Ecological Characteristics of Invasive Alien Plants

John H. Brock

ABSTRACT

An influx of alien plant material to the North American flora accompanied the settlement of the continent by immigrant peoples during the latter part of the 19th century. Plant materials were introduced as ornamentals, agronomic crops, land conservation material, and many were accidentally introduced as contaminants in seeds of desirable plants such as small grain crops. In the early 20th century introductions continued as people wanted to improve on the natural vegetation, and have plants that seemed to be better adapted to habitats than were components of the native flora. Several of these well-intended introductions are now considered as invasive. This paper presents information about some of the general characteristics of invasive plants including: pollination strategies, regeneration strategies, seed and propagule dispersal, formation of ecotypes, the lag time from introduction until the plant is termed invasive, and some aspects of the physiology of invasive plants. Many alien plants have naturalized to the environment of North America, and are so widespread that vegetation management strategies to control the whole population are probably not feasible. However, strategies to control the further invasion by the alien species are needed and will most likely incorporate integrated weed management techniques that are socially and politically acceptable.

INTRODUCTION

When taking a global view, there is a question among plant ecologists if a species is ever truly an “alien”. However, in studying invasion ecology, an introduced species of a flora must be treated as alien to an ecosystem because it would not be there without human intervention (Pysek 1995). Some alien plants grow only for one season and fail to establish and these are termed “accidentals” if included in a floristic survey. Some of the alien plants establish but are very passive in their new ecosystem, while others adapt with a broad ecological amplitude and invade man-made and natural areas. When native plants widen their historic range the term expanding is suggested, and when an alien plant is becoming more common on the landscape the term invasive is more appropriate (Pysek 1995). Where and under what circumstances alien plant species are likely to attain a weed status has emerged as a central question for those studying plant ecology.

1. Environmental Resources Department, School of Planning and Landscape Architecture, Arizona State University, Tempe, AZ
Alien invasive plants have been a concern to land managers in the western United States for the past 100 years. The largest immigration of alien plant species to the United States accompanied the "taming-of-the-west" from about 1870 through 1900. Alien invasive plants are also a global concern, since plant materials have been relatively freely exchanged between varying ecosystems and the continents. In many cases the alien plants have provided many benefits to mankind, but some of the plants have displayed an invasive nature which has created management problems.

Alien invasive plants often have ecological characteristics that allow them to be colonizers on disturbed sites, and in some cases are truly invasive, by literally invading existing stands of native vegetation. Through direct competition they become dominant plants in the habitat. Many alien invasive plants are classed as weeds, or as colonizers, that is, they are often plants found in the pioneering stages of succession (Rejmanek 1995). There is another class of alien plants that while not particularly invasive, alter the environment in undesirable ways. Lesica and DeLuca (1996) discuss a plant of this nature, which is probably the most commonly planted exotic grass in western North America, *Agropyron cristatum*, *A. desertorum* (crested wheatgrass). *A. cristatum* is a strong competitor that modifies soil resources to the disadvantage of native species limiting their recruitment and establishment in mature stands of this exotic grass (Lesica and DeLuca 1996).

The receptor area where alien plants colonize has often undergone some type of disturbance that has allowed open niches or spaces in the community. The type of disturbances are mostly man induced, but variations in weather patterns, natural fire frequencies, and flooding can result in receptive areas for alien plants to become established. Man-induced disturbances include anything that contributes to bare soil such as: agriculture, urbanization, development of transportation corridors, modification of natural landscapes through extraction of minerals, timber harvest, and poorly managed livestock grazing. For successful establishment of alien plants the following factors (Mooney and Drake 1986) are required: (1) An opening in the community, (2) Climatic conditions at the receptor area similar to the source area, (3) Vegetation lifeforms of both areas should be similar, (4) Soils of the areas are not significantly different, and (5) Similar latitudinal range is also a good predictor of invasiveness (Rejmanek 1995).

While these factors are very important for an alien plant to establish on the new area, the ecological traits of alien invasive plants are what is largely responsible if the new plant is to function as a weedy species. Baker (1986) presents information related to patterns of plant spread into North America, and Pysek et al. (1995) evaluated invasion success in relation to plant traits by analysis of flora in the Czech Republic. The purpose of this paper is to review the ecological characteristics of alien invasive plants. The characteristics of the plants to be discussed include: (1.) Pollination strategies of alien invasive plants, (2). Regeneration and development of seed banks, (3). Seed and propagule dispersal, (4). Adaptability of alien species through ecotype formation, (5) Lag time from introduction to invasive status, and (6). Physiological ecology of invasive plants.

**DISCUSSION**

**Pollination Strategies**

Alien invasive plants that are most successful have generalist pollination strategies. They may be wind pollinated as is often the case with invasive grasses of the western United States, such as *Bromus tectorum* (downy brome), *Eragrostis lehmanniana* (Lehmann's lovegrass), *Cenchrus ciliaris* (buffelgrass), and *Taeniatherum asperum* (medusahead rye). Plants may be self pollinated, or like...
Tamarix chinensis (salt cedar), may be a generalist for insect pollination. In general, successful alien invasive plants do not have specific insect pollinators, or specific pollination requirements.

Regeneration

Typically successful alien invasive plants produce either large numbers of viable seeds that will readily germinate, or seeds with dormancy requirements so that when dormancy is overcame they produce large populations of seedlings. T. chinensis fits the first case, in that it produces a nearly continual seed rain during the growing season, and the seeds will rapidly germinate on a moist media (Brock 1994). E. lehmanniana may fit the second case, in that the plant produces many small hard seeds that contribute to a seed bank. Conditions for favorable germination of E. lehmanniana is achieved on almost a yearly basis in its adopted ecological range, but seems to be more prolific in seedling establishment following a period of soil heating resulting from fire (Ruyle et al. 1988). Invasive plants often display early sexual maturity, such as can be observed in T. chinensis. Rejmanek (1995) reported on the genus of Pinus and found that invasiveness in this genus is predictable based on a small number of factors such as small seed mass, short juvenile growth periods, and short mean intervals between seed crops. This may well apply to other woody species of seed plants in disturbed landscapes (Rejmanek 1995).

Not all alien invasive plants spread because of successful sexual regeneration. In some cases, alien plants with no or very little viable seed production are invasive and have become noxious weeds. The case in point is illustrated by Reynoutria japonica (Japanese knotweed), listed as Polygonum cuspidatum in Whitson’s (1991) “Weeds of the West” book, and also as Fallopia japonica in European weed science literature. This plant in North America and Europe reproduces almost exclusively by vegetative means (Bailey et al. 1995). The most commonly known reproduction strategy of R. japonica is from its extensive rhizome/root system (Beerling 1990). Brock and Wade (1992) reported that even pieces of rhizome tissue of 1 cm provided about 40% regeneration success. In 1991, vegetative regeneration from stem portions of R. japonica was only hypothesized. Greenhouse research was initiated in the spring of 1992 to test this hypothesis. From the greenhouse research by Brock et al. (1995), it was found that R. japonica also regenerates from stem tissue. Over all treatments, R. japonica had the capability to successfully reestablish rooted shoots from 6% of the stem portions, but in water (the most probable dispersal mechanism for stems along water courses) 63% regeneration success was observed. R. japonica occurs in the United States in areas of temperate and humid climates. It is known in the Pacific Northwest and is found in the deciduous forest ecosystem of the eastern United States.

Seed and Propagule Dispersal

Seed and propagule dispersal is the result of both passive and active processes. Passive seed dispersal results from seed being blown about by wind as is very common for seeds of the Asteraceae family, and T. chinensis. Passive dispersal is often accomplished by seed falling into moving water which is important for riparian and wetland plants. Seed dispersal by water provides a spread mechanism for T. chinensis and is considered to be a major way R. japonica stem segments spread along riparian corridors. A third passive agent for seed dispersal is gravity.

Active seed and propagule dispersal is primarily aided by members of the animal kingdom (Rejmanek 1995). Many animals eat plant fruits containing seeds and the seeds may pass through the digestive system largely intact and germinate from the fecal deposits of the host animal. This is
one of several dispersal mechanisms employed by *B. tectorum* (Bazzaz 1986). Seeds attach to the skin or pelts of animals and spread across landscapes as the animals either migrate, or establish new territories. In the case of domestic animals, the seeds may be deposited where the animals are first introduced to the new habitat. This seed dispersal strategy is one working hypothesis concerning the introduction of *Halogeton glomeratus* (halogeton) from Asia to the Great Basin region of the western United States, possibly in the wool of Karakul sheep (Mack 1986).

In many cases, the main seed dispersal mechanism of alien invasive plants has been the willful, or unknowing action by people. Many plants have been introduced accidentally because of contaminated agronomic or forage crop seeds. This is believed to be the case for *B. tectorum* which probably was a contaminate in winter wheat. The phenology of *B. tectorum* fits the culture of winter wheat and the rapid spread of this plant is considered to be from many introduction loci rather than one large locus (Bazzaz 1986). *Salsola iberica* (Russian thistle) and *Kochia scoparia* (kochia), two species of the Chenopodiaceae family introduced from Eurasia are also tied to the introduction of small grain crops to North America. People are further implicated in the spread of these 2 species since they were repeatedly first observed along transportation corridors (railroads and highways) in landscapes remote to agricultural areas.

Many invasive weeds are actively spread during construction in man built areas. The spread of *R. japonica* follows this pattern in urbanized areas of Europe. It is also interesting to note that Kowarik (1995) stated that *Ailanthus altissima* (tree-of-heaven) expressed its invasive nature after the industrial revolution was firmly in place in Germany and the "heat island" effect had developed in the cities (annual average temperature is 1.5°C greater in metropolitan Berlin). Man both accidentally and knowingly spreads alien invasive plants. The saving argument in some cases for plants like *E. lehmanniana*, *C. ciliaris*, *T. chinensis*, and *R. japonica* is that the alien plants were being introduced as beneficial organisms, and their weedy nature came as a surprise.

**Ecotype Formation**

Many alien plants adapt to their receptor areas and after several generations experience ecotype differentiation (Baker 1986). This action probably involves genetic recombination and as a result the species becomes better adapted to the environment of the new habitat. This is hypothesized to be the case for *B. tectorum* and other plants that have undergone plant breeding selection processes since introduction to the United States. Another hypothesized example involves *E. lehmanniana* ecotypes currently growing in Arizona. These may ecologically react differently compared to the native strains if they were now reintroduced to South Africa. The process of ecotype formation allows the alien plants to more specifically adjust to the environmental characteristics of a new area and perhaps become better competitors.

Kowarik (1995) and Pysek et al. (1995) both reported on woody alien species in Europe. Kowarik (1995) from work in Germany reported that 41% of alien woody plants had successfully moved from their introduction site indicating that successful ecotypes had formed. Of these 41% successful plants, 19% were only naturalized on man made sites, and 12% had successfully naturalized to natural sites. In the report by Pysek et al. (1995), of the 132 alien plants studied in the Czech Republic, 80% were not successful in establishment. For the 20% that were successful, 14% were found on man made sites, with the remainder being found in natural sites. One successful species from North America, invading natural sites in the Czech Republic is *Robina pseudoacacia*, the black locust tree.
LAG TIME FROM INTRODUCTION TO INVASIVE STATUS

There is much variation in the time lag of introduction until a species is clearly recognized as being invasive. Some species that acted as weeds in their original habitats acted as weeds almost immediately after introduction to the United States. This is apparently the case for common crop weeds such as *Amaranthus* sp. (pigweed) and *Chenopodium album* (lambquarters). Other plants experienced lag times to allow for seed dispersal and for populations to reach a critical number for wider dispersion in the new landscape. Research in Europe (Kowarik 1995), indicates that often there is a lag time of 50 years from introduction until a plant is invasive. For tree species introduced to Germany, this time period was found to be an average of 170 years. The development of lag times for species commonly believed to be alien invasive plants to the western parts of North America would provide an interesting research topic.

PHYSIOLOGICAL ECOLOGY OF INVASIVES

Most of the knowledge about the physiological ecology of invasive plants is inferred from studies dealing with colonizer type plants compared to those of late successional stages. In general, the physiological ecology of specific alien invasive plants is not well understood. Generally, early successional plants have high photosynthetic, respiration, transpiration rates, and behave opportunistically to disturbance. These plants have great ability to acclimate to changes in the environment, and quick response to changes in environmental resources, water and nutrients as examples.

Climatic change may also be having a large impact on plant physiology and the invasive nature of some plants. This topic was reviewed by Mayeaux (1995) with plant invasiveness related to changes in the earth’s atmosphere and by Patterson (1995). Both Mayeaux and Patterson indicated that global warming and related climatic changes would affect the growth, phenology, and geographic distribution of weeds. Carbon dioxide (CO$_2$) at the current level of about 350 ppm is increasing in the atmosphere at about 0.4% per year from a pre-industrial revolution level of 280 ppm (Ashmore 1990). Another greenhouse gas, methane (CH$_4$) is increasing at 0.9% per year from the current level of 1.7 ppm (Ashmore 1990). Crop plants with C$_3$ and C$_4$ photosynthetic pathways have increased average biomass by 40% for C$_3$ plants and by 11% for C$_4$ crop plants (Kimball 1983). Response in doubling CO$_2$ in the air of C$_3$ and C$_4$ weedy plants resulted in a mean biomass increase of 130% and 115% respectively (Patterson 1995). With increased CO$_2$ (350 to 675 ppm) and limited water, the following weedy grasses, *Echinochola crus-galli* (barnyardgrass), *Eleusine indica* (goosegrass), and *Digitaria sanguinalis* (crabgrass) increased dry matter production by 43, 46, and 37% respectively (Patterson 1986). These data support Mayeaux’s and Patterson’s hypothesis that changing atmospheric conditions will alter the physiology of invasive plants and perhaps change their distribution, so that the geographic range will expand northward, such as *Impatiens glandulifera* (Himalayan balsam) and *F. japonica* (Japanese knotweed) in the British Isles (Beerling 1994), and a subtropical alien plant like *Pueraria lobata* (kudzu) will invade deeper into the North American continent.

The following material related to physiological aspects of plants is adopted from Bazzaz (1986) and summarizes some of the characteristics shared by invasive species: (1). High rates of photosynthesis, respiration, and transpiration, (2). Rapid response to available environmental resources, (3). Fast population growth rates, (4). Relatively short life cycle, (5). Early reproduction capability, (6). Allocation of growth activity to reproduction in favor of foliage growth, (7). Self, wind, or serviced by generalized insect pollinators, (8). Seed dispersal mechanisms that provide for
establishment of large ecological ranges, (9). Generalists in resource use (broad niches), and (10). Readily adapt to changes in the environment.

CONCLUSION

Alien invasive plants have changed many of the habitats of the western United States. In many cases there may have been an associated loss of biodiversity, and that loss may be at a rate that is barely discernible. For example, what is the impact of Bromus rubens (red brome grass) on the recruitment of Carnegiea gigantea (saguaro cactus) in desert habitats? It is a rare riparian plant community in Arizona that does not have either or both Cynodon dactylon (Bermuda grass) or T. chinensis represented in the vegetation. On the uplands, especially in southeastern Arizona, E. lehmanniiana is common. In the Phoenix area, many horticultural plants are currently displaying invasive characteristics. Some of these plants include the tree Rhus lancea (African sumac) and Cenchrus setaceum (fountain grass). Alien invasive plants have become parts of our landscapes, and land managers need to learn how to manage those lands in the presence of those plants, or devise strategies to return native plants to the habitats through the practice of ecological restoration.

Alien invasive plants have become firmly naturalized in most of the habitats of the United States and the world. Management attempts that extol eradication of these alien plants most likely will be futile. Management to control the plants on critical portions of the habitat can be achieved with economic, ecological, social, and perhaps political costs. Many times the ecological and economic costs are bearable, but the social and political costs curtail widespread successful vegetation management programs. It is my belief that existing management tools will effectively control alien invasive plants if there is both a political and social consensus for vegetation management.

REFERENCES


