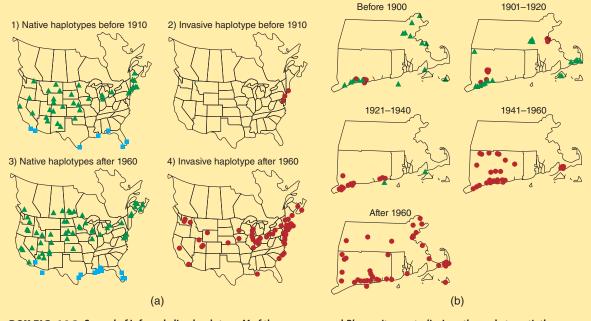# HOT TOPICS IN MARINE BIOLOGY 14.2

The Molecular Sleuth: Invasion of a Very Aggressive Genotype

Grassy plants dominate almost any wetland in North America in fresh or saltwater. In fresh water, cattails dominate marshes with their lovely brushlike flowers, they sway gently in the breeze and provide essential habitat for fishes, ducks, and many other species. Atlantic and Gulf coast marine marshes are dominated by *Spartina* grasses which form enormous meadows, sometimes over hundreds of square kilometers. Until recent decades, one also encountered to a lesser extent the common reed, *Phragmites australis*, which is typically found on the upper wet fringes of salt marshes and commonly in very disturbed roadside wetlands. Although its name suggests an invasion from the Southern Hemisphere, *P. australis* has been in eastern North America for thousands of years. In the southwestern United States, fossil evidence demonstrates its presence for at least 40,000 years, so it is hardly a recent invader.

But something strange began to happen. The work of Orson and colleagues (1987) in southern Connecticut documents the appearance of salt marshes about 3,800 years ago and the first appearance of *P. australis* about 3,500 years ago. It was found only in the upper fringe of the marsh for most of this time, but during the last 100 years, *P. australis* has been found to completely dominate marshes (Orson, 1999). Records from the early nineteenth century show this species to be rather rare, but it began to increase into the twentieth century and became a hallmark of disturbed edges of ponds, lakes and rivers. Since about the 1960s it has spread into more established marshes and appears to be displacing both freshwater and salt marsh plants. But what has made a species, once rather rare, a source of sudden dominance?

Enter the molecular sleuth, in the form of Kristin Saltonstall (2002). She used the PCR technique (see Chapter 7 for a discussion of this molecular method of amplifying DNA) to amplify and sequence chloroplast DNA from living populations of *Phragmites australis* around the world and compared these to specimens taken from museum herbaria in collections in the United States that were made before 1910. She found 27 unique sequences, or haplotypes, around the world in living populations. Eleven native North American haplotypes were common in the samples throughout North America before 1910. Another type *I* was found to dominate in the southern United States. By contrast, a rarer type *M* was found only in a few sites in the mid-Atlantic states before 1910 (**Box Figure 14.3**). After 1910, type *M* was widespread throughout the world. Before 1920, variation between populations in North America was quite high, but after 1910 the populations were much more similar genetically, which was a reflection of the invasion and spread of type *M* around the United States. The invasion and spread of type *M* can be seen in microcosm in southern New England, where it arose to dominance in the twentieth century (**Box Figure 14.3b**). In the Hudson River estuary, *Phragmites* patches have been appearing in marshes and outcompeting local plants (**Box Figure 14.4**). The type *M* haplotype most likely came from Europe or Asia.

Was type *M* also native to North America? This is unlikely. Details of the DNA sequence show no real similarities between the type *M* haplotype and the 11 native haplotypes. It is more likely that type *M* came in ballast in ships from either Europe or Asia. Plant material was common in ballast in the early twentieth century and before.

(a)

(b)

BOX FIG. 14.3 Spread of inferred alien haplotype *M* of the common reed *Phragmites australis* since the early twentieth century. (a) Distribution of native North American haplotypes (green and blue) and haplotype *M* (red) in North America before 1910 and after 1960. (b) Spread of haplotype *M* in southern New England over time. (From Saltonstall, 2002, Copyright National Academy of Sciences, U.S.A.)

HOT TOPICS IN MARINE BIOLOGY 14.2 CONT

BOX FIG. 14.4 Patch of *Phragmites australis* growing and spreading at the expense of surrounding cattail vegetation in a tidal freshwater salt marsh in the Hudson River estuary. (Photograph by Jeffrey Levinton)

Why has this genetic type so successfully displaced all of the native haplotypes across an entire continent? This is not clear as yet, but some features of the type *M* haplotype provide clues. First, this invasive genotype can have explosive growth from seed in a single growing season. It also responds much more to nutrient enrichment. Type *M* haplotypes outgrew native genotypes, produced more stems, and ultimately had 3–4 times more biomass. Salt marshes are now commonly near sources of nutrients, owing to human development. It is not clear, however, that this is a sufficient explanation for the wide spread of this haplotype. It may simply be

a better competitor than the natives. It is also possible that salt marsh communities today are more disturbed and less diverse, which may make them more vulnerable to invasion.

This study provides a discomforting notion of invasion. It may well be that many cryptic genotypes of many species have invaded from elsewhere. In some of these cases, what appear to be native species are essentially new, with distinctly different ecologies and possibly radically different roles within their respective communities. The molecular sleuth has a great deal of work ahead. ■

greater than 20°C, but no less than 16°C in the coldest month (**Figure 14.40**). They range in size from enormous tracts of forest, mudflats, and creeks covering an order of 10^2–10^3 km^2 to tiny cays in shallow seas such as the Caribbean. They are dominated by shrub- or treelike mangroves, which are rooted in anoxic muddy sediment that is waterlogged with seawater. Once established, they greatly decrease wave energy of the shorelines on which they live. Waterlogging is a very profound physiological problem for mangroves, especially because the sediment pore water is often anoxic. Mangrove belowground tissue is, therefore, subjected to long periods of exposure to anaerobic conditions, which slows nutrient uptake and allows the accumulation of toxins such as hydrogen sulfide, methane, carbon dioxide, and reducing metals. Exposure to decomposing bacteria is also a problem, which may explain the high tannin concentrations in mangrove tissues that function to protect against bacterial invasion. Mangrove species have evolved independently from ancestors in a number of plant

evolutionary groups, but are united in their tolerance of waterlogging and salinity stress.

■ Mangroves are adapted to the anoxic sediments by air-projecting and shallow roots.

Mangroves are usually broadly rooted but only to a shallow depth. This may be a response aimed at avoiding exposure to deeper-lying anoxic sediments. Above the water level, mangroves are in many ways typical terrestrial shrubs, with trunks, stems, leaves, and flowers. Their root system, however, is adapted to the anoxic sediment, and all mangrove species have root extensions that project into the air so that the underground parts of the plant root system can obtain oxygen.

The variety of root morphologies maintained by a single tree allows differentiation of function. Mangroves can have prop roots, structures that extend midway from the trunk and arch downward for support, roots that direct upward into the air (knee roots or larger pneumatophores,