FIGURE 4 *Phakopsora pachyrhizi* (soybean rust) is a soybean pathogen that originated in East Asia and is increasingly common in soybean production worldwide. (Photograph courtesy of Dr. Glen Hartman, USDA-ARS National Soybean Research Laboratory, Urbana, Illinois.)

disease follows, wiping out entire crops. The primary defense against this, and many other plant pathogens, is to breed resistant crop varieties.

Prevailing winds can carry fungal spores hundreds of miles. Soybean rust (*Phakopsora pachyrhizi*; Fig. 4), native to East Asia, was first identified in the U.S. soybean production region in 2004. Soybeans are the main economic species affected by this fungus, but there are many alternate hosts, including another invader, kudzu (*Pueraria montana*), and so soybean rust can overwinter easily and infect new plants. Wind then disperses new spores to uninfected regions. Fortunately, fungicides have proven very effective against this pathogen.

Sometimes, one pest may facilitate another. In the case of maize dwarf mosaic virus (MDMV), three pests interact to complete the disease cycle. Aphids that feed on infected maize can be infected within minutes; they then carry it to other maize plants or *S. halepense*, an alternate host. Because *S. halepense* is a perennial, it provides an excellent overwintering location for MDMV to begin the infection cycle anew the following growing season.

PREVENTING FUTURE AGRICULTURAL INVASIONS

Preventing agricultural invaders is considered the best strategy for reducing their impacts on both agriculture and natural ecosystems. This should involve careful screening of new crop species and varieties for potential invasiveness and to ensure that insects and diseases are not introduced along with crop material. Increased interest in biofuel production means active interest in new crop introductions in many parts of the world. Biofuel crops share many characteristics with invasive plants and should be subjected to particularly stringent review.

There is much scope for managing agricultural systems to reduce the opportunity for invasion, the impacts of invaders, and the invaders that agricultural systems supply to natural areas. These include improved sanitation to prevent transport of propagules from one field to another, improved monitoring to facilitate early detection and eradication or containment of invaders, and increased crop and landscape diversity, which can improve biotic resistance to invaders.

SEE ALSO THE FOLLOWING ARTICLES

Genotypes, Invasive / Herbicides / Integrated Pest Management / "Native Invaders" / Parasitic Plants / Pathogens, Plant / Seed Ecology / Weeds

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AGROFORESTRY

SEE FORESTRY AND AGROFORESTRY

ALGAE

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Algae are an exceptionally diverse group of generally autotrophic marine, freshwater, and terrestrial organisms that lack true tissues and organs and are thus not typically considered true plants. They comprise a group of eukaryotic

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uni- or multicellular organisms that possess nuclei and chloroplasts bound with one or more membranes. While cyanobacteria (blue-green algae) were once lumped into the group "algae," they are not eukaryotes and so are not treated as algae here. Small single-celled algae are often described as phytoplankton, while larger multicellular species are described as macrophytes, if growing in freshwater, or seaweeds, if growing in the ocean. In this article "invasive introduced algae" are treated as any species of marine, freshwater, or terrestrial algae that has been introduced into a region where it does not naturally occur, has become highly successful, and is causing ecological or economic harm.

ALGAL INVASIONS

Algae can take on numerous growth forms and can exist as single cells, colonies, or more complex multicellular forms (e.g., filamentous forms, cylindrical forms, sheets, crusts, etc.). These primary producers are common components of most ecosystems around the world and are responsible for producing more than 70 percent of the world's oxygen. Algae can form blooms in their native environments, where they may grow excessively in response to some biotic or abiotic trigger (e.g., nutrient enrichment, pollution), and they may form blooms associated with being introduced into new environments.

While many species of algae have been introduced around the world to new environments, marine algae appear to be the most invasive. Marine algal invasions have occurred and continue to occur around the world as a result of many vectors, including intentional aquaculture introductions as well as accidental introductions associated with shellfish aquaculture and ship traffic. While few introduced algal species become invasive, those that do have been shown to have large negative impacts on associated species and communities. Control or eradication of algal invaders is extremely costly and has been successful in very few cases.

GLOBAL PATTERNS

The majority of documented cases of invasive introduced algae involve marine seaweeds. Out of some 277 species of marine algae that have been introduced around the world, only 13 can be considered invasive. However, many of these species are invasive in more than one locale, region, or ocean basin. Invasive introduced marine algae include members of the Chlorophyta (3), Phaeophyta (3), and Rhodophyta (7), with the number of invaders being proportional to the size of the taxonomic group. While many phytoplankton species can form massive blooms in their native ranges and cause adverse ecological impacts, very few species have been definitively identified as being invasive, probably because of difficulties in taxonomy and incomplete distributional data. Among freshwater taxa, many flowering plants are known to be invasive, but only a few species of algae, specifically some diatoms, have become successful invaders.

Despite the large number of algal species that are considered to be nonnative introductions, very little is known about most species. In fact, the majority of studies that have examined invasive algae have focused on a few high-profile species. Furthermore, many algal invasions are likely to have occurred prior to scientific study or the emergence of the field of "invasion biology." Thus, the results and summaries presented below should be treated with caution, as it is difficult to make generalizations about the effects of invasive introduced algae on invaded communities.

SPECIES OF CONCERN

Among the marine algae or seaweeds, only two species are currently listed on the IUCN Invasive Species Specialist Group's list of the 100 worst invaders in the world (see Appendix); these are the green alga *Caulerpa taxifolia* and the brown alga *Undaria pinnatifida* (Figs. 1A and B, respectively). *Caulerpa taxifolia*, otherwise known as the "killer alga" for its reputation in the Mediterranean Sea, has been introduced to three oceanic basins: the Mediterranean, Australia, and the west coast of North America. In all cases, it has become highly invasive. *Caulerpa* is native to tropical waters around the world, but a cold water–tolerant strain was first introduced to the Mediterranean via accidental release from the Monaco Aquarium in the 1980s. This aquarium strain grows nearly ten times larger than *Caulerpa* in its native habitats and is known for monopolizing soft-bottom and seagrass habitats, where it outcompetes native species and impacts the livelihoods of fishermen. The kelp *Undaria pinnatifida* is native to Asia and has been introduced to Europe, the Mediterranean, Australia, New Zealand, and the west coast of North America, where it has become highly successful in most cases. This species is cultivated in Japan (where it is known as *wakame*) for human consumption, and it was intentionally introduced to parts of Europe. Causes of *Undaria* introductions in other parts of the world remain unknown but are believed to be associated with ship traffic (hull fouling and ballast water). Impacts of *Undaria* on native communities remain undocumented in many cases, but it has been shown to alter community structure and reduce native species diversity.

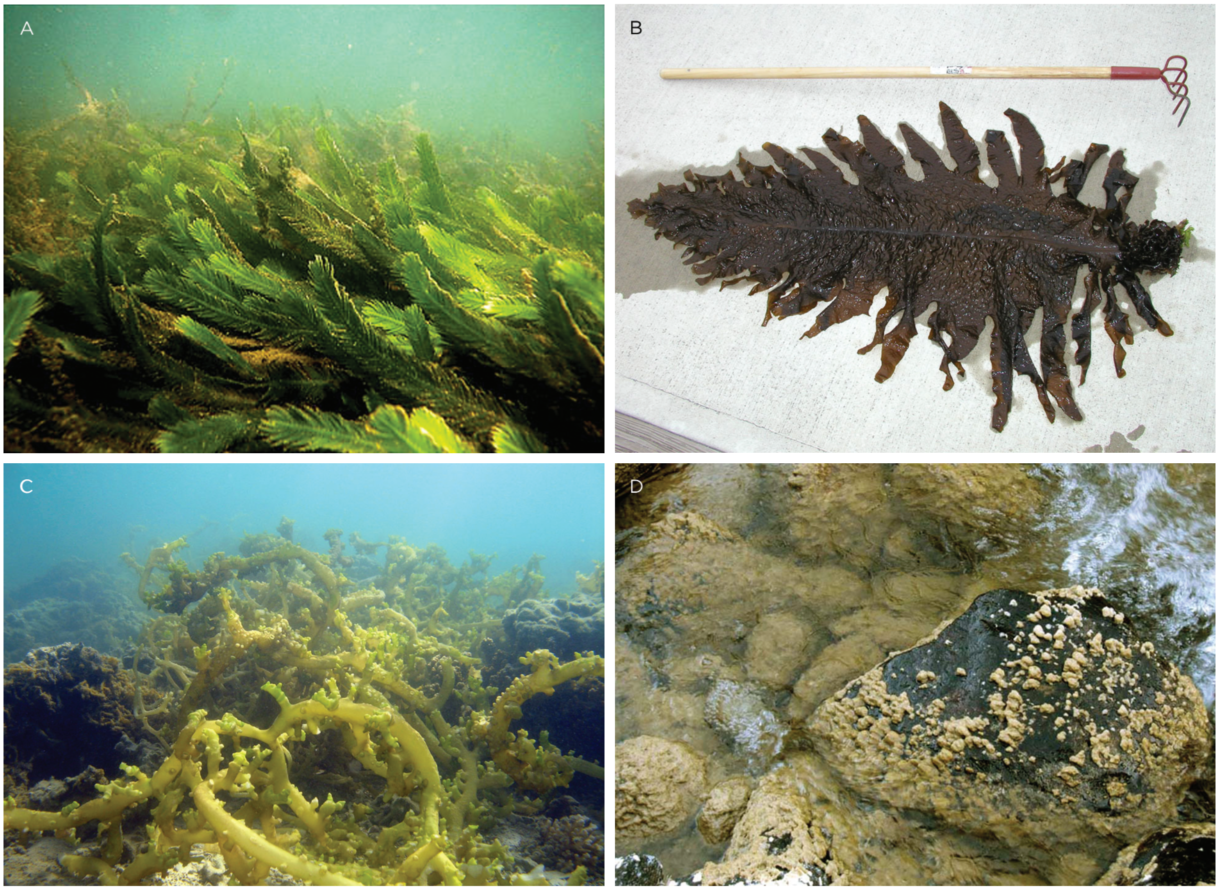

FIGURE 1 Photographs of some of the most invasive introduced algae from around the world. (A) *Caulerpa taxifolia* (the killer alga) dominating habitat in the Mediterranean; (B) the invasive kelp *Undaria pinnatifida* from Monterey Bay, California; (C) *Kappaphycus* spp. in Kane'ohe Bay, Hawaii; and (D) the invasive freshwater diatom *Didymosphenia geminata* in lakes of the northeastern United States. (Photographs courtesy of the author.)

Numerous other species of marine algae have been considered to be invasive based on studies that have explicitly examined the ecological impacts of the invaders on communities in which they have been introduced. These include (1) the red algae *Gracilaria salicornia*, *Dasya sessilis*, *Acrothamnion preisii*, *Womersleyella setacea*, *Kappaphycus alvarezii* (Fig. 1C), and *Eucheuma denticulatum*; (2) the brown algae *Fucus evanescens* and *Sargassum muticum*; and (3) the green algae *Codium fragile* and *Caulerpa racemosa*.

The freshwater diatom *Didymosphenia geminata*, otherwise known as Didymo or "rock snot," is native to the cool temperate regions of the northern hemisphere (Fig. 1D). However, it was recently found in New Zealand and appears to be spreading out within its native range in North America and Europe; it is now considered to be one of the worst freshwater invasive introduced algal species. Although it is a single-celled alga, it can form large colonies that attach to the bottom of both lakes and streams where it smothers native biota including fish, plants, and invertebrates. It is described as having an unpleasant appearance and may cause adverse effects to the fishing and tourism industry. Didymo is believed to spread to new locations though human activity, primarily as a result of algal cells hitchhiking on footwear or fishing gear.

VECTORS OF INTRODUCTION

Based on a recent review of seaweed invasions around the world, a number of vectors were identified and ranked according to prevalence. Interestingly, the mode of introduction for the majority of introduced seaweeds has been undocumented. Of those introductions where the vectors have been identified, ship traffic (including both ballast water and hull fouling) was the most significant source of algal introductions. Because algae are photosynthetic organisms and require sunlight to grow, ballast introductions are not as likely as hull fouling to transport algal propagules. A number of algal introductions have also occurred as a result of aquaculture. Several seaweed species are cultivated around the world in open water cultures both for human consumption and for production of colloids (agar and carrageenan), which are used as thickening agents in a number of human products such as toothpaste, shaving cream, hair products, low-fat foods, ice cream, and even beer. In most cases, these seaweed introductions have not resulted in severe invasions. However, in the Hawaiian Islands, a number of seaweeds introduced for experimental aquaculture in the 1970s have become invasive on the coral reefs, where they cause large ecological and economic impacts (Fig. 1C; see section below on impacts of seaweed invasions). A number of other invasive introduced algae arrive in new locations indirectly through shellfish aquaculture. Algae can "hitchhike" on the shells of oysters and other shellfish, and as these species are transported around the world for human consumption, the algae go with them. Algae have also been commonly used as packing material to pad shellfish when they are transported from one location to the next. Other common vectors for the introduction of algae to new locations include fishing gear, SCUBA gear, and clothing, as small algal fragments can become entangled in these items when they move from location to location. Aquarium introductions have also occurred accidentally though discharge pipes or intentionally when people want to free or discard the organisms living in their home aquaria. Lastly, in the past researchers introduced algae to new environments for the purpose of research, but today, intentional introductions are no longer common outside of the aquaculture industry.

IMPACTS OF INVASIVE INTRODUCED ALGAE

Despite the large number of algae (277 species of marine algae and an unknown number of freshwater algae) that are known to have been introduced to new locations around the world either intentionally or accidentally, very little is known about the impacts these species are having since introduction. A recent review of the scientific literature revealed a total of 68 published studies that have explicitly examined the ecological impacts of seaweed invaders on the invaded communities. A variety of response variables have been used to assess impacts, including changes in the abundance and diversity of the native biota and changes in productivity, community structure, community function, and feeding and performance of native species. The majority of these studies reported that the seaweed invaders caused negative impacts or changed community structure in the invaded communities. However, in some cases, seaweed invaders have been shown to increase the abundance, diversity, and feeding rates of native species. It is important to note here that although the majority of studies have documented negative impacts of invaders on the native biota, only a very small number of seaweed invaders have been studied in any detail. Of the 277 species of introduced marine algae, only a small number of these species are truly considered invasive, but those that are invasive have had large negative impacts. *Caulerpa taxifolia* is the best studied of the invasive seaweeds, and it has been shown to negatively affect performance, feeding, diversity, community function, and abundance of native species. Other species that have been shown to have negative effects on invaded communities in at least ten different cases include *Codium fragile* ssp. *tomentosoides*, *Sargassum muticum*, *Caulerpa racemosa*, and *Euchema denticulatum*. In the case of freshwater algal invasions, few studies have quantified impacts, but anecdotal evidence suggests that when the diatom Didymo blooms, it may reduce oxygen levels in water bodies at night while the algae are respiring and cause hypoxia and subsequent harm to native species. Didymo blooms also reduce light levels and may negatively affect other plant or algae species growing nearby. Didymo blooms, along with many other algal blooms, appear unpleasant to tourists and may negatively impact recreational activities.

At least one study has documented the economic costs associated with an invasive introduced alga. The red seaweed *Hypnea musciformis* was first introduced to the island of Oahu in the Hawaiian Islands in the 1970s for experimental aquaculture. Over the next several decades, this species spread to a number of other islands in the main Hawaiian Islands, and it began forming extensive, large blooms on the island of Maui. The blooms, which are believed to be associated with nitrogen and phosphorus pollution occurring in the nearshore environment, result in large amounts of rotting algal biomass that accumulates on the beaches and creates an unpleasant environment and a very foul odor. In a formal economic analysis, Van Beukering and Caesar (2004) determined that the city and county of Maui were losing an estimated $20 million per year in costs associated with beach cleanups, reduced property values, and reduced occupancy rates in hotels and condominiums in bloom-affected areas. The authors concluded that the costs associated with preventing the introduction of this invasive alga would likely have been far less than the costs associated with managing the current problem. Several other studies have anecdotally noted economic impacts of seaweed invaders as a result of colonization and fouling of aquaculture facilities, but no quantitative data are currently available.

MANAGEMENT AND ERADICATION

Invasive introduced algae can be managed in a number of ways and during a number of different stages (i.e., transport, establishment, and spread) of the invasion process. By far, the best form of managing invasive introduced algae is to prevent introductions from occurring altogether. This is especially true for algal species that have proven to be invasive in other locations around the world or for species that are closely related to known invasive species. Taxonomy has in some cases been used to predict species that are more likely to become invasive than others, and taxonomic risk assessments are often used for other taxa (e.g., flowering plants) as a screening mechanism to prevent introductions. Species traits have also been used to predict invasive algal species for 113 species of macroalgae in Europe. Trait categories were grouped according to dispersal ability, establishment, and ecological impact, and introduced species were compared with native species to determine whether some traits were good predictors of invasiveness. Certain characteristics, such as an alga's ability to disperse through vegetative propagation, were common among many invasive introduced algal species. Other mechanisms that can help to prevent the introduction of algae into new locations include strict guidelines for the shipping industry to manage both ballast water and hull fouling introductions; these regulations will of course need to operate at an international level. Aquaculture activities should be strictly regulated to prevent algae from (1) "hitchhiking" on the shells of invertebrates, and (2) escaping from farm plots in open water systems. Finally, educational programs can help to inform people of the dangers of introducing nonnative species and can help to prevent intentional dumping of aquarium organisms into the natural environment.

Once an alga has been transported to a new location, it may either persist and establish or die. The "tens rule" has been used to describe the invasion process, whereby only one in ten species introduced to an area typically successfully grows, and of these succeeding species, usually only 10 percent become prolific and spread. If an introduction is detected early enough, then a rapid response activity can result in complete eradication. After the killer alga *Caulerpa taxifolia* was found in waters near San Diego, California, a rapid response was initiated, and using a combination of reduced light and chlorine, the Southern California *Caulerpa* Action Team was the first to eradicate a marine alga. The eradication was declared in 2006, some five years after the infestations were initially detected, and the estimated cost upon completion was approximately $8.3 million. The success of the *Caulerpa* story in San Diego was likely due to the quick response and the dedicated effort by a number of individuals representing state and federal agencies as well as consulting firms and nongovernmental organizations. A number of eradication attempts have been made with other species of algae, but none has been successful.

In most cases, by the time an introduced alga has been detected and declared invasive, it is too late for successful eradication. In these cases, control is really the only management option. A variety of control strategies have been used and include simply removing the plants manually, by hand or underwater suction device (see information on the "super sucker": www.nature.org/wherewework/northamerica/states/hawaii/press/press2376.html); controlling them with chemicals, such as algicides or bleach; changing water temperatures; reducing the light; and even employing biological control methods by using native or nonnative herbivores. For many of the most invasive algal species, control strategies are used either to reduce the impacts of the invaders on the native communities or to prevent further spread of algal invaders into new areas.

SEE ALSO THE FOLLOWING ARTICLES

Aquaculture / Aquaria / Ballast / Eutrophication, Aquatic / Freshwater Plants and Seaweeds / Invasion Economics / Seas and Oceans / Taxonomic Patterns

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