The rise and fall of eastern hemlock

Majestic hemlock groves evoke reverence, affection, and poetry (Frost 1923). Eastern hemlock (*Tsuga canadensis*), one of the most long-lived, shade-tolerant trees in North America, dominates about 1 x 10^6 ha of forest from the southern Appalachians to southern Canada and west to the central Lake states (McWilliams and Schmidt 2000). In the north, hemlock typically occurs in nearly pure stands with species-poor understories.

In the south, hemlock grows in mixed stands in narrow riparian strips and moist coves, often with dense understories of rhododendron (*Rhododendron maximum*). In hemlock-dominated stands, the combination of deep shade and acidic, slowly decomposing litter results in a cool, damp microclimate, slow rates of nitrogen cycling, and nutrient-poor soils (Jenkins *et al*. 1999). Canopies of evergreen hemlocks have a higher leaf area index and lower transpiration rates per unit leaf area than canopies of co-occurring deciduous trees (Catovsky *et al*. 2002).

Although hemlocks have much greater whole-tree respiration rates in the spring and fall, when deciduous trees are leafless, during the summer hemlocks transpire about 50% of the total water released by deciduous trees (J Hadley unpublished). These characteristics of hemlock, along with its high snow-interception rates, mediate soilmoisture levels, stabilize stream base-flows, and decrease diel variation in stream temperatures. As a result, streams flowing through hemlock forests support unique assemblages of salamanders, fish, and freshwater invertebrates that are intolerant of seasonal drying (Snyder *et al*. 2002).

Hemlock stands also shelter deer and other wildlife. Populations of eastern hemlock have declined precipitously three times since the Pleistocene glaciation: approximately 5500 years ago, coincident with regional climate change and an outbreak of an insect similar to the extant eastern hemlock looper (*Lambdina fiscellaria*; Bhiry and Filion 1996); about 200 years ago, following forest conversion to agriculture, increases in fire, and extensive logging for timber and tannin (McMartin 1992); and from the mid-1980s to the present, due to an introduced insect, the hemlock woolly adelgid (*Adelges tsugae;*).

This rapidly spreading insect kills trees of all sizes and age-classes within 4–15 years of infestation (Orwig *et al*. 2002). Hemlock has no apparent resistance to the adelgid; it rarely recovers from attack (Orwig *et al*. 2002), and there are currently no effective biological or chemical controls of the adelgid in forested ecosystems. The insect's impact is further exacerbated by pre-emptive salvage logging, in which hemlock, which has modest economic value, is cut in anticipation of future infestation (Orwig *et al*. 2002).

Hemlock could functionally disappear from eastern forests in the next several decades. This species generally does not re-establish following adelgid-induced mortality, but is replaced throughout its range by hardwood species, including birch (*Betula* spp), oaks (*Quercus* spp) and maples (*Acer* spp) (Orwig *et al.* 2002). In the southeastern United States, hemlock is replaced by yellow poplar (*Liriodendron tulipifera*; J Vose *et al*. unpublished) when *Rhododendron* is absent. Decline of hemlock may lead to the local loss of its uniquely associated ants (Ellison *et al*. 2005) and birds (Tingley *et al*. 2002), cause regional homogenization of floral and faunal assemblages (Ellison *et al*. 2005), change soil ecosystem processes (Jenkins *et al.* 1999;), and alter hydrological regimes.

The effects of adelgid-induced hemlock mortality on stream ecosystems will be extensive. For example, hemlock streams support significantly more taxa of aquatic invertebrates than paired mixed-hardwood stands, and nearly 10% of the taxa are strongly associated with the presence of hemlock (Snyder *et al*. 2002). Hemlock death may result in a rapid pulse of large amounts of wood that decays more slowly than coarse woody debris from hardwoods.

Large hemlock logs in streams retain sediment and organic matter and create novel habitat types. In general, large hemlock logs are abundant in streams draining forests where hemlock is an important riparian species. Although logs from adelgid-killed hemlocks may persist in streams for decades to centuries, eventually the loss of hemlock will reduce in-stream wood, leading to a decline in sediment retention and productivity.

Logging of hemlock initiates more rapid and greater ecosystem changes than the adelgid because of the abrupt vegetation and environmental changes, removal of wood, soil scarification, and the presence of extensive slash left by logging operations (Kizlinski *et al*. 2002). Nitrogen availability and nitrification rates are significantly higher in cut forests than in adelgid-damaged ones, increasing the threat of nutrient losses and changing food availability in nearby aquatic systems (Kizlinski *et al*. 2002; C Swan unpublished.