# THE EVOLUTION OF FREEZING TOLERANCE IN OAKS (*QUERCUS*)

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## PURPOSE AND SCOPE

Freezing tolerance is a critical factor controlling the broad-scale distribution of organisms. The American oaks (*Quercus*) are an important representative lineage for studying the evolution of freezing tolerance given their biogeographic history, assembling at high latitudes in the Americas and expanding southward as they diversified (Cavender-Bares et al. 2018, Hipp et al. 2018). Freezing temperatures result in intra and extracellular ice crystal formation, which can cause physical damage and cellular dehydration, resulting in losses of xylem function. Within the nonliving cells of the xylem, freezing temperature is likely to cause cavitation resulting in losses of xylem function, depending on the size of the conduits as well as the freezing temperature and tension in the xylem. The capacity of plants to tolerate freezing varies widely and many species have evolved adaptations that allow them to survive episodic freezing (Zanne et al. 2014). How rapidly plants can adapt to changing climate and whether there are tradeoffs between freezing tolerance and growth remain poorly understood.

## METHODS AND APPROACH

We grew 48 species of oaks from five sections of the genus under temperate and tropical growth conditions and measured their stem freezing tolerance and growth rate. We used the electrolyte leakage method to determine stem freezing sensitivity. The electrolyte leakage method measures changes in electrical conductivity to predict cell lysis in response to freezing. To assess whether current adaptation influenced freezing evolution in the oaks, we performed a comparative analysis modeling traits as evolving under an Ornstein-Uhlenbeck model of evolution in a maximum likelihood framework.

## FINDINGS AND IMPLICATIONS

We found significant differences among species in their freezing tolerance and capacity to cold acclimate. We found that species from colder regions have higher freezing tolerance and slower growth rates than species from warmer climates. Nevertheless, a direct evolutionary tradeoff did not emerge because

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deciduousness rather than freezing tolerance appears to constrain growth rates. Deciduous species have consistently slower growth rates than evergreen species regardless of climatic niche but vary markedly in freezing tolerance in step with the broad climatic range they span. In contrast, evergreen species occur only in warm climates and have low freezing tolerance. Species from colder regions also have higher acclimation potential than species from warmer areas, indicating that cold-climate species have evolved higher capacity to acclimate to seasonal fluctuations in climate, and warm-climate species have constraints to surviving in colder climates. Freezing tolerance in the oaks is relatively close to its optimal evolutionary state ($r = 0.77$), yet the phylogenetic half-life is 8.9 million years. Consequently, despite a high level of adaptation to the climates in which species occur, evolution towards optimal freezing tolerance has a considerable lag time. Freezing tolerance thus appears to evolve independently from growth rate and investment in freezing tolerance does not impose a constraint on growth. However, leaf phenological habit plays a crucial role in both growth and freezing avoidance. All species, regardless of their climatic origin, have higher growth rates in the tropical treatment where season length is longer. Deciduous species pay a price of losing the opportunity to gain carbon after leaf drop, a price the evergreen species do not pay. Deciduous species are able to persist in both cold and warm latitudes, though evergreen species are relegated to mild climates. At the same time, stem freezing tolerance—and the loss of freezing tolerance—has evolved in coordination with climate and cold tolerant species are not found in warm regions. These findings suggest there may be tradeoffs associated with freezing tolerance, other than growth, that make freezing-resistant species less competitive in warm climates.

Figure 1—Oaks in winter on the banks of the Mississippi River, Minneapolis, MN. (Courtesy photo by Jeannine Cavender-Bares, Department of Ecology, Evolution and Behavior, University of Minnesota)

## LITERATURE CITED

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