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Biology of Pathways for Invasive Weeds[1]

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Abstract: Biological processes and characteristics are important factors in the introduction, spread, and establishment of invasive weeds. These biological traits include reproduction, dispersal, phenology, physiology, protection from herbivores, tolerance to environmental extremes, and interspecific interactions. Measures and methods to prevent dispersal, establishment, and persistence of nonnative invasive weeds include knowledge of the most vulnerable growth stages, management strategies, maintenance of weed-free areas, and sanitation of vehicles, transportation equipment, animals, and other modes of dispersal.

Additional index words: Dispersal, ecology, invasive weeds, reproduction.

Invasive weeds possess a variety of characteristics that enable them to disperse rapidly into new areas and outcompete crops and native or desirable nonnative vegetation for light, water, nutrients, and space (Westbrooks 1998, 2001). The success of a weed's biological pathway is dependent on several factors including the method or mechanism of dispersal, longevity of propagule, adaptiveness to varying environmental conditions, and competitive and reproductive ability. Botanists, ecologists, and weed scientists have long been aware of the problem of the establishment of nonnative weed species and have gleaned knowledge of how some species reproduce, spread, and interact with crops and native and acceptable nonnative species. To prevent economic and ecological diversity losses, it is necessary to prevent additional introductions and invasions of plant species that have the potential to become serious pests of agriculture, forest, urban, and native areas. Understanding the basic biology and ecology of weeds is important to determine pathways of entry, spread, establishment, and persistence. Biology of pathways varies depending on the species and environmental surroundings. Biological processes and characteristics that are most important for weeds to thrive are dependent on reproduction, dispersal, phenology, physiology, protection, habitat requirements, tolerances to environmental stress, and interspecific interactions (Table 1).

Humans are often directly or indirectly responsible for most introductions, whether intentional or unintentional, but animals and natural processes also disperse plants (Reed 1977). The most common pathways of movement associated with humankind include contaminated soil, food, feed, fiber, ballast, and packing and bagging material. However, pathways for introduction and spread may be from ornamentals, forages, or plants used for erosion control that were once thought to be acceptable but have become weedy. Natural processes including wind, hurricanes, tornadoes, earthquakes, and floods are also responsible for plant dispersal but to a lesser extent than human activities.

Natural barriers and restricted migration routes prevent many plant propagules from dispersing over great distances; however, the current speed and ease of world transportation by humans and their cargo has increased the rate and distance of dispersal of plant propagules. After introduction, a plant species may remain near the point of introduction without becoming a pest or the plant may continue dispersing from the initial point of entry. Unfortunately, newly introduced weeds are often unnoticed until after their numbers and range increase greatly. The period of time between introduction and invasion is termed the lag phase (Radosevich and Holt 1984). The duration of the lag phase depends on a number of biological factors including size of population, dynamics of reproduction, and adjusting to environmental factors that may be slightly different from those in the plant's native range. The lag phase may range from a few to many years and may depend on new pathways for dispersal, introduction of new pollinators or dispersal vectors, environmental change such as disturbances (e.g., tillage), and local adaptation of the population through

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Table 1. Biological and ecological characteristics of weeds, in part adapted from Baker (1965, 1974), Muenscher (1955), Radosevich and Holt (1984), Stuckey and Barkley (1993), and Westbrooks (1998).

Reproduction
Copious production of small seeds
Profuse vegetative reproduction and fragmentation
Self-compatible or if cross-pollinated then by wind or unspecialized floral visitors
Survival and the ability to produce seed under adverse environmental conditions
Seed size similar to associated crops or native plants
Small inconspicuous flowers
Dispersal
Multiple vectors for dispersal
Short- and long-range dispersal mechanisms
Structural modifications facilitating dispersal
Habitat
Ability to invade new habitats
Germination and survival in a wide range of habitats
Interspecific interactions
Ability to parasitize other plants
Shade other vegetation
Alternate host for insect pests and pathogens of crops
Resistance to pathogens
Phenology
Early maturation
Extended seed dormancy and discontinuous germination
Long life of propagules in soil or during dispersal
Multiple generations annually
Photoperiodic flowering
Rapid growth
Short juvenile period
Physiology
Accumulation of large food reserves in roots, rhizomes, or other plant structures
High photosynthetic rate (C_4 photosynthesis)
Increased water-use efficiency (C_4 photosynthesis)
Production of phytotoxins to prohibit or suppress growth of other plants (allelopathy)
Protection from herbivores
Production of toxic secondary compounds that deter herbivores
Structural modifications (e.g., thorns, prickles, spines, urticating hairs, etc.) that cause injury and repel animals or herbivores
Tolerance to environmental stress
Germinate and grow through harsh environmental zones
Survive environmental and chemical extremes, including fire, herbicides, soil disturbances, salinity, etc.

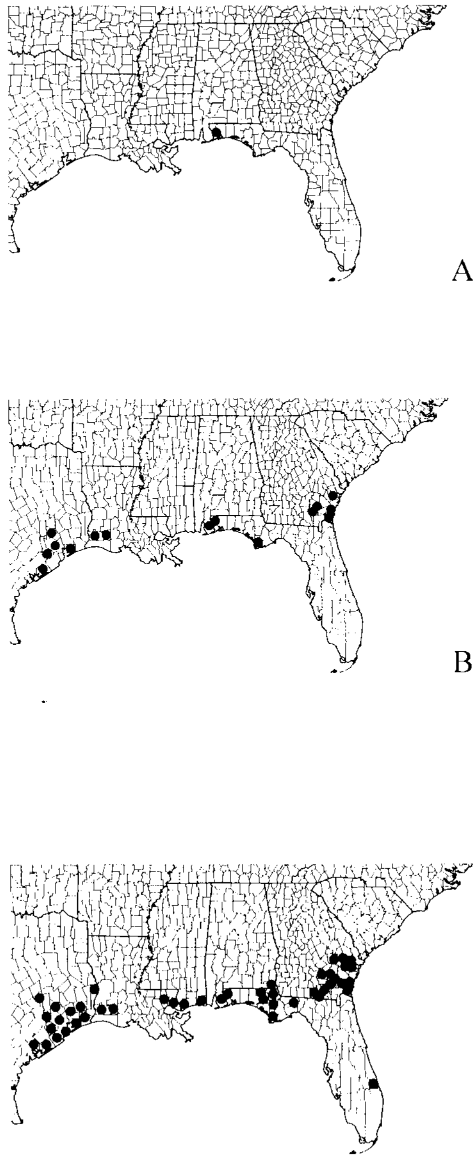

Figure 1. The dispersal of deeprooted sedge in the United States: (A) 1941–1979, (B) 1980–1989, (C) 1990–2003.

natural selection (Cronk and Fuller 1995). Nonnative invasive weeds may become established in areas with similar habitats or become adapted to new habitats through natural selection. The time for selection may vary depending on the genetic diversity in the population. Heterosis resulting from hybridization with related species may also be a factor in facilitation of establishment and spread of weeds (Carter 1990; Daehler and Strong 1997).

Dispersal of sexual or asexual propagules varies among plant species. Copious production of sexual and asexual propagules, i.e., seeds, rhizomes, bulbs, tubers, etc., is the most common biological characteristic in pathways of dispersal. Deeprooted sedge (*Cyperus entrerianus* Boeck.) populations are estimated to produce up to 1 to 2 million seed annually (Bryson et al. 2003a). Deeprooted sedge has spread rapidly along major highways (especially Interstate 10) in the southeastern United States during the past decade (Carter and Bryson 1996) and now occurs at sites in 45 counties in six states (Figure 1). Many other native and nonnative invasive weeds produce copious seeds and propagules annually. Once seed and propagules are dispersed, they may germinate immediately or remain dormant until environmental conditions are favorable for germination and plant growth. However, not all seeds and propagules germinate when conditions are favorable, which results in seed and propagule reservoirs in soil. These soil reservoirs are a survival mechanism, and once established in an area, weed seeds may remain viable in soil seed banks for many years. For example, seeds of Johnsongrass [*Sorghum halepense* (L.) Pers.] and many other invasive weeds may remain viable for 15 yr or more in soil (Egley and Chandler 1983). Seeds from perennial vines, shrubs, and trees may remain in the soil for years, and their spread and survival are enhanced because seed or propagules can be produced annually over a long period of time.

Spread of seeds, fruits, or asexual propagules may occur through natural processes, natural mammal and bird migrations, and human activity. Morphological structures on seed or fruit can enhance dispersal. Modified plant structures that attach to hair of mammals and feathers of birds during migrations or to human clothing are important biological traits that enhance long- and short-range dispersal of many species of invasive weeds. Common cocklebur (*Xanthium strumarium* L.) is commonly known as nature's "Velcro," and its fruit readily attach to hair and clothing for dispersal (Armstrong 1979). Small seeds in soil, such as *Cyperus* spp., can attach temporarily to the hooves or feet of animals and to soles of shoes, vehicle tires, or equipment and can be moved from one site to another (Westbrooks 1998). Contaminated hay and straw blown for erosion control and from mowing equipment can also move weed seed from one area to another (Westbrooks 1998). Cogongrass [*Imperata cylindrica* (L.) Beauv.] seed can be dispersed by wind at distances up to 25 km or as seed and rhizome-contaminated soil (Byrd and Bryson 1999).

Weed seed may remain viable after passage through digestive tracts of animals and birds. Tropical soda apple (*Solanum viarum* Dun.) is a prime example of weed dispersal through the digestive tract of domesticated animals over long distances and within smaller areas by wildlife in the southeastern United States (Mullahey and Cornell 1994). Excretion of scarified seed may take up to 3 d after ingestion of tropical soda apple fruit. Within years after its first detection, tropical soda apple spread to and infested more than 500,000 ha in nine states in the southeastern United States (Mullahey 1996; Mullahey and Cornell 1994).

Humans are vectors for turkeyberry (*Solanum torvum* Dun.) and swamp morningglory (*Ipomoea aquatica* L.). Fruits of turkeyberry are used in stir-fry dishes, and the leaves of swamp morningglory are eaten like spinach or greens. Both are listed as Federal Noxious Weeds in the United States based on their biology and potential to be invasive in their native lands.

Phenology parameters of some species may provide a biological advantage over other species. Short generation times and high seed production favor rapid dispersal, large seed reservoirs in the soil, and high population levels (Vaillant 1967). Plants that flower and produce seed throughout the growing season may be able to produce multiple generations per year, which increases the likelihood of successful dispersal, establishment, and increases in population sizes. Smallflower umbrellasedge (*Cyperus difformis* L.) has the ability to complete its life cycle in 4 to 6 wk (Holm et al. 1977). In rice production areas of California, multiple smallflower umbrellasedge generations per year and production of large seed numbers and reservoirs in the soil seem to be the primary factors in the development of herbicide resistance to bensulfuron (Hill et al. 1994; Pappas-Fader et al. 1993, 1994).

A biotype of nonnative bloodscale sedge (*Cyperus sanguinolnentus* Vahl) flowers and produces seed in the fall until frost or in the early spring in the southeastern United States (Carter and Bryson 2000). Seasonal seed production may be one reason that this species has not become a problematic weed in the United States like several other nonnative annual sedges such as annual sedge (*Cyperus compressus* L.) and rice flatsedge (*Cyperus iria* L.), which flower and produce seed throughout the growing season in the southeastern United States. Common cocklebur seed production is also day length dependent. Common cocklebur seed contain two or occasionally three viable embryos that germinate at different times, often years apart. A recently discovered common cocklebur biotype evolved the ability to produce additional seed (up to 25) per bur (Abbas et al. 1999). Additional seed per bur enable this common cocklebur biotype to produce more progeny and the ability to germinate over a longer period of time.

Plants with specialized physiological processes may produce a number of chemicals that promote biological advantages in competing with other vegetation. Purple nutsedge (*Cyperus rotundus* L.), yellow nutsedge (*Cyperus esculentus* L.), cogongrass, and other plant species produce alleopathic compounds that reduce germination and growth of adjacent crop or noncrop plants (Friedman and Horowitz 1971; Inderjit and Dakshini 1991; Koger and Bryson 2004; Koger et al. 2004; Mallik and Tesfai 1988; Martinez-Diaz 1997). C_4 plants possess a competitive advantage under conditions of high temperature, high light intensity, and water stress when compared with C_3 plants. C_4 plants have a lower transpiration ratio and, thus, higher water-use efficiency, than C_3 plants.

Although many weeds are C_3 plants, some of the most competitive and invasive weeds are characterized by C_4 photosynthesis (Black et al. 1969; Elmore and Paul 1983) including some of the world's worst weeds, purple nutsedge, yellow nutsedge, and rice flatsedge (Holm et al. 1977), whereas smallflower umbrella sedge is C_3 (Hesla et al. 1982).

Prickles, spines, thorns, and glandular hairs on stems, leaves, fruit, and seed may protect plants from herbivores and ultimately enable plants to produce more viable seed per plant than species that lack these specialized structures. Likewise, plants may produce chemical repellants and toxins that protect them from herbivores. Nipplefruit nightshade (*Solanum mammosum* L.) and red soda apple (*Solanum capsicoides* Cav.) produce fruits with a high animal toxicity that have been used as rodenticides and insecticides in tropical North and South America (Nee 1991). Because of animal toxicity many contaminated crop seeds are rejected from sale, such as rattlebush [*Sesbania punicea* (Cav.) Benth.] and showy crotalaria (*Crotalaria spectabilis* L.) contaminated soybean [*Glycine max* (L.) Merr.] (Burrows and Tyrl 2001; Thomas 1934).

Biological mechanisms and structures are important in survival strategies during periods of adverse environmental conditions including heat, cold, drought, flooding, or inadequate aeration. Purple nutsedge rhizomes form tubers that may remain dormant, give rise to new aerial plants, or produce other rhizomes that can form additional tubers without an aerial plant (Wills 1987). Thus, purple nutsedge is very difficult to control in crops and is easily spread in contaminated soil (Bryson et al. 2003b). Cogongrass and many other perennials are fire tolerant and provide an advantage over other plants that are not fire tolerant (Byrd and Bryson 1999). Fire temperatures at cogongrass canopy top can reach 400 C and burn all aboveground foliage; however, cogongrass rhizomes remain viable below the soil surface and germinate under favorable conditions (Bryson and Carter 1993; Byrd and Bryson 1999). Purple nutsedge, cogongrass, and many other species not only can survive periods of adverse environmental conditions such as drought but also can penetrate and grow through fleshy subterranean organs of root crops and harsh environmental zones such as rocky soils or even asphalt pavement (Hauser 1962a, 1962b; Thullen and Keeley 1979).

Competition and interference with native plants and crops vary among weed species. Some weeds compete for water and nutrients, whereas others displace or shade adjacent vegetation. Hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. ex A. W. Hill] shade can reduce cotton yields by as much as 50% (Bryson 1990). Kudzu [*Pueraria montana* (Lour.) Merr.], Japanese climbing fern (*Lygodium japonicum* L.), and old world climbing fern, (*Lygodium myriophyllum* L.) grow over adjacent vegetation. Ultimately these invasive weeds cover and cause death to other vegetation (Westbrooks 1998). Some plants such as Japanese honeysuckle (*Lonicera japonica* L.) and Chinese tallow (*Sapium sebiferum* L.) successfully invade natural areas, whereas purple nutsedge invades mowed and tilled disturbed areas (Westbrooks 1998).

To prevent nonnative invasive weeds from becoming problematic, it is important to become knowledgeable about the plant's biological and ecological mechanisms and characteristics. Determining the plant's most vulnerable stage of growth is the most important factor in developing control strategies. Best management strategies that include prevention, early detection, rapid response, eradication for small or isolated populations, and control methods (cultural and chemical) are dependent on biological and ecological knowledge gleaned from research and implementation of effective weed control strategies. Sanitation measures can eliminate the biological pathway for dispersal and prevent the spread of weeds. Practices such as cleaning vehicles, equipment, animals, or maintaining livestock in weed-free areas before moving them can prevent dispersal, establishment, and persistence of weed seeds or rhizomes in previously weed-free areas.

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