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WEEDS AND INVASIVE PLANTS

Weeds exist as a category of vegetation because of the human ability to select desirable traits from among various members of the plant kingdom. Just as some plants are valued for their uses or beauty, others are reviled for their apparent lack of these characteristics. Weeds are recognized worldwide as an important type of undesirable, economic pest, especially in agriculture. However, the value of any plant is unquestionably determined by the perceptions of its viewers. These perceptions also influence the human activities directed at this category of vegetation.

Harlan, in the middle of the last century, described how vegetation evolved under the impacts of humans. He suggested that vegetation, in relation to the degree of human involvement with it, exists as three categories: wild plants, weeds, and crops. Crops were domesticated from wild plants while weeds evolved from wild plants as an unintentional consequence of growing crops. Some crops also were once weeds and some have again escaped from domestication. In Harlan's concept neither weeds nor crops can permanently displace wild plants from wild habitats over time (DeWet and Harland 1975).

Invasive plants, unlike agricultural weeds, are those that can successfully establish and spread to new habitats after their introduction, seemingly without further assistance from humans. These plants can spread into new areas already occupied by a native flora and displace those species. Such invasions from the intentional or unintentional transport of plants to new regions now seriously threaten the biodiversity, structure, and function of many of the world's ecosystems. Invasive

Ecology of Weeds and Invasive Plants. By Steven R. Radosevich, Jodie S. Holt, and Claudio M. Ghersa

plants are thus weeds in the broadest sense because they evoke human dislike and often some form of management to eradicate or contain them in their new environments. Not all weeds are invasive, however. In this text, the term *weed* will be used in the broad sense and to describe undesirable plants in agricultural systems, while *invasive plant* will be used for those weeds that can spread beyond their point of introduction, often in natural ecosystems.

WEEDS

A "*plant growing out of place*," that is, plants growing where they are not wanted, at least by some people, is a common, accepted explanation for what weeds are. This notion of undesirability imparts so much human value to the idea of weediness that it is usually necessary to recognize who is making the determination as well as the characteristics of the plants themselves. For example, certain plants growing in a cereal field or pasture or along a fence row may be unwanted by a farmer or rancher, but they also may be wildflowers or a valuable wildlife cover to other people. Vine maple, *Acer circinatum*, is a valued source of deer browse in the spring and a spectacular source of coloration in the Cascade Mountains of Oregon and Washington in the United States, during autumn, but it also is known to hamper forest regeneration. It can be argued that many weeds in agricultural fields, forest plantations, and rangelands are not "out of place" at all but are simply not wanted there by some people.

In Table 1.1 we list many of the "human" characteristics that have been used to describe weeds. Most of these characteristics are based on some judgment of

TABLE 1.1 Definitions and Descriptions of Weeds

Definition	Description
Growing in an undesirable location	A plant growing where it is not desired (Weed Science Society of America 1956)
Competitive and aggressive behavior	A plant that grows so luxuriantly or plentifully that it chokes all other plants that possess more valuable properties (Brenchley 1920)
Persistence and resistance to control	The predominance and pertinacity of weeds (Gray 1879)
Useless, unwanted, undesirable	A plant not wanted and therefore to be destroyed (Bailey and Bailey 1941); a plant whose virtues have not yet been discovered (Emerson 1878)
Appearing without being sown or cultivated	Any plant other than the crop sown (Brenchley 1920); a plant that grows spontaneously in a habitat greatly modified by human action (Harper 1944)
Unsightly	A very unsightly plant of wild growth, often found in land that has been cultivated (Thomas 1956)

Source: Adapted from King (1966).

worth, success, or other human attribute, like aggressiveness, harmfulness, or being unsightly or ugly. Since this anthropomorphic view of weeds is so prevalent (Table 1.1), it may be that weeds are little more than plants that have aroused a level of human dislike at some particular place or time. Unfortunately, the anthropomorphic view of weeds provides little insight into why and where they exist, their interactions and associations with crops, native plants, and other organisms, or even how to manage them effectively. Weeds are found worldwide and have proven to be successful organisms in the environments that they inhabit. Therefore, it is important to explore whether weeds posses common traits that distinguish them from other plants or whether they are only set apart by local notions of usefulness.

A list of biological characteristics that describe weeds was proposed in the 1970s and continues to be used today (Table 1.2) (Baker 1974), but it seems unlikely that any plant species could possess all of those "ideal" weedy traits. However, Herbert Baker, botanist and originator of the list, suggests that a species might possess various combinations of the characteristics in Table 1.2, resulting in a range of weediness from minor to major weeds (Baker 1974). In the latter case, Baker believes that evolutionary processes would compound specific adaptations into highly successful (weedy) individuals, which constitutes an "all-purpose genotype." It must be stressed, however, that ecological success in the form of weediness cannot be measured solely from the perspective of noxiousness. The number of individuals, the range of habitats occupied, and the ability to continue the species through time must be considered foremost when evaluating success of a species. The obvious limitation of the list in Table 1.2 is that almost every plant species has some "weedy" characteristics, but, of course, not all plants are weeds.

TABLE 1.2 Ideal Characteristics of Weeds

Germination requirements fulfilled in many environments
Discontinuous germination (internally controlled) and great longevity of seed
Rapid growth through vegetative phase to flowering
Continuous seed production for as long as growing conditions permit
Self-compatibility but not complete autogamy or apomixis
Cross-pollination, when it occurs, by unspecialized visitors or wind
Very high seed output in favorable environmental circumstances
Production of some seed in a wide range of environmental conditions; tolerance and plasticity
Adaptations for short-distance dispersal and long-distance dispersal
If perennial, vigorous vegetative reproduction or regeneration from fragments
If perennial, brittleness, so as not to be drawn from the ground easily
Ability to complete interspecifically by special means (rosettes, choking growth, allelochemicals)

Source: Baker (1974). *Annu. Rev. Ecol. Syst.* 5:1–24. Copyright 1974 by Annual Reviews, Inc., Palo Alto, CA.

Definitions

As we have just observed (Tables 1.1 and 1.2), weeds can be described in either anthropomorphic or biological terms. Weeds emerge from such descriptions as organisms that may possess a particular suite of biological characteristics but also have the distinction of negative human selection. Thus, a definition of a weed as *any plant that is objectionable or interferes with the activities or welfare of man* (Weed Science Society of America 1956) seems to describe sufficiently this category of vegetation. A sample of definitions of weeds published over the past century was presented by Randall (1997), who also argued that the most important criterion was problem-causing plants that interfere with land use.

Other authors, for example Zimmerman (1976), Aldrich (1984), and Rejmánek (2000), define weeds in more specific terms than the simple definition given above. Zimmerman believes that the term "weed" should be used to describe plants that (1) colonize disturbed habitats, (2) are not members of the original plant community, (3) are locally abundant, and (4) are economically of little value (or are costly to control). Aldrich defines weeds as plants that originated under a natural environment and, in response to (human) imposed or natural conditions, are interfering associates of crops and human activities. Each of these definitions implies that weeds have some common biological traits but also a level of relative undesirability as determined by particular people. Whether or not a plant is a weed depends on the context in which someone finds it and on the perspectives and objectives of those involved in dealing with it. Rejmánek, on the other hand, believes that weeds, colonizers, and naturalized species (including invasive plants) reflect three overlapping concepts. In his view (Figure 1.1), weeds are plants growing where they are not desired (anthropomorphic definition), colonizers occur early in succession (ecological definition), and invasive plants are plants that become locally established and spread to areas where they are not native (biogeographical definition).

The most important criterion for weediness is interference at some place or time with the values and activities of people—farmers, foresters, land managers, and many other segments of human society. However, the abundance of weeds is often of more concern than the mere presence of them. For instance, farmers and land managers are usually less concerned about the occurrence of a few isolated plants in a field, even noxious ones, than the occupation of land by vast numbers of weeds. Therefore, the relative abundance of plants, their location, and the potential use of the land they occupy should also be considered in weed definitions. When abundance is applied as a criterion for weediness, it implies a condition of the land as well as a class of vegetation (Table 1.2) and a form of human discrimination (Table 1.1). Weed abundance also may be an indicator or symptom of land mismanagement or neglect.

Agrestals. Agrestals are weeds of tilled, arable land. They require the nearly continual disturbance of agriculture to occupy the land. Holzner et al. (1982) indicate that every cropping system, for example, cereals, root crops, and orchards, also

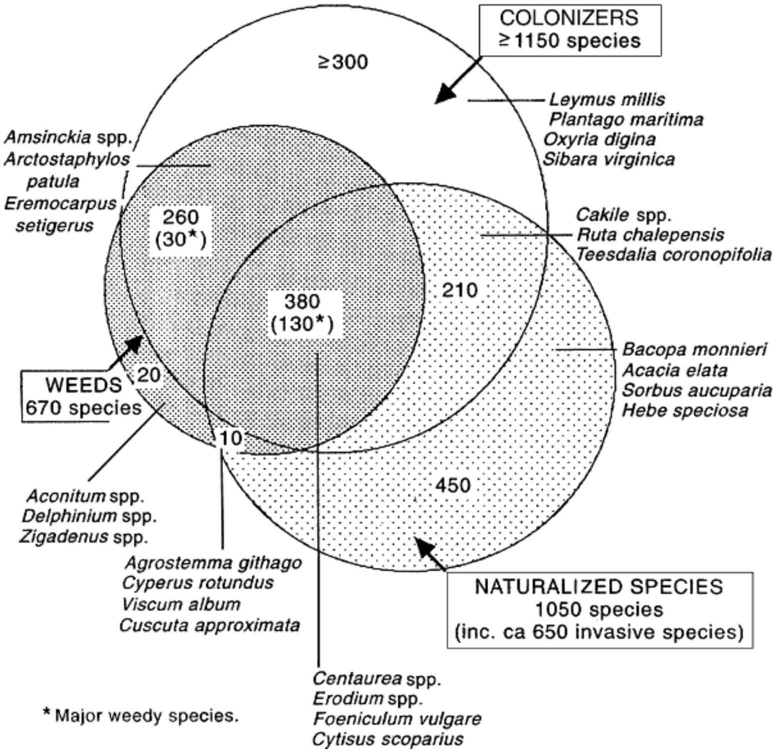

Figure 1.1 Weeds, colonizers, and naturalized species (including invaders) are three overlapping but not identical concepts reflecting three different viewpoints: anthropomorphic (weeds), ecological (colonizers), and biogeographical (naturalized species). Invaders are a subset of naturalized species, namely those nonnative species that are spreading. Estimated species numbers and examples of species representing seven resulting categories of the California vascular flora are given. (From Rejmánek 2000, *Aust. Ecol.* 25:497–506. Copyright 2000, Blackwell Publishing Ltd., reproduced with permission.)

has its special complement of weeds, which may be either native plants or exotics that have been naturalized into the local flora. A list of the 76 worst agricultural weeds in the world was developed by Holm and his associates (1977) and has become the standard by which agrestals are compared. The top 18 weeds on this list are given in Table 1.3. An additional 104 of the weeds that cause the greatest impacts on agriculture was reviewed by Holm et al. in 1997. As a group these 180 agricultural weeds are estimated to cause over 90% of the loss of crop productivity worldwide (Holm et al. 1997).

Holzner and his associates (1982) suggest that agrestals have evolved as either specialists or colonizers during the course of agricultural history. Specialized weeds (*specialists*) have evolved a narrow adaptation to a single crop or sometimes crop cultivar and its particular growing conditions. Perhaps the most extreme example of how human activities influence weed species distribution and

TABLE 1.3 Scientific and Common Names of Certain Annual Weed Species Considered the World's 18 Worst

Species	Common Name
Amaranthus hybridus	Smooth pigweed
Amaranthus spinosus	Spiny amaranthus
Avena fatua	Wild oat
Chenopodium album	Common lambsquarters
Convolvulus arvensis	Field bindweed
Cynodon dactylon	Bermudagrass
Cyperus esculentus	Yellow nutsedge
Cyperus rotundus	Purple nutsedge
Digitaria sanguinalis	Large crabgrass
Echinochloa colonum	Junglerice
Echinochloa crus-galli	Barnyardgrass
Eichhornia crassipes	Waterhyacinth
Eleusine indica	Goosegrass
Imperata cylindrica	Cogongrass
Paspalum conjugatum	Sour paspalum
Portulaca oleracea	Common purslane
Rottboellia exaltata	Itchgrass
Sorghum halepense	Johnsongrass

Source: Adapted from Holm et al. (1977, 1997).

composition are *crop mimics*. These are weeds that have evolved life cycles or morphological features so similar to a crop that the two species cannot be distinguished or separated easily. Chapter 4 considers the influence of humans on the evolution of weed species, including crop mimicry, in much more depth. Since agrestals that are specialists have evolved along with the cultural practices of a particular crop, any change in practices usually disfavors the weed. *Colonizers*, on the other hand, are plants with characteristics that allow them to rapidly occupy and dominate disturbed areas. These species follow the general characteristics listed in Table 1.2 and Figure 1.1.

Weeds are major constraints to crop production, yet as primary producers, they also can be important components in an agroecosystem. It is in this context that weeds are sometimes perceived as an ecological "good" (Gerowitt et al. 2003). Awareness of the importance of weeds on arable land for their role in other trophic levels is growing as natural landscapes become rare or disappear due to the expansion of human-occupied landscapes. The weed flora in many parts of the world has changed over the past century, with some species declining in abundance while others have increased (Haas and Streibig 1982, Marshall et al. 2003, de la Fuente et al. 2006). These changes in the weed flora reflect improved agricultural efficiency, the use of different crops in arable rotations, and the use of more broad-spectrum herbicide combinations (Marshall et al. 2003, de la Fuente et al. 2003). Many weed species of arable land support a high diversity of insects, so the reduction in abundance of weed host plants can affect associated insects and, therefore, the abundance of other taxa. For example, in the United Kingdom a number of insect groups and farmland-associated birds (notably the grey partridge, *Perdix perdix*) have undergone marked population decline, which is associated with changes in agricultural practices over the past 30 years (Marshall et al. 2003). Thus, it seems that weeds may have a general role in supporting biodiversity within agroecosystems.

Invasive Plants. Invasive plants, unlike agricultural weeds, are generally defined as those that can successfully establish, become naturalized, and spread to new natural habitats apparently without further assistance from humans (Randall 1997). They are also generally nonnative or exotic in the new habitat and are often relatively new introductions to an ecoregion (Mashhadi and Radosevich 2003). Invasive plants respond readily to human-induced changes in the environment such as disturbance but also may initiate environmental change through their dominance on the landscape (Pyke and Knick 2003, Hobbs et al. 2006). In addition, the spatial and temporal extent of their impact may be expressed at scales ranging from local to global. Some ecological impacts believed to be caused by invasive plants are as follows (Parker et al. 1999, Alien Plant Working Group 2002):

- Reduction of biodiversity
- Loss or encroachment upon endangered and threatened species and their habitats
- Loss of habitat for native insects, birds, and other wildlife
- Loss of food sources for wildlife
- Changes to natural ecological processes such as plant community succession
- Alterations to the frequency and intensity of natural fires
- Disruptions of native plant–animal associations such as pollination, seed dispersal, and host–plant relationships

It is widely believed that the most effective way to limit plant invasions is to prevent the introduction of exotic species, which may be difficult because of the ongoing expansion in global travel and trade, changes in environments at all scales (local to global), and increasing development of land for human use (Kolar and Lodge 2001).

Although the traits of an "ideal weed" (Baker 1974) have also been ascribed to invasive plants, few empirical studies have tested this concept (Kolar and Lodge 2001). The biological characteristics of invasive plants appear in many cases to be dependent upon the habitat in which they occur (Sakai et al. 2001). Thus, general descriptions of invasive plants remain inconclusive. Some useful generalizations have been made, however, from reviews of empirical evidence or broad-scale analyses of floras or databases. For example, Reichard and Hamilton (1997), using a regression tree analysis of biological and environmental traits of invasive plants, suggest that species known to be invasive elsewhere should be limited in

TABLE 1.4 Biological Characteristics Responsible for Invasiveness

- Fitness homeostasis or the ability of an individual or population to maintain relatively constant fitness over a range of environments. This is equivalent to Baker's (1974, 1995) "general-purpose genotype."
- Small genome size—usually associated with short minimum generation time, short juvenile period, small seed size, high leaf area ratio, and high relative growth rate.
- Dispersed easily by humans and animals.
- Ability to vegetatively propagate. This is an especially important characteristic in aquatic environments (Auld et al. 1983, Henderson 1991) and at high latitude (Pyšek 1997).
- Alien plants belonging to exotic genera are more invasive than are alien species with native congeners. This may be partly because of an absence or limited number of resident natural enemies for that species (Darwin 1859, Rejmánek 1999).
- Plant species without dependence on specific mutualisms (root symbiosis, pollinators, seed dispersers, etc.) (Baker 1974, Richardson et al. 2000).
- Tall plants tend to invade mesic plant communities.
- Persistent seed banks—seeds with different inherent dormancies that provide a random appearance through time and guarantee their survival and persistence.

Source: Adapted from Rejmánek and Pitcairn (2002).

introduction to a new area with a similar environment, where they might also be invasive. Reichard and Hamilton further suggest that a species related to one that is already "invading" a site may share invasive traits through a common ancestor. From a retrospective review of literature, Rejmánek (2000) lists several biological characteristics related to invasiveness, including constant fitness, small genome size, effective dispersal and vegetative propagation, and absence of strong interactions with other taxa (e.g., natural enemies, pollinators, seed dispersers) (Table 1.4). Sutherland (2004) reviewed databases for nearly 20,000 plant species in the United States and concluded that invasive exotic species were more likely to be perennial, monoecious, self-incompatible, and trees than noninvasive exotic species. A broad-scale analysis of the flora of the Czech Republic over 500 years showed that life-form and competitiveness were related to invasiveness (Pyšek et al. 1995). Similarly, an analysis of global datasets revealed some common traits of invasive plants, including nitrogen fixation and clonal growth (Daehler 1998). Other traits that have been shown to be related to invasiveness are described in later chapters.

Terminology

Massive amounts of money, time, and energy are expended on weeds and invasive plants because of their economic and ecological costs and impacts on agricultural and natural systems. Because of the magnitude of these effects, it is important that scientists and land managers consider carefully the metaphors they use to describe these two categories of vegetation. Larson (2005) points out that metaphors allow people to understand abstract or perplexing subjects in term of something they already know about, a common referent. Thus, weeds and especially invasive plants are often described in militaristic terms, which probably date to Elton's (1958) classic *The Ecology of Invasions by Animals and Plants*. Davis (2005) points out that such terms as *alien*, *exotic*, *invader*, and *invasion* commonly used by invasion ecologists contrast markedly to the less evocative terms such as *colonizer*, *founding population*, *introduced plant*, *nonnative*, *spread*, or *migration*, which could be used to describe weeds and "invasive" plants. It should be noted that a similarly militaristic terminology has been used for decades in the pest management field.

From a management point of view, there is little doubt that the "invasion" terminology and metaphors have been useful in pointing out the significance of weeds to land managers and policymakers. From a strictly scientific point of view, however, it is difficult to argue against returning to the more value-neutral terminology used by Baker and Stebbins (1965) in their early classic, *The Genetics of Colonizing Species* (Davis 2005). Since this text is designed to fulfill a dual role for both scientists and land mangers and because the notion of "weed" is itself value laden, we have chosen to use the language of both scientists and managers that is in conventional use to discuss this important class of vegetation.

Classification Systems of Weeds and Invasive Plants

Botanical classification is the systematic grouping of plants using criteria that distinguish among types of vegetation. These criteria may be biologically meaningful, based on phylogenetic or evolutionary evidence, or artificial and based on structural or other visible or functional attributes. Some common methods used to classify weeds are by taxonomic relationships, life history, habitat, physiology, and degree of undesirability. Weeds and invasive plants can also be classified by ecological behavior related to invasion and evolutionary strategies related to carbon allocation.

Taxonomic Classification. Systematics is the scientific study of biological organisms and their evolutionary relationships. Ideally, organisms are classified systematically according to their presumed genetic relationships, although often this information is unknown. The basis of modern classification is taxonomy, the identification, naming, and grouping of plants according to their traits in common. The accepted taxonomic system used today classifies organisms into a hierarchy of categories: kingdom, phylum (also called division in some botany texts), class, order, family, genus, and species. Recent evidence has shown that an additional category, the domain, occurs above the level of the kingdom; the three recognized domains are Bacteria, Archaea, and Eukarya. All land plants are placed in the domain Eukarya and the kingdom Plantae. Most weeds occur in the phylum Anthophyta (angiosperms, flowering plants), although notable exceptions occur (e.g., some ferns, which are seedless, and conifers, seed plants that have no flowers, are considered weeds). Angiosperms are further divided into the classes Dicotyledones (dicots) and Monocotyledones (monocots).

The next level of classification is the order. Although systematists do not agree on the exact number of orders, the commonly accepted Cronquist system recognizes 64 orders of dicots and 19 orders of monocots (Cronquist 1988). The orders are divided further into families, which, like classes and orders, are comprised of plants whose morphological similarities are greater than their differences. Approximately 383 angiosperm families are currently recognized (318 dicot and 65 monocot). The level of genus includes plants that have common characteristics and that are presumed to be genetically related. The narrowest category of classification is the species, which consists of plants that can interbreed freely (the biological species concept). For practical purposes, however, most species are grouped largely on the basis of anatomical and morphological characteristics (the morphological species concept).

At this point in taxonomic classification, the plant group is given a name, called a scientific name or *Latin binomial*, which consists of both the genus and species names of the plant. For example, Table 1.3 is a list of common agricultural weed species and their Latin binomials. This method of classification is the basis for the organization of all taxonomic texts and many books used to identify weeds.

There are approximately 250,000 species of flowering plants in the world (depending upon which authority is used). However, less than 250 of these, about 0.1%, are troublesome enough to be called major agricultural weeds throughout the world (Holm et al. 1977). It is far more difficult to estimate the number of invasive plant species in nonagricultural habitats worldwide. In the United States, by one estimate, introduced invasive plants comprise from 8 to 47% of the total flora of most states (Rejmánek and Randall 1994). Of the 250 recognized major agricultural weeds, nearly 70% occur in only 12 plant families and over 40% are found in only two families, Poaceae (grass family) and Asteraceae (aster or composite family). Although these observations are fruitful areas of speculation for plant evolutionary biologists, it should be noted that about 75% of world food production is provided by only a dozen crops: barley, maize, millet, oats, rice, sorghum, sugarcane, wheat, cassava, soybean, sweet potato, and white potato. Eight of these crops (the first eight in the list above) are also members of the grass family. The distribution of both the world's worst agricultural weeds and its major crops is quite taxonomically restricted, again pointing to the extreme discrimination and selection that humans apply to vegetation.

It is sometimes necessary to distinguish only broadly among weed species, for example when broad-scale methods of weed control are used. In such situations, distinction among grasses and sedges (monocot) and broadleaf (dicot) plants may be sufficient, and a much abbreviated system of classification is satisfactory. Such a system was once in common use by weed control specialists; a typical description of weeds by this method is shown below (Ross and Lembi 1985, 1999):

Dicots. Plants whose seedlings produce two cotyledons or seed leaves. Usually typified by netted leaf venation and flowering parts in fours, fives, or multiples thereof. Examples include mustards (*Brassica* spp.), nightshades

(*Solanum* spp.), and morningglory (*Convolvulus* spp.). Commonly called broadleaved plants.

Monocots. Plants whose seedlings bear only one cotyledon. Typified by parallel leaf venation and flower parts in threes or multiples of three. Most weeds are found in only two groups, grasses and sedges, although other groups exist.

Grasses. Leaves usually have a ligule or at times an auricle. The leaf sheaths are split around the stem with the stem being round or flattened in cross section with hollow internodes.

Sedges. Leaves lack ligules and auricles and the leaf sheaths are continuous around the stem. In many species the stem is triangular in cross section with solid internodes.

Classification by Life History. Another method used to classify weeds is by the life cycle of the plant. The length of life, season of growth, and time and method of reproduction are used to classify weeds in this way.

Annuals. An annual plant completes its life cycle from seed to seed in one year or less (Figure 1.2). Annuals are often divided into two groups, winter and summer, according to the plant's time of germination, maturation, and death:

Winter Annuals. These plants usually germinate in the fall or winter, grow throughout the spring, and set seed and die by early summer.

Summer Annuals. These plants germinate in the spring, grow throughout the summer, set seed by autumn, and die before winter.

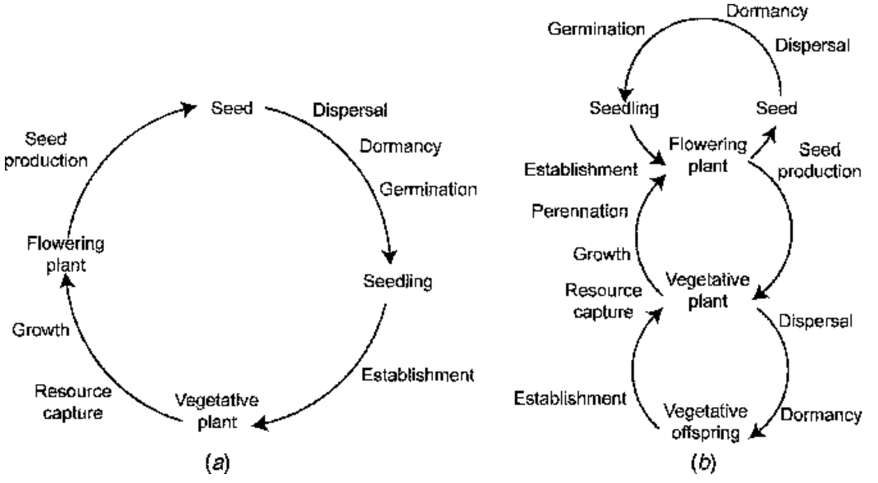

Figure 1.2 (*a*) Life cycle of an annual flowering plant. (*b*) Perennial plant producing both seed and vegetative progeny. (Adapted from Grime 1979, *Plant Strategies and Vegetation Processes*. Copyright 1979 by John Wiley & Sons, Chichester.)

In mild climates, however, it is usual for some winter annuals to germinate in late summer or autumn and for some summer annuals to live throughout the winter. Annual plants are the largest single category of weeds.

Biennials. These plants live longer than one but less than two years. During the first growth phase, biennials develop vegetatively from a seedling into a rosette. Because of this growth habit, biennials sometimes can be confused with winter annuals. After a cold period, vegetative growth resumes, and floral initiation, seed production, and death occur. Biennials are often large plants when mature and have thick fleshy roots. Relatively few weed species are biennials, but some annual plants may behave as biennials under certain conditions and some biennials may behave as short-lived perennials in mild climates.

Perennials. Perennial plants live for longer than two years and may reproduce several times before dying (Figure 1.2). These plants are characterized by renewed vegetative growth year after year from the same root system:

Simple Herbaceous Perennials. Simple herbaceous perennials reproduce almost exclusively from seed and normally do not reproduce vegetatively. However, if the root system of these plants is injured or cut, each piece usually regenerates into another plant. Dandelion (*Taraxacum officinale*), plantain (*Plantago lanceolata*), and sulfur cinquefoil (*Potentilla recta*) are examples of simple herbaceous perennials.

Creeping Herbaceous Perennials. Creeping herbaceous perennials survive over the winter and produce new vegetative structures (ramets) from asexual reproductive organs such as rhizomes, tubers, stolons, bulbs, corms, and roots. These plants also reproduce sexually from seed (genets). Most aquatic weeds, except algae, are creeping perennial plants.

Woody Plants. This is a special category of perennial weed. Plants in this group are characterized by stems that have secondary growth, producing wood and bark, which results in an incremental increase in diameter each year. Some tree, some shrub, and many vine species are considered to be woody weeds.

Classification by Habitat. Weeds can be classified according to where they grow. Most weeds are terrestrial, that is, found on land, but some are restricted to the aquatic environment. Some weeds only infest a particular crop or cropping system, complex of plant communities, or growing condition. Therefore, it is common to find lists and descriptions of weeds that are usually found in particular environments, such as arable land, pastures and rangeland, forests, rights-of-way, or wildlands. These classifications can also be land uses and are described in a following section of this chapter:

Aquatic Weeds. Aquatic weeds are plants that are modified structurally to live in water. They have been categorized further based on their location in the

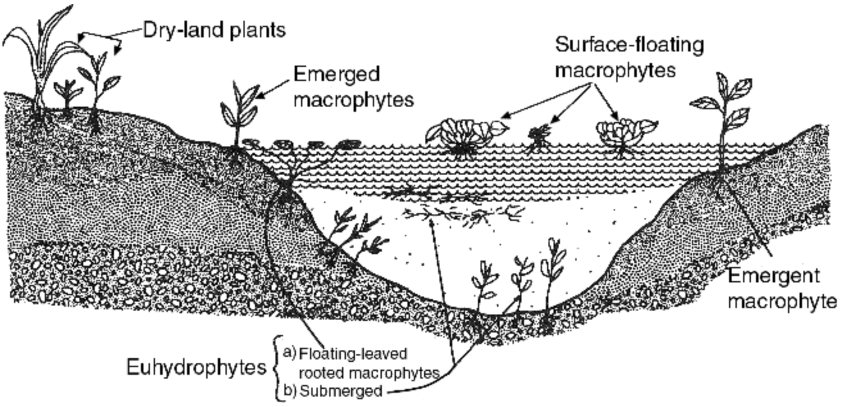

Figure 1.3 Habitats of aquatic weeds. (From Akobundu 1987, *Weed Science in the Tropics: Principles and Practices*. Copyright 1987 by John Wiley & Sons, New York. Reproduced with permission.)

aqueous environment. These categories are depicted in Figure 1.3 as *floating*, *emergent*, and *submerged.* Algae are also considered to be aquatic weeds.

Floating Weeds. These plants rest upon the water surface. Their roots hang freely into the water or sometimes attach to the bottom of shallow ponds or streams.

Emergent Weeds. These typical plants of natural marshlands are often found along the shorelines of ponds and canals. They stand erect and are always rooted into very moist soil.

Submerged Weeds. Although a few floating stems or leaves may exist on the water surface, these plants grow completely under water.

Some weeds and invasive plants occur mainly in riparian habitats, along rivers, streams, or other watercourses. These terrestrial plants, such as Japanese knotweed (*Polygonum cuspidatum*), Himalaya blackberry (*Rubus armenicus*), reed canarygrass (*Phalaris arundinacea*), and saltcedar (*Tamarix* spp.), require the frequent disturbance or high water table associated with rivers, streams, lakes, or ponds. These plants can alter the hydrology of an area and also reduce human access to areas where they occur.

Physiological Classification. Plants differ in their responses to temperature, light, day length, and other factors of the environment. These differences in plant physiology and biochemistry have also been used as a basis for weed classification.

Photosynthetic Pathway. Most plants, called C_3 plants, use the Calvin–Benson cycle exclusively as a method of fixing carbon dioxide, water, and light energy into sugars. This terminology is used because the first stable product of photosynthesis in such plants (phosphoglyceric acid) has three carbon atoms. In some plants, called C_4 plants, the first stable photosynthetic products are four-carbon atom sugars, such as oxaloacetate, malate, and aspartate. This physiological distinction may not seem significant as a means of categorizing weeds. However, these differences in photosynthetic pathway result in substantial biochemical, anatomical, and morphological variation among species. Because of these differences, C_4 weeds are often more efficient at photosynthesis and can be more competitive than C_3 weeds and crops, especially in hot, dry climates. Of the 18 worst weeds in the world noted by Holm et al. (1977), 14 have the C_4 pathway of carbon fixation.

Day Length. Classification by day length is based on a photoperiodic response of flower initiation in plants. Three distinct classes of day length response are known: short day, long day, and day neutral. Although these responses are named for the length of the light period, it is now known that plants detect and respond to the length of the dark period (e.g., short-day plants are actually long-night plants). Weeds that have a short-day response to day length, such as lambsquarters *(Chenopodium album*) and cocklebur (*Xanthium* spp.), are stimulated to flower when days are short and maintain vegetative growth when days are long. Long-day weeds, like henbane (*Hysocyamus niger*) and dogfennel (*Eupatorium capillifolium*), maintain vegetative growth when days are short but are induced to flower under long-day conditions. Other weeds (e.g., nightshades) remain vegetative or flower irrespective of the photoperiodic condition.

Classification According to Undesirability. The term *noxious* weed is a legal term that refers to any plant species capable of becoming detrimental, destructive, or difficult to control. Legally, a noxious weed is any plant designated by a federal, state, or county government as injurious to public health, agriculture, recreation, wildlife, or property (Sheley et al. 1999). Many states, provinces, and countries maintain at least one official list of such weeds so that their introduction can be prevented or restricted. Noxious weeds usually create a particularly undesirable condition in crops, forest plantations, grazed rangeland, or pastures. For example, the presence of noxious weed seed in seed crops can prevent the sale and distribution of that crop across national and international boundaries. Poisonous weeds, which can be landscape ornamentals or occur in pastures and rangeland, represent a special kind of undesirability, since they can be a direct threat to human or animal health.

Ecological Classification. Weeds, and in particular invasive plants, are often classified using ecological categories related to population behavior. As shown in Figure 1.1, the flora of California includes many weeds, which may also be colonizers (taxa appearing early in vegetation succession) or naturalized species (exotic species that form sustainable populations without direct human assistance). By this classification scheme, invasive plants are a subset of naturalized species that are spreading. Not all naturalized taxa are invasive, however, nor are all colonizers considered to be weeds.

Groves (1986) and Cousens and Mortimer (1995) divide the process of invasion by an exotic species into the phases of *introduction*, *colonization*, and *naturalization*. These three phases of invasion are defined as follows:

Introduction. As a result of dispersal, propagules arrive at a site beyond their previous geographical range and establish populations of adult plants.

Colonization. The plants in the founding population reproduce and increase in number to form a colony that is self-perpetuating.

Naturalization. The species establishes new self-perpetuating populations, undergoes widespread dispersal, and becomes incorporated into the resident flora.

Richardson et al. (2000), however, argue that colonization as used by Cousens and Mortimer is a component of naturalization, and the term *invasion* should be distinguished from naturalization and used to describe widespread dispersal and incorporation of an exotic species into the resident flora. Such differences of opinion on terminology pertaining to invasion will likely diminish as further knowledge is gained about the ecological processes involved. The steps of the invasion process are discussed later in Chapters 2 and 3.

***Classification by Evolutionary Strategy*.** Weed species can be organized according to evolutionary strategies that are based on genetically determined patterns of carbon resource allocation. One prevalent theory holds that two fundamental external factors limit the amount of plant material (vegetation) that can accumulate within an area. These factors are *stress* and *disturbance* (Grime 1979). When the extremes of these factors are considered (Table 1.5 and Figure 1.4), the following possible strategies of evolutionary development emerge (see Chapter 2 and Figure 2.10 for a more thorough explanation of this classification approach):

Stress Tolerators. These are plants that survive in unproductive environments by reducing their biomass allocation for vegetative growth and reproduction and increasing their allocation to maintenance and defense. They exhibit characteristics that ensure the endurance of relatively mature individuals in

TABLE 1.5 Plant Evolutionary Strategies Resulting from Disturbance and Stress

	By Intensity of Stress	
Intensity of Disturbance	High	Low
High	Plant mortality	Ruderals
Low	Stress tolerators	Competitors

Source: Grime (1979). *Plant Strategies and Vegetation Processes*. Copyright 1979 with permission of John Wiley and Sons, Inc.

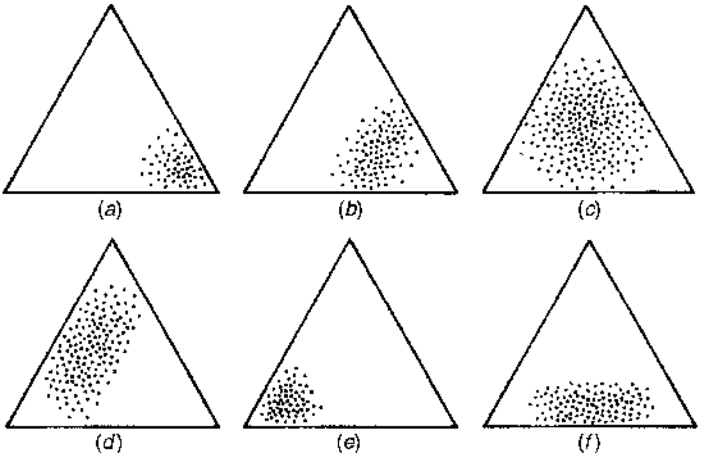

Figure 1.4 Diagram describing range of strategies encompassed by (*a*) annual herbs, (*b*) biennial herbs, (*c*) perennial herbs and ferns, (*d*) trees and shrubs, (*e*) lichens, and (*f*) bryophytes. For the distribution of strategies within a triangle, see Figure 2.10. (From Grime 1977, *American Naturalist* 111:1169–1194. Copyright 1977 by the University of Chicago.)

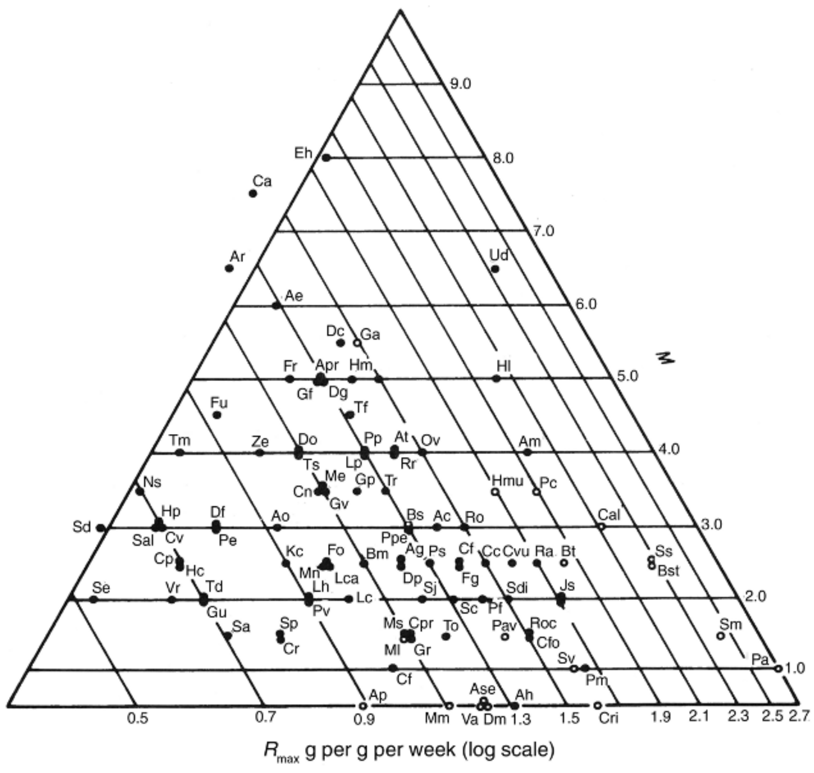

Figure 1.5

harsh, limited environments. The environmental limitation may be caused by physical factors, such as reoccurring drought or flood, or biotic factors, such as use of resources by neighboring plants or herbivory. Species with these characteristics are prevalent in continually unproductive environments or during the late stages of succession in fertile environments.

Figure 1.5 Triangular ordination of herbaceous species. (○), annuals; (●), perennials (including biennials). The morphology index (*M*) was calculated from the formula $M = (a + b + c)/2$, where a is the estimated maximum height of leaf canopy (1, <12 cm; 2, 12–25 cm; 3, 25–37 cm; 4, 37–50 cm; 5, 50–62 cm; 6, 62–75 cm; 7, 75–87 cm; 8, 87–100 cm; 9, 100–112 cm; 10, >112 cm); b is the lateral spread (0, small therophytes; 1, robust therophytes; 2, perennials with compact unbranched rhizome or forming small (<10 cm diameter) tussock; 3, perennials with rhizomatous system or tussock attaining diameter 10–25 cm; 4, perennials attaining diameter 26–100 cm; 5, perennials attaining diameter >100 cm); c is the estimated maximum accumulation of persistent litter (0, none; 1, thin discontinuous cover; 2, thin continuous cover; 3, up to 1 cm depth; 4, up to 5 cm depth; 5, >5 cm depth (Grime 1974). Key to species: Ac, *Agrostis canina* ssp. *canina*; Ae, *Arrhenatherum elatius*; Ag, *Alopecurus geniculatus*; Ah, *Arabis hirsuta*; Am, *Achillea millefolium*; Ao, *Anthoxanthum odoratum*; Ap, *Aira praecox*; *Apr*, *Alopecurus pratensis*; Ar, *Agropyron repens*; As, *Agrostis stolonifera*; Ase, *Arenaria serpyllifolia*; At, *Agrostis tenuis*; Bm, *Briza media*; Bs, *Brachypodium sylvaticum*; Bst, *Bromus sterilis*; Bt, *Bidens tripartita*; Ca, *Chamaenerion angustifolium*; Cal, *Chenopodium album*; Cc, *Cynosurus cristatus*; Cf, *Carex flacca*; Cfl, C*ardamine flexuosa*; Cfo, *Cerastium fontanum*; Cn, *Centaurea nigra*; Cp, *Carex panicea*; Cpr, *Cardamine pratensis*; Cr, *Campanula rotundifolia*; Cri, *Catapodium rigidum*; Cv, *Clinopodium vulgare*; Cvu, *Cirsium vulgare*; Dc, *Deschampsia cespitosa*; Df, *Deschampsia flexuosa*; Dg, *Dactylis glomerata*; Dm, *Draba muralis*; Do, *Dryas octopetala*; Dp, *Digitalis purpurea*; Eh, *Epilobium hirsutum*; Fg, *Festuca gigantea*; Fo, *Festuca ovina*; Fr, *Festuca rubra*; Fu, *Filipendula ulmaria*; Ga, *Galium aparine*; Gf, *Glyceria fluitans*; Gp, *Galium palustre*; Gr, *Geranium robertianum*; Gu, *Geum urbanum*; Gv, *Galium verum*; Hc, *Helianthemum chamaecistus*; Hl, *Holcus lanatus*; Hm, *Holcus mollis*; Hmu, *Hordeum murinum*; Hp, *Helictotrichon pratense*; Js, *Juncus squarrosus*; Kc, *Koeleria cristata*; Lc, *Lotus corniculatus*; Lca, *Luzula campestris*; Lh, *Leontodon hispidus*; Lp, *Lolium perenne*; Me, *Milium effusum*; Ml, *Medicago lupulina*; Mm, *Matricaria matricarioides*; Mn, *Melica nutans*; Ms, *Myosotis sylvatica*; Ns, *Nardus stricta*; Ov, *Origanum vulgare*; Pa, *Poa annua*; Pav, *Polygonum aviculare*; Pc, *Polygonum convolvulus*; Pe, *Potentilla erecta*; Pl, *Plantago lanceolata*; Pm, *Plantago major*; Pp, *Poa pratensis*; Ppe, *Polygonum persicaria*; Ps, *Poterium sanguisorba*; Pt, *Poa trivialis*; Pv, *Prunella vulgaris*; Ra, *Rumex acetosa*; Rac, *Rumex acetosella*; Ro, *Rumex obtusifolius*; Rr, *Ranunculus repens*; Sa, *Sedum acre*; Sal, *Sesleria albicans*; Sc, *Scabiosa columbaria*; Sd, *Sieglingia decumbens*; Sdi, *Silene dioica*; Sj, *Senecio jacobaea*; Sm, *Stellaria media*; Sp, *Succisa pratensis*; Ss, *Senecio squalidus*; Sv, *Senecio vulgaris*; Td, *Thymus druceri*; Tf, *Tussilago farfara*; Tm, *Trifolium medium*; To, *Taraxacum officinalis*; Tr, *Trifolium repens*; Ts, *Teucrium scorodonia*; Ud, *Urtica dioica*; Va, *Veronica arvensis*; Vr, *Viola riviniana*; Ze, *Bromus erectus*. Estimates of R_{max} are based on measurements during the period 2–5 weeks after germination in a standardized productive controlled environment conducted on seedlings from seeds collected from a single population in Northern England. (In Grime 1974, from Grime 1979, *Plant Strategies and Vegetation Processes*. Copyright 1979 with permission of John Wiley & Sons Inc.)

Competitors. These are plants that have evolved characteristics that maximize the capture of environmental resources in productive but relatively undisturbed conditions. These plants have extensive vegetative growth and are abundant during the early and intermediate stages of succession.

Ruderals. Ruderals are plants that are found in highly disturbed but potentially productive environments. These plants are usually herbs, characteristically having a short life span, rapid growth, and high seed production. They occupy the earliest stages of succession.

Grime (1979) suggests that most herbaceous weed species fall into one of two combined strategies, *competitive ruderals* or *stress-tolerant competitors*. Plants possessing the competitive ruderal strategy have rapid early growth rates and competition between individual plants occurs before flowering. Such plants occupy fertile sites and periodic disturbance (e.g., annual tillage) favors their abundance and distribution. Many annual, biennial, and herbaceous perennial weed species found on arable land fit the criteria for the competitive ruderal tactic (Figure 1.4 and Chapter 2).

Stress-tolerant competitors are primarily trees or shrubs, although some perennial herbs also fall into this category (Figure 1.5). Common characteristics of these weeds are rapid dry-matter production, large stem extension, and high leaf area production.

WEEDS AND INVASIVE PLANTS IN PRODUCTION SYSTEMS

There are many books that describe and identify weeds. Some weed species have even achieved worldwide prominence (Table 1.3) (Holm et al. 1977, 1997). Most weeds are important, however, from a more local perspective. The local distribution of weeds is influenced by biotic and abiotic environmental factors that determine habitat types and human activities. Abiotic factors that affect weed occurrence are soil type, soil pH, soil moisture, light quantity and quality, precipitation pattern, and variation in air, soil, and water temperatures. Disturbed areas (either by natural or human causes) also are higher in susceptibility to invasion than habitats that exist for long periods of time in late succession. Biological factors, such as the incidence of insects and diseases on either weeds or associated crops, grazing activities of animals, and plant competition, also can influence the distribution of weeds. It is for all of these reasons that human land uses, such as farming, forestry, range management, and recreation, are major causes of local and regional patterns of weed distribution. Plant species react in different ways when their habitats are disturbed by humans; some species flourish because of the disturbance, whereas others migrate or die and are replaced.

Weeds on Agricultural Land

Many textbooks about modern weed control are quick to point out that weeds have been with us since settled agriculture began, perhaps 10,000 years ago. Weeds must have been known to early farmers because hoes and other “grubbing” implements, artifacts of those ancient times, have been found at archeological sites. In addition, many references account for the detrimental effects of weeds on crop yields, from the early writings of Theophrastus and the Bible to more recent books. These writings have shaped our ideas and definitions of weeds as we saw earlier in this chapter (Table 1.1). Even today, weeds are considered to be just an incidental part of food production in most parts of the world, where farmers are simply people with hoes. The use of modern mechanical and chemical tools to control weeds is actually little more than a century old, even though weeds have been associated with humans since agriculture began. The many reasons to control weeds are described below, while methods and tools for weed management are discussed in detail in Chapters 7 and 8.

Holzner and Immonen (1982) and Marshall et al. (2003) indicate that human action is the most important factor determining the occurrence and distribution of agricultural weed species. They note that many agrestals that accompanied crops for centuries in Europe have now become locally extinct, retreating to their climatic optimum where most survive outside cultivated fields. Haas and Streibig (1982) also note that other weeds have increased in both prominence and abundance as agricultural practices change. Holzner and Immenon suggest several causes for such changes in weed species composition:

- Improved seed cleaning, which results in the local eradication of "specialists" that are unable to grow outside arable land and depend on being sown with the crop
- Abandonment of crops, which leads to loss of specialized weeds
- "Leveling" of environmental conditions, which results in a uniform weed flora
- Increased reliance on crop monocultures, which tends to simplify the weed flora
- Combine harvesting, which allows some weed species to shed seed in the field and distributes the seed of others
- Reduced-tillage and "no-tillage" operations, which promote perennial species
- Reduced competitive ability of short-stature crops and crops treated with chemical growth regulators
- Extensive use of herbicides, which causes sensitive species to become locally extinct or to evolve resistance to the chemical

Reasons for Weed Control. A goal of agriculture for the last half century or more has been to develop efficient methods of weed control in crops, forest plantations, rangelands, and noncrop situations. The search for cost-effective ways to control weeds has often focused on tillage and herbicides as a means to reduce labor requirements and production costs or increase yields. Below are some reasons to control weeds in cropland.

Improve Crop Production. The threat of weeds to crop productivity accounts for most of the human effort devoted to weed control. It is estimated that 10–15% of the total market value of farm products in the United States is lost because of weeds. This loss amounts to about $8 billion to $10 billion per year. Direct losses to forests and rangeland are more difficult to estimate than agricultural losses. Walstad and Kuch (1987) believe that nearly 30% reduction in wood productivity could result because of weed occupation during the early stages of forest plantation formation. The U.S. Forest Service estimates that about 3.5 million acres of National Forest System lands are infested with invasive plants (U.S. Forest Service 2001).

Enhance Product Quality. Weeds have a detrimental effect on crop quality as well as quantity, especially crops that must meet size, color, nutrient content, or contamination-free standards. For example, yields of alfalfa hay in California are often highest during the first cutting when annual weeds are present. However, hay quality is also low when weeds are present in the crop. For example, protein content can fall from over 20% to below 10% when the hay contains large amounts of weeds. Such decreases in grade or quality often mean lowered revenue for growers, since a premium price is usually paid for commodities of high quality.

In some cropping systems, the crop seed and weed seed are so similar in weight and shape that separation at harvest is difficult. Examples are alfalfa and dodder (*Cuscuta* spp.) seed, soybean seed and nightshade fruits, and pea seed that are mixed with the immature flowers of Canada thistle (*Cirsium arvensis*). If the weed material is not removed from these crops by screening, lower price for the commodity will result. For seed crops, the presence of a few noxious weed seed, even less than 1%, usually makes the commodity unmarketable.

Reduce Costs of Production. Weed control is a major reason for many cultural practices associated with crop production. For example, weeds are killed during plowing and cultivation (tillage) to prepare seedbeds for planting. A report by the U.S. National Research Council (2000) indicates that 92–97% of the acreage planted to corn, cotton, soybean, and citrus are treated with herbicides each year. In addition 87% of all citrus acreage and 75% of potato and vegetable crops acreage in the United States are chemically treated for weed control. According to the U.S. Environmental Protection Agency, 60% of the total pesticide sales in the United States in 1999 was for herbicides. There is no doubt that weed control is a costly endeavor in the production of most crops.

Weeds also interfere with harvesting operations, often making harvest more expensive and less efficient. For example, weeds sometimes get wrapped around rollers or cylinders of mechanical harvesters, causing equipment breakdowns and longer harvest times. Up to 50% loss in efficiency and 20% loss of yield can result from weed presence at harvest time.

Reduce Other Pests. Some weed species act as alternate hosts or harbor insects, pathogens, nematodes, or rodents that are crop pests. Numerous specific examples exist of various pest organisms that benefit from the presence of weeds. For example, aphids and cabbage root maggots live on wild mustard, later attacking cabbage and other cole crops. Nightshades are hosts of the Colorado potato beetle. Disease organisms, such as maize dwarf mosaic and maize chlorotic dwarf virus, use Johnsongrass (*Sorghum halepense*) rhizomes to overwinter. Black stem rust uses barberry (*Berberis thunbergii*), quackgrass (*Agropyron repens*), and wild oat (*Avena fatua*) as hosts prior to infesting cereal crops. Rodent damage to orchards can be prevented by weeding around trees before winter.

It also is possible for weeds to aid in the prevalence or spread of certain beneficial organisms that are used to control other pests. In such cases, the weeds act as an alternate source of food or cover for the beneficial organisms, allowing them to survive when the preferred host is not available.

Improve Animal Health. Some weeds are poisonous to animals. However, plants toxic to one species of animal may be harmless to others. For example, larkspur (*Delphinium* spp.) will kill cattle if eaten in sufficient quantity, but sheep and horses are relatively unaffected by this rangeland weed. In contrast, fiddleneck (*Amsinckia* spp.) is highly toxic to horses, while other livestock are relatively tolerant of it. It is estimated that up to 10% of range-grazing livestock may become afflicted by poisonous plants at some time during each growing season.

In addition to direct poisoning, animals may experience other discomforts from association with certain weed species. Some plants [e.g., St. Johnswort (*Hypericum perforatum*), buckwheat (*Eriogonum longifolium*), and spring parsley (*Alchemilla arvensis*)] contain chemicals that make animals abnormally sensitive to the sun, a phenomenon called photosensitization. Other plants contain teratogenic materials that result in fetal malformations. For example, malformed lambs can result if false hellebore (*Veratrum californicum*) is ingested by sheep around the fourteenth day of gestation. Bracken fern (*Pteridium aquilinum*) causes a disease of cattle called "red water" because of the blood-colored urine that is its symptom. This weed causes cancer of the bladder if eaten in sufficient quantities.

Enhance Human Activities. Weeds affect a number of human activities that are difficult to assess in monetary terms. The presence of weeds can reduce real estate values because of the unkempt and unsightly appearance of the property. Dense moisture-holding weed growth aids the deterioration of wooden and metal structures and machinery, further reducing property value. In fire-prone ecosystems, weeds can provide fuel to carry fire, further endangering structures and property. Access and enjoyment of recreation areas are also reduced by weed presence. Other weed impacts and nonmonetary reasons to control weeds are noted in the section on wildlands later in this chapter.

Reduce Effects on Transportation. Some rivers and lakes in the tropics and subtropics are clogged by aquatic weeds, making travel on them nearly impossible. Ross and Lembi (1985) provide an interesting example of how weeds influence transportation costs. They indicate that in 1969 and 1970, 487,000 tons of wild oat seed were inadvertently transported from Canada to the United States along with 16 million tons of grain. The transportation costs for the wild oat were estimated at $2 million, which did not include the $2 million cost for cleaning the grain to remove contamination.

Weeds are kept free from highway intersections to prevent accidents. Airports and railways also keep signs and lights free of weeds so that maximum visibility can be maintained. Power line rights-of-way are kept free of tall growing vegetation to prevent power outages if trees contact power lines during storms and to increase access to downed power lines.

Reduce Risks to Human Health. Toxicants or irritants produced by weeds can cause serious health problems for some people. These discomforts or illnesses include hay fever, dermatitis, and direct poisoning. Hay fever afflicts millions of people each year. It is caused by an adverse effect of proteins associated with the pollen of certain plants on the respiratory system of susceptible people. Ragweed (*Ambrosia* spp.) is best known for causing hay fever. However, pollen from many other broadleaved plants, grasses, trees, and shrubs causes similar allergic reactions. Each year, many people are troubled by poison ivy (*Rhus radicans*), poison oak (*R. diversiloba*), and poison sumac (*R. vernix*). These plants produce and store a toxic substance called urushiol that causes intense itching and rash upon contact with the skin. Many plants contain toxic substances that when ingested cause sickness or death to humans. Toxic substances in weeds include alkaloids, glycosides, oxalates, resins and resinoids, volatile oils, acrid juices, phytotoxins (toxalbumens), and minerals. There are few poisons, including synthetic substances and minerals, that approach the strength and violence of illnesses caused by some plant-produced toxins.

Weeds in Managed Forests

There are many natural conditions such as climate, soil type and fertility, topography, and events like hurricanes and wildfire that shape forested landscapes. Following "catastrophic" disturbances, it is common for forests to undergo a sequence of vegetation changes that result in a forest nearly identical to the one previously destroyed. This process of natural forest reestablishment through successive changes in vegetation composition is called secondary succession (Chapter 2). Following a radical disturbance, like a fire or clearcut, a new patch in the physical environment is once again available for colonization by plants. In such situations, "pioneer" tree (e.g., poplar, birch, alder, and some conifers) or shrub species (e.g., ceanothus or manzanita) (Figure 1.6) are quick to colonize the disturbed areas and can dominate them for years to decades. This rapid recolonization by usually native pioneer species, although a normal stage in succession, can delay the revegetation of disturbed sites with more economically desirable trees (Balandier et al. 2006).

The major disturbance to forests of any region is the harvesting of wood by humans. It was estimated in 1989 that each year the world loses 37 million acres of forest in this manner (Perlin 1989) and current estimates remain unchanged [Food and Agriculture Organization (FAO) 2001]. In temperate conifer forests

Figure 1.6 A young Douglas-fir plantation following logging and artificial regeneration. (Photograph by S. R. Radosevich, Oregon State University.)

logging, especially without any follow up reforestation activities, led to the gradual replacement of conifers by less desirable herbaceous, shrub or hardwood species. Sutton (1985) pointed out that in Canada large-scale weed problems have occurred due to exploitation forestry, which strives to maximize profits and minimize costs. Weed problems were exacerbated by poor choice of forested stands to harvest, season and method of harvesting, intensity of utilization, and lack of attention to regeneration (Sutton 1985). Walstad and his associates (1987) similarly indicated that hardwoods occupy 32% of the prime timberland in western Oregon that was once dominated by conifers.

Forest Regeneration. Most forests regenerate naturally following disturbance given enough time. However, logging activities and land clearing are the principal disturbance factors that both set up and modify the natural patterns and time frames of succession so that native and exotic weed species are favored and even dominate many forest types (Balandier et al. 2006, Wagner et al. 2006). The ability of a site to regenerate, as well as the composition of species following such disturbances, is most dependent on the type, frequency, and severity of the tree removal operation (Kimmins 1997). In the coastal Douglas-fir forests of the

U.S. Pacific Northwest, the impact of both native and exotic plants is currently restricted to the earliest stages of forest succession that follow logging and fires. Ruderal exotic forbs, such as Canada thistle or woodland groundsel (*Senecio jacobaea*), and some exotic shrubs, such as Scotch broom (*Cytisus scoparius*), displace native early seral vegetation in some locations and reduce tree regeneration in others. Though exotic plants are typically eliminated from the plant community after a few years to a decade of forest stand development, exotic shade-tolerant species are capable of persisting and/or invading forest understories if relatively open stand conditions are maintained through clearcutting or severe silvicultural thinning. In particular, false-brome (*Brachypodium sylvaticum*) poses a serious threat to forest understory communities in that region (Zouhar et al. 2007).

Several techniques, collectively known as *artificial regeneration*, have been used successfully to replant many logged-over areas in many countries. This method usually involves collecting seed of preferred tree species, germinating and growing the seedling trees in nurseries, outplanting them to field sites, and following this by intensive chemical weed control. Wagner et al. (2006), surveying 60 studies, found that the most intensive vegetation management treatments always improved crop tree growth, although results varied by location, tree species, and length of time from experiment initiation. Despite these successes in projected crop tree biomass yield, important questions still remain about the ecological (Balandier et al. 2006), social, and economic desirability of converting vast acreages of naturally regenerated forests into tree farms.

Weeds in Rangelands

The destruction and replacement of vegetation by humans are now common occurrences over most of the world, with a loss in primary productivity and floristic diversity often being the result. The invasion of exotic plants is both a cause and a consequence of such environmental manipulation. However, it is rare that invaders cause the replacement of most or all of the plant and animal species in a disturbed ecosystem (Billings 1990). A possible exception to this generalization is rangeland weeds. In this system of production, species replacement following disturbance has been so complete that only a sketchy picture of predisturbance conditions remain. We offer the sagebrush (*Artemisia tridentata*)–cheatgrass (*Bromus tectorum*) steppe as an example (Figure 1.7).

The chance introduction of cheatgrass before the turn of the last century to the Great Basin of North America altered the entire native shrub ecosystem of that region. D'Antonio and Vitousek (1992) after Billings (1990) indicate that its introduction provides a classical case of biological impoverishment where the concomitant environmental change allows successful replacement of indigenous vegetation. In this case, native perennial bunchgrasses and shrubs, particularly sagebrush, were first grazed by large herbivores, then invaded by cheatgrass, and subsequently subjected to range fires (Figure 1.8).

Figure 1.7 Cheatgrass (*B. tectorum*) in former sagebrush–bunchgrass range. (Photograph by S. R. Radosevich, Oregon State University.)

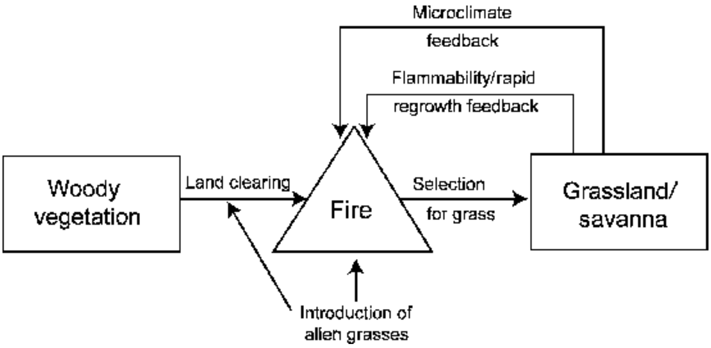

Figure 1.8 Conceptual diagram of land clearing and grass–fire cycle (modified from Fosberg et al. 1990) to illustrate influence of alien grass invasion. In some cases grass invasion itself is sufficient to initiate grass–fire positive feedbacks; more often, it interacts with human-caused land use change. (From D'Antonio and Vitousek 1992, *Annu. Rev. Ecol. Syst.* 23:63–87. Copyright 1992. Annual Reviews Inc.)

Original Vegetation and Early Land Use History of Great Basin. Billings (1990) and others (Klemmedson and Smith 1964, Mack 1984) indicate that the western Great Basin was not part of the bison range of the North American Great Plains because the rhizomatous C_4 grasses on which the bison thrived cannot grow on the summer-dry steppes of this region. Rather, perennial C_3 bunchgrasses of the genera *Poa*, *Festuca*, *Agropyron*, and *Stipa* dominated the grass stratum of this sagebrush ecological formation. Apparently, the native bunchgrasses of the region also did not carry fire well because range fires in the sagebrush–bunchgrass steppe, in contrast to the Great Plains, were rare.

The native ungulate herbivores were antelope, deer, desert bighorn sheep, and elk which, because of their smaller size and numbers than bison, created a relatively light impact on the sagebrush–grass community. During the 1840s and 1850s, the first overland wagon trains to Oregon and California introduced domestic livestock to the region. Thus, the first grazing impacts in the area appeared along the Oregon and California Trails. For example, Beckwith, (1854) (in Billings 1990) pp. 305–306 an early explorer, noted the following in June 1854: "Fine droves of cattle, which had been wintered near Great Salt Lake, passed today on their way to California, and one or two large flocks of sheep are but a few miles behind them. The more experienced stock-drovers to California send their cattle back from the river to feed on the nutritious grass of the hills."

Watson (1871) made one of the first good botanical descriptions of the area, listing 59 species of Poaceae. Cheatgrass was not among the species listed, suggesting that it had not yet arrived to the intermountain region of North America. In the summer of 1902, Kennedy (1903) made the first survey of range conditions in northern Nevada and 50 years later Robertson (1954) retraced Kennedy's route. Billings (1990) compared the writings of both men and noted the following differences in range conditions that occurred over that 50-year time period:

- Desirable livestock browse shrubs decreased.
- Bluebunch wheatgrass (*Agropyron spicatum*), a prime forage bunchgrass, decreased from "abundant" to "generally absent" or "less than 5% density."
- Annuals, notably cheatgrass, not present in 1902 had increased to an "extreme degree."
- Burn scars were "absent or unimportant" in 1902. In 1952 much of the route was bordered or crossed by "burned-off range" and covered by cheatgrass or little rabbitbrush (*Chrysothamnus viscidiflorus*).
- Big sagebrush replaced "bluegrass meadows" at lower elevations.
- "Stream channels had eroded deeper and wider."

All of the conditions in the above list indicate heavy grazing, cheatgrass invasion, and occurrence of repeated fires.

Introduction of Cheatgrass and Fire. According to Mack (1981, 1986), the first collections of cheatgrass in the Great Basin were from Spenses' Ridge, British

Columbia, in 1889; Ritzville, Washington, in 1893; and Provo, Utah, in 1894. Each location is in a wheat-growing area, which suggests that cheatgrass seed may have arrived as a contaminant of crop seed. From these beginnings, the species spread throughout eastern Washington and Oregon, southern Idaho, northern Nevada, and Utah. By the 1930s, it was abundant throughout the entire sagebrush steppe. Billings believes that the rapid spread of the grass across the region was aided by railroad stock cars and grazing animals that were subsequently driven onto the rangelands. In addition, the climate of the Great Basin was ideal for the new weed, which, being a winter annual, requires moist soils during the cold season and cold winter weather while vegetative in order to flower the following spring.

Billings (1990) and D'Antonio and Vitousek (1992) indicate that once cheatgrass became established, the region was set for wildfires (Figure 1.8). Cheatgrass usually sets seed, dies, and dries up by June in most areas of the region. Thus, a supply of fuel that was nonexistent in the original open sagebrush–bunchgrass ecosystem became available. Without fire, cheatgrass simply invades the overgrazed sagebrush range, where it forms an ephemeral annual stratum in that community. However, once this plant community experiences either lightning or human-caused fire, the sagebrush is killed. Since this shrub cannot sprout following fire, the native shrublands of the Great Basin have been replaced by vast expanses of annual grassland. Upland areas of the Great Basin, notably the pinyon pine–juniper biome, are now increasingly threatened by a similar process of vegetative change.

Management of Cheatgrass. The assemblage of features that allowed cheatgrass to invade the Great Basin have also largely prevented its eradication. For example a plant capable of germinating over an eight-month period, as cheatgrass can, is nearly impossible to control completely in the seedling stage. Mowing or grazing in early spring makes little difference since developing seed of the species are readily viable and capable of germinating the following autumn. Even when fire removes all vegetative plants, new ones emerge from seed reserves in the soil and, of course, further reentry is always possible. Furthermore, as we will see in Chapter 4, the plant has little problem adapting to the wide variety of environmental conditions of both rangeland and cultivated fields. While cheatgrass is clearly a permanent member of the Great Basin vegetation, it may now be possible to restore local areas of cheatgrass infestation to a more pristine and desirable state (Briske et al. 2003, Sheley and Krueger-Mangold 2003).

On the other hand, and from the standpoint of volume of herbage produced and extent of area covered, cheatgrass is unquestionably the most important forage plant in the Great Basin now (Klemmedson and Smith 1964). It provides the bulk of early spring grazing for all classes of livestock on millions of acres in the arid West. While it is not easy to comprehend the economic importance of this ecological change, the extent and permanence of it are readily comprehensible.

INVASIVE PLANTS IN LESS MANAGED HABITATS AND WILDLANDS

Certain forests, deserts, prairies, beaches, marshes, estuaries, and riparian areas have been protected from disturbance or designated as wilderness throughout the world. Wilderness and similarly managed natural areas, such as national parks and monuments, provide many benefits to society. These benefits include the preservation of biodiversity, unique natural features, and watersheds as well as opportunities for recreation and personal fulfillment. Although land management agencies place a high priority on protection of natural ecosystems and wilderness areas, some of these benefits are threatened by increasing levels of human activity within and outside areas designated for protection. The introduction of exotic species into such areas is of particular concern due to the potential for irreversible impacts on the natural ecosystems that such areas represent (Aldo Leopold Wilderness Research Institute 2003, D'Antonio et al. 2004).

Three research areas were identified by the Aldo Leopold Wilderness Research Institute to address the question of exotic plant invasion into wilderness:

- Understanding the introduction, spread, and distribution of exotic species within wilderness
- Understanding the effects of exotic species on wilderness values
- Identifying and evaluating management options and their consequences

Parks and her associates (2005a,b) examined the patterns of invasive plant diversity in mountainous ecoregions of the northwestern United States. Their analysis found that altered riparian systems and disturbed forests were especially vulnerable to exotic plant invasion. Conversely, alpine areas, forests, and grasslands designated as wilderness were still relatively unaffected by invasive plants, with introductions often being restricted to campsites, roads, or trails. The predominance of wilderness throughout much of the western United States is believed to contribute to the lower incidence of invasive plants in mountainous ecoregions of that area compared to other regions. Human settlement and intense land use at low elevations were identified as factors that enhance invasive plant introductions (Parks et al. 2005a,b, Mack et al. 2000).

Local versus Regional Perspectives about Weeds

Most of the previous discussion has focused on weeds and invasive plants at the individual plant, species, or field level of scale. However, weeds may extend much farther than individual fields and the benefits and costs of weed control may extend much further than to individual farmers, foresters, or land managers. For example, consumers of agricultural products or users of natural resource areas may benefit from lower priced food, more abundant lumber, or greater access to recreational areas as a result of weed control. These same people also may have legitimate concerns about the presence of chemical residues in food or water, public safety, soil erosion, or other impacts that weed control techniques have on them or their environment. Others may be concerned about the overall vitality of an industry or profession as new technologies are introduced and others are regulated. All of these issues extend beyond the aims of individuals to the needs, wants, and expectations of a society. These issues are explored further in Chapters 2 and 9.

Weeds in Regional and Global Context

There are many examples of the widespread regional or even global distribution of weeds. One of the earliest examples is that of Hitchcock and Clothier (1898), which describes the distribution of native and introduced weeds in Kansas as that land was being developed for agriculture. A similar study was accomplished by Mason (1932), who described the occurrence of wild oat throughout several provinces of central Canada (Figure 1.9). These studies are augmented by more recent descriptions of widespread infestations of weed species, for example, leafy spurge (*Euphorbia esula*), purple loosestrife (*Lythrum salicaria*), downy brome (also known as cheatgrass) (*B. tectorum*), Paterson's curse (*Echium platagineum*) (Auld and Tisdel 1988), and lantana (*Lantana camara*) (Figure 1.10) (Cronk and Fuller 1995). The ability to disperse widely is a common characteristic of many weed and invasive plant species, which has been exacerbated in recent decades by increasingly global movement of humans and goods. Any harmful organism that is spreading or has the capacity to spread poses a threat to uninfested areas without regard for ownership boundaries. Thus, a spreading species represents a problem to more people than just those whose land it currently occupies. Such situations make a strong case for legislation (weed laws), quarantine districts, or other governmental interventions to reduce or slow the spread of weeds and

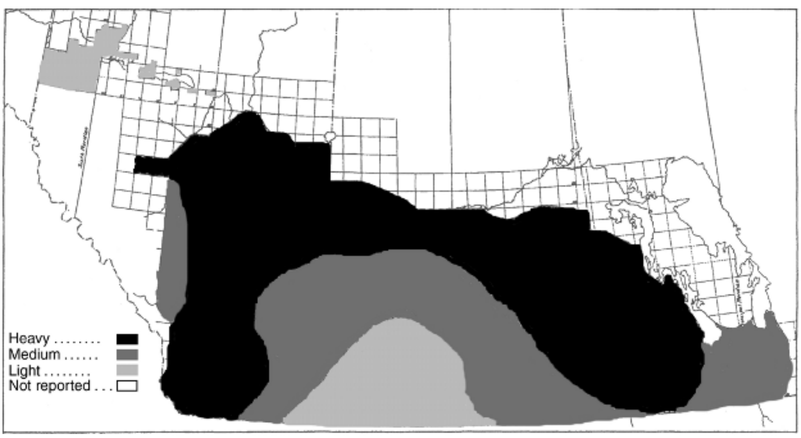

Figure 1.9 Distribution and prevalence of wild oat in Alberta, Saskatchewan, and Manitoba in 1931. (Modified from Mason 1932.)

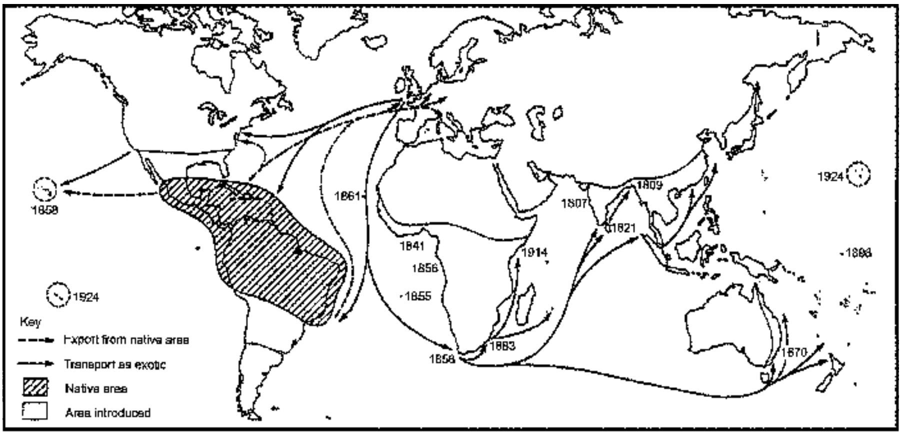

Figure 1.10 Some invaders, such as the shrub *L. camara*, have been introduced repeatedly in new ranges, the result of global human colonization and commerce. As the array of estimated years indicates, lantana was introduced throughout the nineteenth and twentieth centuries in many subtropical and tropical areas. In each new range it has become highly destructive, both in agricultural and natural communities. (Cronk and Fuller 1995, from Mack et al. 2000, *Ecol. Appl.* 10:179–200. Copyright 2000. Ecological Society of America.)

invasive plants. Furthermore, governmental objectives for weed suppression may be less constrained by cash flow than those of individual farmers, ranchers, or forest land owners (Auld and Tisdel 1988).

SUMMARY

Weeds are a category of vegetation that exists because of the human ability to select among plant species. In most cases, the value of a weed is determined by the perception of its viewer. Weeds have been described and defined in both anthropomorphic and biological terms. They also may describe a condition of the land or environment and they affect almost everyone at some time or place. Some of the negative aspects of weeds are lowered crop yields, animal discomfort and death, poor product quality, increased costs of production and harvest, higher incidence of other pests, and reduced human health and activities. Invasive plants, unlike many agricultural weeds, can successfully occupy and spread to new "natural" habitats apparently without further assistance from humans.

Weeds and invasive plants have been classified in numerous ways. Some methods used to classify weeds are by taxonomic relationships, life history (annuals, biennials, perennials, etc.), habitat, physiological differences, degree of undesirability, ecological behavior, and evolutionary tactic. Weeds are distributed widely throughout the world, inhabiting most agricultural, and managed forest and rangeland systems. However, weeds account for less than 0.1% of the flowering plants of the world. Many environmental, biological, and human factors influence distribution of weed species, although humans are the main factor for the continued evolution of weeds and spread of invasive plants into new regions of the world.