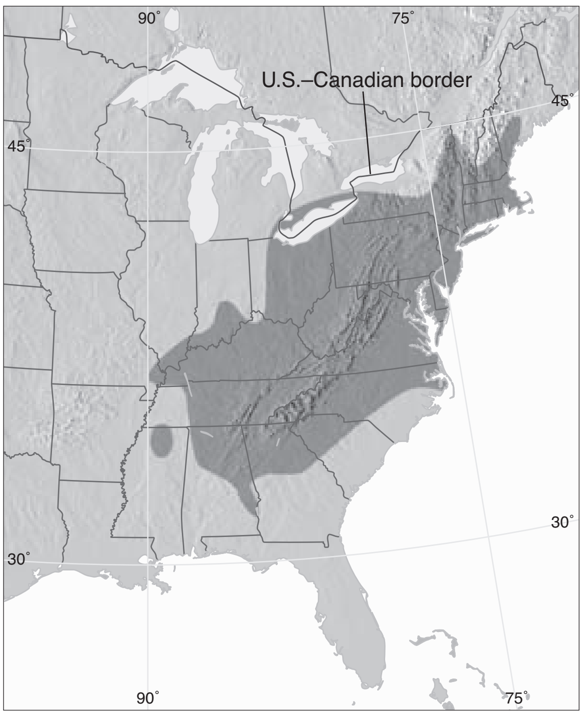

Figure 7.2 Historical distribution of the American chestnut.

Not only were the chestnut trees decimated, but several insect species that live only on the chestnut are now endangered or extinct. Most of its natural habitat is still infected with the chestnut blight, therefore, preventing any restoration efforts by replanting American chestnut back into these infested forests.

Restoration of the American chestnut is in progress using genetic resources of the few populations of the American chestnut that still exist. The crux of this work has involved developing blight-resistant hybrids using traditional breeding techniques in which the disease-resistant Asian chestnut is crossed (hybridized) with the American chestnut. The hybrid is resistant to the chestnut blight. Backcrossing is then completed when Asian-American hybrids are crossed with pure American trees to increase the genome of the American chestnut in the hybrid. The main aim of this work is to transfer blight resistance to the hybrid and then phase out most of the Asian trait of the hybrid. The first chestnut blight-resistant trees saplings are already growing. Seed will be available for large-scale restoration after 5 to 15 years. The hybrid must then be transplanted strategically into forests of its former range. Eventually, mass production in nurseries of the hybrid tree will follow. This project has good potential, but enormous work lies ahead.

Invasive non-native species can also prey directly on native species with disastrous consequences. For example, the introduced Nile perch (*Lates niloticus*) in Lake Victoria is responsible for the extinction of many endemic cichlid fish species (family Cichlidae). Another example is that of the brown tree snake (*Boiga irregularis*), a native to New Guinea and Australia, which was introduced accidentally to the island of Guam. Without natural enemies on Guam the brown snake population multiplied exponentially and caused extensive preying on the island's native birds. Almost 73% of native forest bird species on the island are now extinct.

7.3 Methods of Control

Prevention

Prevention measures against invasive non-native species is the first step to stop them from spreading (**Figure 7.3**). This includes education and public awareness about the damaging effects of invasive species. Also, it is critical to gain public support for a prevention program. Prevention is reinforced by legislation on introduction of invasive non-native species (discussed further in Chapter 14). Preventive measures can focus on the source of introduction. For instance, preventive measures have been implemented to avoid accidental introduction of aquatic organisms. These include ballast-water treatment and on-ship treatment targeting all living organisms in the ballast water. It is important to ensure political support, especially from the public and stakeholders before a preventive program is initiated. Sufficient funding must be secured for preventive programs and also for subsequent monitoring and restoration of native ecosystem.

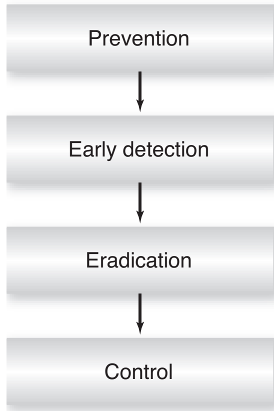

Figure 7.3 Factors to consider in the invasion process of non-native species. (Reproduced from *Invasive Alien Species: A New Synthesis (SCOPE 63)*, edited by Harold A. Mooney, Richard N. Mack, Jeffrey A. McNeely, Laurie E. Neville, Peter Johan Schei, and Jeffery K. Waage, copyright SCOPE, Island Press, 2005.)

It is much more difficult to deal with invasive species once they have established than it is to prevent their arrival. In this respect it is critical to obtain basic biological information on potential invasive species. This includes species introduced for agricultural, horticultural, or recreational purposes. Such information should include details on life cycle and potential vectors of dispersal. Early detection of potentially invasive species is critical for preventing its spread and facilitating its eradication before it becomes unmanageable.

If prevention fails invasive species may represent a challenge for restoration ecologists, especially when eradication is required. Three main strategies are available to deal with invasive species that have already become established (**Figure 7.4**): eradication, containment, and control. Selection of appropriate strategies depends on the extent of the problem and the aggressiveness of the species in question.

Eradication

Eradication involves the elimination of all individuals of an invasive species. Methods of eradication are fairly well established and are used successfully on a large scale in different ecosystems. Monitoring sites that have been eradicated of invasive non-native species should be considered as a part of the eradication program. This should be followed by restoration of native ecosystems.

Flora Methods for the eradication of plants include mechanical methods, which involve removing individuals of the non-native species by using tools (shovel, cutters, or machete) or by using specifically designed machines (mowers,

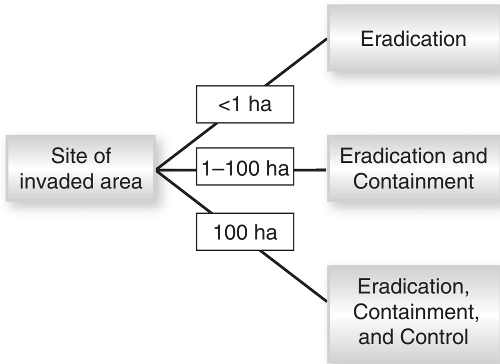

Figure 7.4 Management options to control non-native invasive plants. (Reproduced from *Invasive Alien Species: A New Synthesis (SCOPE 63)*, edited by Harold A. Mooney, Richard N. Mack, Jeffrey A. McNeely, Laurie E. Neville, Peter Johan Schei, and Jeffery K. Waage, copyright SCOPE, Island Press, 2005.)

plows, or harrows). All sites are not easily accessible by machinery and therefore require more labor-intensive methods. Eradicating plants by using hand tools is only practical when dealing with small isolated populations but is impractical if such populations are dispersed within a large area of native plants. Also, pulling of deep-rooted or rhizomatous plants is not practical, and minor soil disturbances could promote further invasion. Notorious invaders that form monospecific stands are typically eradicated by mowing, frequent harrowing, deep plowing, or bulldozing the entire site. Mowing is most effective when applied at a sensitive growth stage, such as just before flowering. Grazing management is another method that can effectively eradicate populations of invasive species. For instance, goats and native bison have been used to reduce kudzu infestation on a small scale in the southern United States.

Valuable experience has been gained in eradication of many agricultural pests. This effort has typically involved different combination of methods such as quarantine, chemical controls, and education. Such strategies can certainly be used in eradication of invasive species. It is critical for successful restoration to select effective combination of methods of eradication for non-native invasive species. Such methods should ideally have minimum impact on native ecosystems and should facilitate restoration of native plants. Successful eradication of invasive plants has been achieved in various ecosystems by using a combination of methods. For example, about 260 hectares of the noxious invasive shrub camelthorn (*Alhagi pseudalhagi*) was eradicated in California by combining eradication methods (herbicides and grazing). Eradication of the notorious French and Scotch broom (*Cytisus monspessulanus* and *C. scoparius*) provide a good example of using combinations of methods. Both broom species are N_2-fixing shrubs that are native to Europe but have invaded North America and formed dense, monospecific stands. The brooms have a strong impact on the structure and function of native ecosystem. Herbicides are typically used to eradicate brooms as they invade forests. Other methods of eradication include more labor-intensive hand pulling, cutting, and prescribed burning. Brooms are also cut using heavy machinery (a tractor or bulldozer); however, plants may resprout and therefore repeated cutting is required. Cutting is typically applied on extensive stands where burning is not possible due to close vicinity to residences. Hand pulling is labor intensive and cutting is not as effective. All these methods are, however, effective at reducing cover of broom. It is important to repeat these methods, however, because the brooms have large seed bank in the soil and can resprout after minor soil disturbances. Combining methods was especially effective in eradicating the brooms. Cutting broom in summer and burning it in the fall is a promising method of control. After initial eradication, sites are typically burned repeatedly to remove new broom seedlings. Frequent fires are, however, counter-effective because they can promote invasion by other non-native species. Close monitoring for the emergence of the brooms is, therefore, essential. Repeated burning and pulling of the brooms are, however, effective methods in promoting passive restoration of native plants.

Another approach is "integrated pest management," which involves a combination of control methods selected for a particular invasive problem. This approach often provides the most effective and acceptable control measures. Combining methods of eradication must be carefully selected and tested in small scale trials for each target invasive species before being implemented on a large scale.

Fauna Eradication of invasive vertebrates involves direct hunting and use of bait stations with toxic chemicals. Eradication of invasive freshwater fish species involves the use of toxins specific to fish, for instance, lampricide was successfully used against the sea lamprey in the Great Lakes. Invasive insects are usually eradicated by the use of insecticides or biopesticides. In small contained areas, baits or traps are used. However, widespread application is needed if the target insect is invading rapidly. The mass release of sterile male flies referred to as the "sterile insect technique" is effectively used against insect outbreaks affecting agricultural production such as screwworm fly *(Cochliomyia hominivorax)* and Mediterranean fruit fly (*Ceratitis capitata*). Use of the sterile insect technique may, however, be prohibitively expensive in small-scale restoration projects.

Not all eradication programs have been successful. For example, the attempt to eradicate the introduced fire ant from the southern United States has so far been unsuccessful. If the fire ants could be totally eliminated, the native ants would recolonize affected sites. The initial chemical control (using heptachlor) in 1957 resulted in deaths of wild animals and livestock. This was followed by a large-scale application of another chemical in baits (mirex), but the fire ant rapidly reinvaded areas from which it had once been eliminated. Moreover, mirex residues were discovered in other nontarget organisms and its use was soon terminated. Meanwhile, the fire ants have advanced their invasion dramatically.

Containment

Containment measures aim at restricting the invasion of non-native species to certain well-defined areas. The invasion of non-native species is restricted by using methods of eradication described above around populations of the non-native species. Any non-native species invading out of this defined area should ideally be eradicated. Monitoring the invasive species is important in this respect because the target invasive species might exist in small interconnected populations. In such cases an effective strategy is to disrupt small interconnected populations of invasive species.

Chemical and Biological Control

Control measures are implemented if eradication does not work. The invasive species is controlled to contain a certain level of economic and/or ecological damage. Methods of control are often the same as those previously described for eradication programs. Chemical control, especially insecticides and herbicides or toxic baits for animals, are widely used for this purpose. Chemical control (herbicide) on plants is often used in conjunction with other mechanical methods (mowing or cutting). The success of control measures such as herbicide application is much greater if followed by restoration efforts. Applications of herbicides are most effective when chemicals are translocated to underground tissues. Therefore, timing of herbicide application is critical to coincide with movement of carbohydrates to plants' underground storage tissues. This usually takes place during late summer to early fall. Herbicides are used directly (spot spraying) on targeted non-native species or by spraying it over large monopopulations of invasive species. The former method is more agreeable as the latter might affect other species than invasive organisms. Spot-spraying plants is ideal for small infestation and is accomplished by trained labor. Large-scale spraying is accomplished, for instance, by using crop dusters (small aircraft). One drawback of relying on chemical control is that repeated application is usually required. Also, the high cost of chemical control might be prohibitive. The environmental impact of chemical control is discussed in Chapter 10.

Biological control (biocontrol) is traditionally achieved by the introduction of natural enemies into invaded sites from the original range of the invasive species in question. Benefits from biological control programs in the United States are estimated to exceed $180 million annually. Some environmental risks (release of pests), however, are associated with this method. Leafy spurge (*Euphorbia esula*) is a non-native species that has invaded more than 2 million hectares in United States and Canada. Programs aiming at biological control of leafy spurge in the United States were initiated in the 1960s, and today

15 non-native insect species are used for this purpose. These insects limit growth of leafy spurge by consuming foliage, roots, and seed. Biological control can effectively reduce leafy spurge stem densities by as much as 90% over large areas.

Control of invasive non-native animal species can potentially be achieved by building up populations of native predators. Nevertheless, controlling invasion of non-native animals can be viewed as a step toward total eradication and eventual ecosystem restoration.

7.4 Restoration to Constrain Invasion

Restoring ecosystems to their full potential can be used as a strategy to control invasive species.

Niche Preemption

Niche preemption is the main principle behind restoration efforts that aim at reducing the impact of invasion. This approach establishes native species in the same functional group as the invasive species in question. This approach is also called "integrated restoration management." A good example is derived from studies on a notorious perennial tussock grass (*Agropyron cristatum*) that was introduced to the northern Great Plains of the United States after the 1930s. Today, this grass dominates about 17 million hectares of semiarid lands. Invaded stands of *A. cristatum* typically show reduced biodiversity, and the soil chemistry is also altered. Soil below *A. cristatum* stands has lower levels of available nitrogen and about 25% less total carbon than native prairie soil. This grass forms monospecific stands, some of which have lasted for more than a half century and therefore represent an alternative ecosystem state. The potential of using ecological restoration as a strategy to control this invasive grass was tested in an old field in the Grasslands National Park, Saskatchewan, Canada. The intensity of invasion of *A. cristatum* was compared between non-restored abandoned grassfield and restored prairie grasslands. Restoration was accomplished by broadcasting seed of native prairie grasses in the same functional group as *A. cristatum*. This effort reduced the invasion of *A. cristatum* by one-third. Furthermore, restoration practices could perhaps be improved by determining the optimal density of species in native functional groups and implementing eradication of the invasive species before large-scale restoration.

Niche preemption also includes restoration efforts after eradication of non-native species. After the invasive species is eradicated, restoration of the site by native species is essential to avoid reinvasion. Eradication of the invasive salt cedar in New Mexico by mechanical and chemical methods is most successful when this effort is followed by restoration of native trees such as cottonwood and black willows.

When eradication of invasive species is followed by restoration of native species, the prevalence of invasive species is usually reduced. For instance, in the Great Smoky Mountains National Parks, populations of non-native pasture plants are gradually being eradicated. For this purpose an integrated restoration management involving herbicide treatment, prescribed burning, and seeding native plants has effectively decreased the abundance of several non-native species. At the same time abundance of several native species that were previously not found in these pastures has increased. Eradication of invasive plants must therefore be followed by restoration of native species as quickly as possible to fill the empty niche and prevent the re-invasion of any invasive species.

In another example, the effect of eradication on invasive species for 1 year without any restoration was compared with repeated eradication efforts over 5 years followed by active restoration. This study took place in invaded forests in Ontario, Canada, dominated by sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*). Different methods of eradication such as application of glyphosate (herbicide), hand pulling, cutting inflorescence, and adding a thick layer of mulch were tested on monopopulations of invasive understory species. These methods of eradication were tested once or repeated over 5 years followed by restoration efforts. The invasive species were garlic mustard (*Alliaria petiolata*), dame's rocket (*Hesperis matronalis*), and celandine (*Chelidonium majus*). Restoration efforts involved planting mature plants of the following native species: trout lily (*Erythronium americanum*), sharp-lobed hepatica (*Hepatica acutiloba*), mayapple (*Podophyllum peltatum*), and bloodroot (*Sanguinaria canadensis*) at a density of two shoots per square meter. The one-time use of glyphosate and hand pulling had adverse effects; the population of the invasive plants increased. The cutting and adding a mulch layer was also ineffective in eradicating the invasive species, but at least their populations did not increase. The repeated control efforts over 5 years followed by restoration effort were, however, effective in reducing the population of the invasive species and also by increasing the abundance of native plants. This example demonstrates that incomplete eradication without any restoration efforts can make matters worse. Also, long-term commitment is necessary in eradicating invasive species that should be followed by restoring native ecosystems.

Fire Management

Fire management, including fire suppression or prescribed burning, is used as a tool in restoration of invaded sites. Increasing the frequency of fire can intensify invasion. Curbing induced disturbances such as fire is often necessary to eliminate invasion of non-native species. For instance, an African grass jaragua (*Hyparrhenia rufa*) was deliberately introduced during the past century into pastures in Central America to improve cattle pastures. This grass can build up dense and tall (up to 2 m) stands. The grass litter is pyrogenic during the dry season, and frequent outbreaks of fire maintained this grass after cattle grazing was abandoned in what is now part of the national park system in Costa Rica. Fire is not a natural component of these forests and fire constrained restoration of native forest. It was, however, noticed that by suppressing fire outbreaks forest species began to recolonize the pasture and gradually outcompeted the shade-sensitive jaragua grass. It may, however, take the next half-century before an abandoned pasture is recolonized by the intact tropical dry forest species. On the other hand, prescribed burning is used effectively to eradicate invasive plants. Prescribed burning is most effective just before flowering of the invasive plant. Prescribed burning is commonly used in the United States to manage invasive species such as the Australian pine (*Casuarina equisetifolia*).

Increasing Biotic and Abiotic Resistance

It is assumed that restoring degraded ecosystems will reduce the risk of invasion. A degraded ecosystem is generally more prone to invasion because invasive species are usually preadapted to disturbed habitats. It follows then that degraded ecosystems have generally higher proportion of invasive species than less degraded or pristine ecosystems. Studies in the United Kingdom have shown that the proportion of non-native plants increases with degradation of the ecosystem. Restoration of invaded sites should focus on increasing biotic and abiotic resistance of the degraded ecosystem. Biotic factors such as the thickness of a forest canopy usually affect composition and density of understory species and is a strong determining factor for the forest's vulnerability to invasive species. In this case the shade of the canopy represents biotic resistance of the ecosystem. Invasive non-native understory species that are adapted to disturbed, open habitats are typically shade intolerant and can therefore be curtailed by restoring a thick canopy of native trees. The density of the canopy of native trees is one of the most important factors in determining an ecosystem's invasibility. An alternative method of eliminating the jaragua grass mentioned above from abandoned tropical pastures is, therefore, to out-shade it by planting dense stands of gmelina (*Gmelina arborea*), a fast growing non-native tree. A dense canopy is formed in about a year and the jaragua grass is eliminated (out-shaded) from the pastures in 3 to 5 years. The gmelina promotes recolonization of native understory species. The gmelina is typically cut down after 6 to 8 years, and this facilitates establishment of the rain forest. This method of using rapidly growing commercial trees as nurse plants is a powerful restoration tool that is commonly used for restoration of abandoned tropical pastures.

Ecological restoration places emphasis on **biotic resistance** as a strategy to slow down or inhibit invasion. Non-native invasive species interact with native species, pathogens, and herbivores that can potentially limit their impact on the ecosystem. Native pathogens may sometime reduce the invasiveness of non-native species. Communities containing high species diversity will most likely harbor high diversity of pathogens. Such assemblages of native pathogens will probably with time increase the pathogen load of the invasive species, which will in turn possibly reduce their invasiveness. Increasing biotic resistance therefore reduces an ecosystem's invasibility.

Summary

Problems associated with invasive non-native species are on the rise. This is in part due to increased long-distance dispersal vectors that did not exist before and also due to increased degradation of native ecosystems. Notorious invading species can permanently alter the structure of an ecosystem by forming monospecific stands. Invasive species also alter ecosystem function such as nutrient cycling, hydrology, and fire regime. It is important to identify potential invasive species before they spread into native ecosystems because eradication is in some cases prohibitively expensive. Eradication of invasive species is possible using a variety of mechanical and chemical methods. Integrated restoration management involves using combination of methods to eradicate invasive species. This work must be followed by restoration of native ecosystem to prevent re-invasion. Native ecosystems can show resistance (biotic or abiotic) to invasive species. Biotic resistance might not only be affected by species richness of the native ecosystem but also by the presence of native species belonging to the same functional group as the invasive species. Restoration of degraded ecosystems can also be used as a strategy to halt invasion of non-native species.

7.1 Case Study

Kudzu—The Notorious Invader of Southern United States

Patricia Kinney, Georgia Power, Savannah, GA

In a less-than-affectionate term, kudzu (*Pueraria montana*) is often referred to as "the vine that ate the South." In its native Asia, kudzu was used to make food, medicine, and paper for thousands of years. Kudzu was introduced to the United States in 1876 at the Philadelphia Centennial Exposition and appeared at the New Orleans Exposition in 1883. It quickly became a popular ornamental among southern gardeners, gracing porches with its sweet-smelling purple flowers. During the early 1900s kudzu seeds and root crowns were commonly available in mail-order catalogs. Farmer C.E. Pleas of Florida operated one such mail-order catalog, marketing kudzu as nutritious, high-protein forage for livestock. The U.S. government also played a significant role in the spread of kudzu. Historically, the South had an agrarian economy, and many years of intensive crop production and inappropriate agricultural techniques left poor, eroded soils. To combat soil erosion the U.S. government created the Soil Erosion Service, which subsequently encouraged farmers to plant kudzu to stabilize the soil. From the 1930s to 1940s the Soil Erosion Service distributed approximately 85 million kudzu seedlings to farmers, paying them $19.75 per hectare planted. Concurrently, the Civilian Conservation Corps planted kudzu to control erosion on slopes, roadsides, and public lands. Altogether, more than 1.2 million hectares of kudzu was planted through government programs.

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Case Study (*continued*)

As farming became less profitable, people moved from rural to urban areas, leaving fields of kudzu unattended. Kudzu rapidly became widespread in the Southeast, and by 1953 the government stopped advocating its use. The U.S. Department of Agriculture (USDA) declared kudzu a weed in 1972, and it was placed on the Federal Noxious Weed List in 1997. Although most prevalent in Georgia, Alabama, and Mississippi, kudzu's current range extends from Florida to New York and west to Texas. Kudzu now blankets more than 3 million hectares in the Southeast and is spreading at an alarming rate (**Figure 7.5**).

Because of kudzu's rapid vegetative growth and ability to outcompete native plants, it is classified as an invasive species in the Southeast. Invasive plant species display certain growth characteristics that facilitate their spread, and kudzu is no exception. Taking advantage of warm temperatures and plentiful rainfall, kudzu can grow up to 0.1 m per day or 20 m per year. Kudzu spreads primarily through runners,

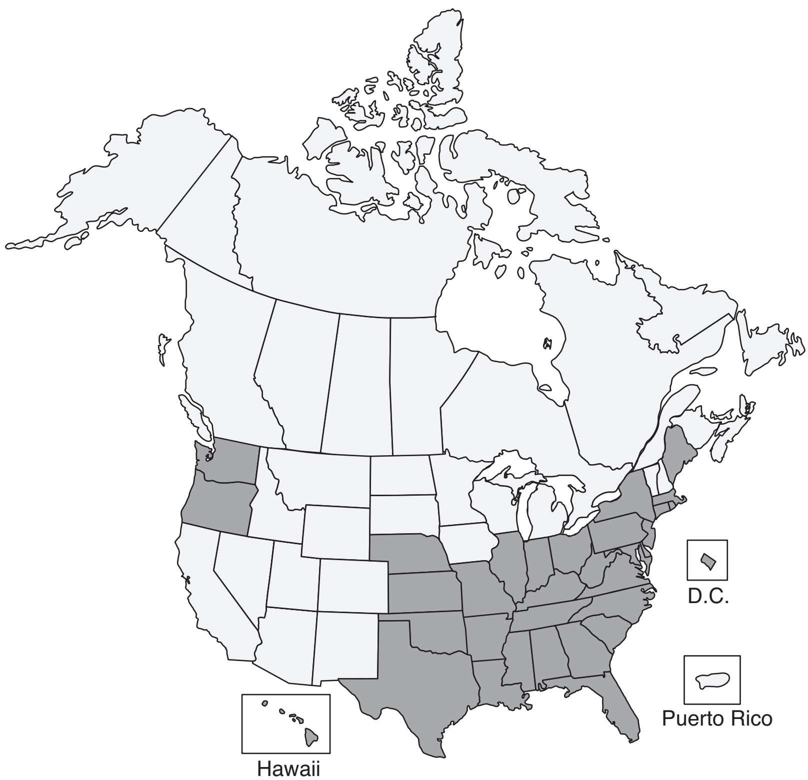

Figure 7.5 Kudzu distribution in North America. (Reproduced from USDA/NRCS. *The PLANTS Database*. Baton Rouge: National Plant Data Center, LA, March 30, 2010 [http://plants.usda.gov].)

rhizomes, and new plants that root at vine nodes. Kudzu also produces a limited amount of seed, with flowers forming mainly on hanging vines in sunlit areas. However, anecdotal evidence suggests that kudzu may be producing more seeds as it adapts to its new environment. Kudzu's rapid vine growth is supported by carbohydrate stores in massive taproots that can weigh up to 180 kg and reach depths of 3 m. Up to 30 vines can stem from one root crown, and individual vines can extend for 33 m. These vines can wreak havoc on native ecosystems, shading the forest floor and reducing biodiversity.

Kudzu damages natural ecosystems by literally smothering native vegetation (**Figure 7.6**). It limits the space, water, sunlight, and nutrients available to native species. Young trees and shrubs are killed by girdling as vines wrap tightly around them. Kudzu easily tops tall pine trees, where its intertwining vines form thick canopies that prevent sunlight from reaching the forest floor. Mature trees eventually die from shading or are uprooted by the weight of the vines, while understory vegetation struggles unsuccessfully to survive in shady conditions. Many native animals and insects also are negatively affected as kudzu displaces native forage and habitat. A common hypothesis to explain the success of invasive plants suggests that exotic species flourish in their new homes because of the absence of their natural enemies, including herbivores, insects, parasites, and bacterial and fungal diseases. But like other invasive non-native plant species, kudzu also may take advantage of mutualistic relationships to enhance its invasive ability.

Kudzu's prolific vegetative growth requires large amounts of macronutrients (nitrogen and phosphorus), and its ability to acquire these nutrients, even in poor environments, makes kudzu a successful invader. Many exotic plant species form symbiotic relationships with soil microorganisms to establish, and this symbiosis with local soil microbes can

Figure 7.6 Kudzu invading a native forest and forming a dense thicket. (© Danny E. Hooks/ShutterStock, Inc.)

(continued)

Case Study (*continued*)

facilitate successful invasions. In general, if the exotic plant's new habitat contains indigenous species that are taxonomically related to the exotic one, then the soil may likely contain suitable symbiotic partners. Studies have shown that invasive legumes obtain nutritional benefits from interactions with *Rhizobia* bacteria and mycorrhizal fungi.

Rhizobia are nitrogen-fixing bacteria that form nodules on the roots of legumes such as kudzu. In exchange for fixing atmospheric nitrogen for the plant, *Rhizobia* receive carbon from the plant. The diverse strains of *Rhizobia* species actually have varying effects on plant growth. Although some legumes can partner with only a few rhizobial genotypes, other legumes can form a beneficial symbiosis with a wide range of rhizobial strains. It is likely that the ability of kudzu to be a successful invader may depend on its ability to form symbiotic associations with a wide variety of *Rhizobia* species.

Invasive plants also form symbiotic relationships with arbuscular mycorrhizal fungi (AMF), which facilitate phosphorus (P) uptake and plant growth. Although AMF can associate with a wide variety of plants from various geographical regions, the magnitude of the response in plant nutrition depends on the specific combination of plant and fungus genotypes. The success of kudzu may depend on its ability to form effective symbiotic relationships with resident AMF populations of native ecosystems. In actuality, kudzu's distinct advantage may be attributed to the tripartite *Rhizobia*–AMF–plant symbiosis.

Aside from being a scientifically daunting task, controlling kudzu also presents an economic challenge. The forest industry, utility companies, farmers, and state and federal parks are all impacted by the cost of controlling kudzu. Dr. Coleman Dangerfield of the University of Georgia estimates a cost of $500 per ha per year over 5 years to control kudzu on forest land, which is apparently higher in value than the lumber. According to Dr. James Miller of the USDA Forest Service, power companies alone spend over $1.5 million per year repairing damage caused by kudzu. Because kudzu poses such a significant threat to native ecosystems and industry, drastic measures must be taken to control and eradicate it. Current control methods involve mechanical, chemical, and biological options.

Impractical on a large scale, mechanical methods involve mowing or cutting vines and destroying the cuttings. Mowing must be repeated multiple times over several years to exhaust the roots' carbohydrate stores. Prescribed burning is another mechanical method that can be used in combination with chemical methods. Burning can allow easier access to heavily infested areas, making chemical application simpler and more effective.

Chemical control methods usually involve the use of herbicides, which kills both foliage and roots. Picloram is highly effective at controlling kudzu when applied from July to October. Other options include metsulfuron methyl, clopyralid, and triclopyr. Although successful, herbicides must be used with extreme caution, because they can damage nontarget species and persist in the soil. Choosing the most appropriate herbicide to use depends on factors such as the age and density of the infestation, the proximity of nontarget species, and physical features of the area such as slopes and streams. Repeated applications over several years are necessary for the complete eradication of kudzu.

Perhaps the oldest natural biological control of kudzu is overgrazing. Livestock will happily graze on kudzu, which is high in protein. Three to 4 years of continuous grazing is usually enough to exhaust root stores and eliminate a kudzu stand. Several introduced biological controls are also being investigated. *Pseudomonas syringae* pv. *phaseolicola,* a bacterial pathogen native to the United States, has been shown to kill kudzu seedlings by causing halo blight. Unfortunately, established kudzu can quickly recover from any damage. Another possibility is *Myrothecium verrucaria* (Albertini and Schwein) Ditmar: Fr., a fungal pathogen isolated from sicklepod (*Senna obtusifolia* [L.] Irwin and Barneby). This fungus attacks kudzu's leaves and stems, acting as a bioherbicide. Field tests showed that when *M. verrucaria* was applied with a surfactant, near total control of a kudzu stand could be achieved in 2 weeks. In fact, *M. verrucaria* proved so successful at kudzu control that USDA scientists Clyde Boyette, Harrell Walker, and Hamed Abbas were issued a patent in 2001. One possible obstacle to its use is the fungus' production of mycotoxins, which are toxic to mammals. However, less toxic strains are currently being developed. Controlling kudzu is difficult at best, but the success of native ecosystems in the South depends on it.

7.2 Case Study

Pale Swallow-Wort: An Emerging Threat to Natural and Seminatural Habitats in the Lower Great Lakes Basin of North America

Dr. Antonio DiTommaso, Department of Crop and Soil Sciences, Cornell University, Ithaca, NY

The invasive perennial vine *Vincetoxicum rossicum* (Kleopow) Barbar. [syn. *Cynanchum rossicum* (Kleopow) Borhidi] (pale swallow-wort or dog-strangling vine) has become a major concern in natural and seminatural areas of central New York State and the Lower Great Lakes Basin of North America within the last 15 to 20 years. This herbaceous vine was introduced into North America from the Ukraine region of Eastern Europe approximately 120 years ago and is currently expanding its range at an astounding rate. In its native range, pale swallow-wort can be found in forest-steppe and steppe zones where it is relatively uncommon. This species was first collected in North America near Toronto, Ontario, Canada, in 1889 and in the northeastern United States in New York State in 1897. It is now distributed from the Atlantic coast west to southern Michigan and northern Indiana and from southern Ontario, Canada, south through southern Pennsylvania (**Figure 7.7**).

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Case Study (*continued*)

Figure 7.7 Pale swallow-wort distribution in North America. (Reproduced from USDA/NRCS. *The PLANTS Database*. Baton Rouge: National Plant Data Center, LA, March 30, 2010 [http://plants.usda.gov].)

This member of the periwinkle family (Apocynaceae) has demonstrated the ability to form dominant, monospecific populations in many upland habitats and readily adapts to a wide range of light and moisture conditions, from full sun in open sites to full shade in mature forest understories. This related species to the milkweeds typically invades disturbed sites and exhibits aggressive growth on lime-derived soils, which are particularly vulnerable to invasion. Anecdotal evidence from private landowners in affected areas suggests that this destructive species can infest new areas over a relatively short period of time once it becomes established (i.e., 3–5 years).

Impact in Its Introduced Environment

Pale swallow-wort is of concern to managers of natural and seminatural lands throughout its range. The species threatens several of New York State's unique or rare ecosystems. For instance, its displacement of the nearly 5,000 ha of globally rare alvar habitats (i.e., shallow limestone barrens) of Jefferson County, New York, threatens 54 rare species of plants, insects, birds, and land snails (**Table 7.1**). Pale swallow-wort is also invading habitats in Onondaga County, New York, where the U.S. federally listed hart's tongue fern, *Phyllitis scolopendrium* var. *americana* occurs. In Connectictut, pale swallow-wort is overgrowing the only New England population of *Asclepias viridiflora*,

Table 7.1 Some of the Rare Species Expected to Benefit from the Management of Pale Swallow-Wort in the Lower Great Lakes Basin

Species/Community	Common Name	Federal or NYS Protected Status
Rare animals		
Lanius ludovicianus migrans	Migratory loggerhead shrike	E
Asio flammeus	Short-eared owl	E
Spizella pallida	Clay-colored sparrow	
Circus cyaneus	Northern harrier	T
Bartramia longicauda	Upland sandpiper	T
Ammodramus henslowii	Henslow's sparrow	T
Rare vascular plants		
Aster ciliolatus	Aster	E
Bouteloua curtipendula	Side-oats grama	E
Ceanothus herbaceous	Prairie redroot	E
Carex garberi	Elk sedge	E
Carex nigromarginata	Black-edge sedge	E
Castilleja coccinea	Indian paintbrush	E
Dracocephalum parviflorum	American dragonhead	E
Epilobium hornemannii	Alpine willow-herb	E
Lilium michiganense	Michigan lily	E
Sphenopholis obtusata var. *obtusata*	Prairie wedgegrass	E
Carex molesta	Troublesome sedge	T
Cypripedium arietinum	Ram's head lady's slipper	T
Carex backii	Rocky mountain sedge	T
Carex crawei	Crawe sedge	T
Corydalis aurea	Golden corydalis	T
Draba reptans	Carolina whitlow-grass	T
Geranium carolinianum var. *sphaerospermum*	Carolina cranebill	T
Geum triflorum	Prairie smoke	T
Hedeoma hispidum	Mock-pennyroyal	T
Panicum flexile	Panic grass	T
Sporobolus heterolepis	Prairie dropseed	T
Stellaria longipes	Starwort	T
Zigadenus elegans sp. *glaucus*	White camas	T

E, endangered; NYS, New York State; T, threatened. Used with permission of Sandra Bonanno and the Nature Conservancy (http://www.nature.org/).

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Case Study (*continued*)

a listed endangered species in Connecticut. The resultant loss of native plant species may reduce biodiversity and delay or redirect succession as well as reduce the value of croplands or wildlife habitats. Many Christmas tree growers and nurseries in affected areas report increased pressure by pale swallow-wort, especially during the past decade. This climbing vine not only competes effectively with favorable species for essential resources such as light and nutrients, but it also makes the plants more susceptible to uprooting and damage during strong winds. Some landowners in New York State have gone as far as abandoning horse pastures after 5 to 10 years of unsuccessful control efforts against pale swallow-wort. Old field locations in Ontario, Canada, colonized by pale swallow-wort have been shown to have much lower arthropod diversity compared with old field locations that have intact native vegetation. Research has also demonstrated that this invasive species may negatively impact reproduction in Monarch butterflies (*Danaus plexippus*) by attracting some ovipositing female butterflies to lay their eggs on this introduced species, but the immature stages of the butterfly are unable to survive on this plant. An added threat of pale swallow-wort to Monarchs is that this invasive may be outcompeting and displacing the native common milkweed (*Ascelpias syriaca*), the natural food host of this butterfly in many old field habitats where the two species co-occur. Pale swallow-wort also has the ability to form symbiotic associations with resident AMF in invaded soils and can alter the composition of AMF populations after colonization, therefore, likely limiting the growth and persistence of other species, including native plants.

Biology

Pale swallow-wort is a twining herbaceous perennial vine that grows 1 to 2 m in height, often in one season. In New York State, flowering begins in late May, peaks in mid-June, and ends in mid-July (**Figure 7.8**). The fruit pods (follicles) release seeds from mid-August to early October. Pale swallow-wort reproduces primarily via seeds, each bearing a coma of silky hairs, which facilitates long-distance wind and animal dispersal. This species may also expand clonally from tillers produced in the root crown, but range expansion appears to occur chiefly by seed production. Seeds are often polyembryonic, a condition in which some seeds give rise to multiple seedlings (up to eight). Polyembryonic seeds are more likely to develop into successfully established seedlings than non-polyembryonic seeds and may present an advantage to pale swallow-wort invasion by facilitating the establishment of new populations from a single seed. In some heavily infested sites of central New York State, seedling densities can be as high as 64,000 seedlings m^{-2}. Pale swallow-wort seeds typically germinate in the spring after production and generally persist in soil for less than 3 to 4 years. Seeds germinate and have high emergence rates (>50%) when buried at soil depths of less than 2 cm or when located on the soil surface. Depending on the level of embryony, pale swallow-wort seedlings have extremely high survivorship (71–100%) relative to most other plant species. This feature may partly be responsible for the high establishment rates and rapid expansion of this species in its introduced range in North America.

Figure 7.8 Pale swallow-wort flowers. (Courtesy of Antonio DiTommaso, Cornell University.)

Another characteristic of this invasive vine that may facilitate its establishment and range expansion is the production of a large and extensive below-ground root system.

Management Tactics

Control of this highly aggressive invasive vine using currently available methods has been difficult, and no single strategy has emerged as most promising. Presently, the control of pale swallow-wort in natural areas is best accomplished through the use of herbicides such as triclopyr. Despite the initial success of herbicide use, follow-up treatments are required to control the plant because of newly emerging seedlings from the seed bank. Thus, the duration and cost of subsequent control efforts largely depends on the size of the seed bank and on the longevity of the seed in soil or near the soil surface. Moreover, the success of restoration efforts within both managed and unmanaged areas will also be influenced by the quantity and type of plants found in the seed bank. Cultural controls have had limited impact upon further establishment or control of pale swallow-wort infestations. Repeated mowing can provide some reduction in plant height but has little impact on overall cover of pale swallow-wort. Cultivation will likely not kill established plants because root crown pieces remaining after cultivation can reroot, even under dry soil conditions.

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Case Study (*continued*)

Grazing and trampling can stimulate sprouting in pale swallow-wort, from leaf axes of stems or from root crown buds. Manual removal of follicles from established plants may also assist in prevention of further seed dissemination, but multiple harvests may be necessary. Pale swallow-wort has few natural enemies in its introduced North American range and has limited impact on its growth and reproductive potential. However, the fact that this species occurs infrequently or sparse in its native range suggests that natural enemies in its native range may be limiting its growth and distribution. Biological control of this invasive vine using effective and host-specific natural enemies collected in its native range may, therefore, provide the best prospect for sustainable long-term management of pale swallow-wort in North America and aid in restoration of affected habitats (**Figure 7.9**).

Figure 7.9 Dr. DiTommaso in pale swallow-wort–infested central New York State site. (Courtesy of Antonio DiTommaso, Cornell University.)

Key Terms

Biological control 161
Biotic resistant 164
Containment 161
Endemic 154
Eradication 158
Invasive species 150
Invasiveness 153
Native species 150
Naturalized 153
Niche preemption 162
Non-native species 150
Preventive measures 157

Key Questions

1. Describe the steps in the invasion of non-native species.
2. What are the main factors behind the rapid growth of invasive non-native species?
3. What are the main effects of invasive non-native species on ecosystem function?
4. What preventive measures can be taken against non-native species?
5. List methods of eradication.
6. What is integrated restoration management.
7. How can restoration of degraded ecosystems inhibit invasive non-native species?

Further Reading

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