

The evolution of cold adapted traits in temperate forest trees

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1. Introduction

Low temperatures in temperate and boreal habitats can pose many risks to plants. Most temperate forest tree species have evolved from tropical origins, where these cold temperatures are far less extreme. From the tropical origins to boreal forests, angiosperm tree species have needed to adapt to the climatic shifts across these temporal and spatial gradients - the most crucial shift being to cold temperatures. Temperatures further north can reach -10°C to -30°C (Larcher, 2005) or even as low as -30°C to -50°C (Howe *et al.*, 2003). Tree species at more northern latitudes, in temperate or boreal regions, spend many months exposed to these very low temperatures. In order to avoid xylem embolism, defoliation, or death, trees must go dormant during this risk time. Over the winter months, leaf buds in northern regions have evolved to harden and tolerate these temperatures. This tolerance is possible through various methods including the synthesis of particular proteins and hormones, such as antifreeze proteins and abscisic acid (Martin *et al.*, 2010). However, in the spring, these specialized proteins and hormones will need to diminish in order to allow buds to deharden so that leaf primordia can be exposed and grow. Temperate tree species are also at risk of freezing and drought events in the spring and must exhibit plastic phenological responses in order to best avoid these risks (Polgar & Primack, 2011). The interplay

of dehardening and frost tolerance has evolved multiple times in many species in order to optimize growth and minimize risk. With anthropogenic climate change, these risks will continue to heighten and become more frequent. Species that evolved more recently and have larger distribution ranges are expected to have higher effective population sizes and increased levels of gene flow. It is anticipated that these advantages will allow species to be more able to track the rapid shifts in climate and, consequently, ecological dynamics.

2. Evidence of Cold Adapted Traits

There are many types of cold adapted traits necessary for deciduous temperate trees to utilize in order to survive winter months and have efficient growing seasons in the spring and summer. One mode of protection is through the dormancy process. There are two types of dormancy: endodormancy and ecodormancy. Endodormancy is the period of winter when temperate trees are inhibited from growing regardless of the outdoor environment. Ecodormancy is the period of time when growth can occur but the external environment is not conducive to growth (e.g. too cold) (Basler & Körner, 2012; Samish, 1954). Temperate trees require a certain number of chilling units in order to leave the endodormancy phase. This protects temperate and boreal trees from stochastic warm spells in winter. Chilling units differ across species and across habitats, which has evolved as one method of protection against late spring frosts. Species in regions that are more susceptible to late spring frosts are more likely to have higher chilling requirements to break dormancy and will likely respond to spring temperature cues more than photoperiod cues for leaf budburst to occur. Another evolved method of survival is by shifts in phenological responses. Variation in leafout phenology across temperate forest trees can be attributed to three factors: phylogenetic effects, historical or epigenetic effects, or adaptive traits (Lechowicz, 1984). These factors are evident through phenotypic, genotypic, and morphological adaptations of cold-tolerant traits in temperate forest trees.

2.1 Phenotypic Evidence

Phenology is closely linked to climatic regimes (Pau *et al.*, 2011) and is therefore a key indicator for the phenotypic variation for cold adapted traits across species. Common garden experiments have shown that individuals from a more northern or higher elevation provenance, tend to initiate budburst sooner, thus increasing the risk for late spring frosts. This could be due to lower chilling requirements or lower forcing requirements since temperatures are less likely to fluctuate as severely at more northern latitudes. Studies also indicate that species growing in these regions tend to respond greater to photoperiod than species growing further south (Caffarra & Donnelly, 2011; Vihera-aarnio *et al.*, 2006; Partanen, 2004). This phenotypic variation signifies varying degrees of selection for cold hardiness over winter versus exposure to frost risk in the spring. In individuals further north, because of these diminished risk of late spring frosts, photoperiodic cues will be more informative and result in heightened efficiency in growth. Individuals growing in regions more susceptible to spring frosts, on the other hand, have longer chilling requirements and respond to both temperature and photoperiodic cues. In these common garden experiments, there is strong evidence for historical and epigenetic effects of seed embryos mimicking phenological trends from their provenance location.

2.2 Genetic Evidence

The evolution of cold hardiness in temperate trees has been driven by three key environmental pressures: 1) shorter photoperiods, 2) greater exposure to colder temperatures and frost events, 3) and in some cases, exposure to extremely cold temperatures (i.e. reaching as low as -50°C). Likewise, deacclimation in the spring, which is cued through longer day lengths and warmer temperatures, has also had to have evolved multiple times across various species. Spring temperature thresholds and the duration of warm temperatures required for leaf buds to burst in spring varies among species. This is evident through the high levels of genetic diversity for cold adapted traits - especially in regards to varying chill-

ing requirements and differing sensitivities to spring forcing temperatures - for spring budburst to occur across temperate and boreal forest tree species (Chuine *et al.*, 2001).

There is an annual cold hardiness cycle in which all temperate tree species undergo (Aitken & Hannerz, 2001). First, all spring and summer growth ceases and buds begin to set in preparation for winter. Once buds are completely set, cold acclimation begins and endodormancy is initiated. As soon as buds are exposed to enough chilling, endodormancy is released and the buds will enter a period where cold hardiness begins to diminish. At this time, buds can burst and initiate primary growth. Winter cold hardiness and fall phenology is genetically uncorrelated to spring cold hardiness and spring phenology, which means the cold adapted traits in the fall are decoupled from the genetic drivers that prepare buds for spring and growth. Spring frosts tend to present the most risk to frost damage, more so than the fall, which may be one reason why the spring and fall phenologies of temperate forest trees are genetically uncorrelated (Howe *et al.*, 2003). Also, cold hardiness in winter typically prepares buds for far lower temperatures than what the buds actually experience, so damage in winter is generally due to drought, not frost damage Sakai & Larcher (1987); Fuchigami *et al.* (1971), making cold deacclimation traits for the spring absolutely critical because they have to deharden even more extrememly than may be necessary. With climate change, temperatures are expected to increase over the winter in temperate regions, making it harder for buds to reach the chilling requirements and, ultimately, deacclimate in the spring.

Studies have shown that there are strong relationships between genetic clines for cold adapted traits along environmental gradients. Such traits include growth initiation and cessation, endodormancy and ecodormancy time periods, and cold hardiness over the winter (i.e. cold temperature threshold in which buds can safely tolerate). This provides strong evidence for natural selection (Morgenstern, 2011; Endler, 1977). Genetic variation for cold adapted traits is also additive (Howe *et al.*, 2003) and variation in cold adapted traits across populations is strongly correlated to climatic and regional regimes.

2.3 Morphological Evidence

2.3.1 *Virentes*: from the tropics to the temperate

Quercus species have originated from the tropics and have an especially long phylogenetic history for angiosperms. They are hearty species that can tolerate very low temperatures in more northern latitudes and often dominate many temperate forests. *Quercus* species are more able to track shifts in climate and have recently out-competed *Castanea* species in dominating most New England forests (Sisco *et al.*, 2009). *Virentes* species, a monophyletic series of *Quercus*, tend to have a shorter growth form in the tropics in order to be more fire-resistant. Frequent fires in the subtropical regions can cause more damage to roots and trunks of taller, single trunk trees, whereas smaller, more sprawling forms can tolerate the fires more successfully. Leaves are generally smaller in tropical systems in order to diminish water loss from photosynthesis and also diminish long-term detrimental effects of fire. Figure 1 demonstrates these shifts in form and phylogeny within the genus *Quercus*, series *Virentes*. Fire can cause severe desiccation within the xylem and leaves, mimicking the adverse effects of late spring frost in temperate forests. This could offer one explanation for the ability of *Quercus* to adapt to various types of environments and to also be a dominant species.

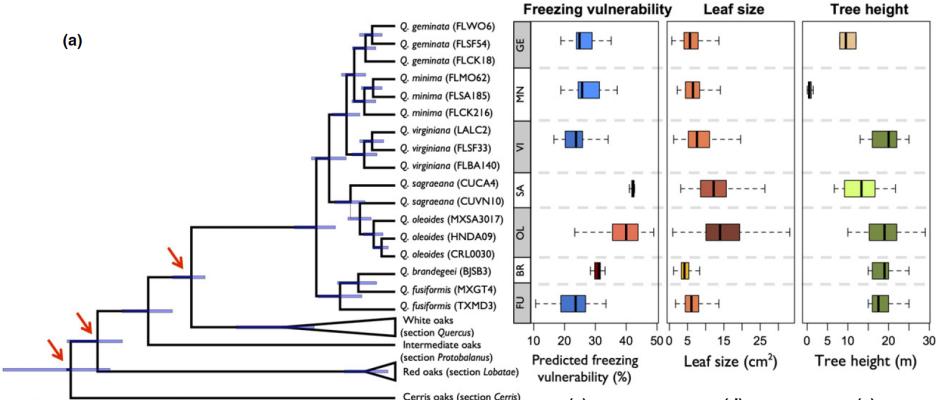


Figure 1: A phylogenetic tree of the genus *Quercus* species based on tree height and phylogenetic history. Box plots signify freezing vulnerability, leaf size, and tree height based on species. Species with blue hues have lower values, whereas species with more red hues have higher values (Cavender-Bares *et al.*, 2015). The clade is made up of 7 species: *Quercus virginiana* Miller, *Q. geminata* Small, *Q. minima* Small, *Q. brandegeei* Goldm., *Q. fusiformis* Small, *Q. oleoides* S. C. and *Q. sagraeana* Nutt.)

2.3.2 Winter Buds

Further evidence of morphological adaptations to cold is through leaf margin shape and structure. Tree species that have large spatial distributions across many latitude lines, tend to express variations in leaf shape morphology. Individuals closer to the tropics generally have entire leaf margins (i.e. no serrations along leaf edge), whereas individuals further north have toothed or lobed leaves. This is possibly due to the 'packability' of leaves into dormant winter buds. Leaf primordia is developed prior to dormancy in the summer and fall. Buds are packed with nutrients and genetic information so that little metabolic energy is required for leaves to develop in the spring. One hypothesis is that more hearty leaves will be able to pack into winter buds if there are serrations along the leaf edge (Edwards *et al.*, 2017). Temperate forest tree leaves generally have more trichomes (i.e. small, unicellular hairs) on them,

which are typically more prevalent in the earlier phenological stages of leaf growth. It is thought that these trichomes offer leaf primordia further protection within the winter buds against cold temperatures and even protection against later spring frosts after budburst has already initiated (Edwards *et al.*, 2017).

Other species can store larger amounts of non-structural carbohydrates in their roots and phloem, permitting multiple flushes of leaves if a damaging frost does occur. These species will usually initiate budburst earlier in the season in order to utilize the diminished canopy cover and ample sunlight to decrease the amount of competition for resources early and have decreased long-term risk of damage to late spring frosts.

Winter buds also use various hormones and proteins as frost protectants. Abscisic acid and antifreeze proteins are used to inhibit ice from forming intercellularly within the bud and leaf tissue. Intercellular frosts are the most damaging to leaf primordia and can result in xylem embolism in leaf stems and even branches in some cases. They can also result in greater cavitation within the entire xylem (Larcher, 2005). Frost damage, for these reasons, often mimics desiccation damage, meaning frost and drought protections are typically congruent.

Subtropical forests, while they may not experience consistently low temperatures, can have episodic frosts, or brief cold spells. This is potentially one manner in which cold-adapted traits first began to evolve. As species distributions continued to spread polewards, these low temperatures and frosts became slightly more typical, permitting more natural selection to act on these tree species (Larcher, 2005). Different species vary in their susceptibility to frost damage, thus inflicting a limiting factor in species distribution size but many have been able to spread their range centers through adaptive radiation and openings in ecological niches.

3. Potential Future Risks

Tree species with smaller distribution ranges and fragmented distributions are more prone to genetic drift due to geographic barriers and higher susceptibility to stochastic events (i.e. frost and drought). The capacity for dispersal and propagation is crucial for local adaptation to occur and for species to be more able to respond to changes in climate (Alberto *et al.*, 2013). Climate change is expected to increase the level of damage from spring frost events around the world due to earlier spring onset and greater fluctuations in temperature (Martin *et al.*, 2010). Therefore, it is essential that temperate forest tree species maintain continuous ranges in order to avoid the impending changes in climate. Trees growing in the wild generally have lower levels of heritability and greater environmental variation, exposing tree species to even higher levels of risk (Conner *et al.*, 2003).

Individuals and species with many loci having small effects, will respond strongly to selection on cold adapted phenotypes (Alberto *et al.*, 2013). With adaptive plasticity, trees will be more able to track climate change and minimize the lag between climatic shifts and rate of selection. However, greater fluctuations in temperature and precipitation will result in weaker selective pressures and, ultimately, a decrease in the rate of adaptation. Although, recent studies indicate that plastic responses to large shifts in climate outweigh the decreased rate of selection (Chevin & Lande, 2010; Lande, 2009).

The effects of climate change may be harder for fragmented populations to track. However, if there is sufficient gene flow, such populations should be able to track changes as well as continuous populations. This said, some continuous populations may have greater genetic variation than their fragmented counterparts, rendering them more competitive in the long-term.

4. Conclusion

Cold winter temperatures, seasonal variation, spring frosts, and droughts can all be limiting factors for tree species to extend their geographic ranges. Most angiosperm species have evolved from sister taxa originating from the tropics and have been able to adapt to these more northern pressures. As species ranges extend polewards, episodic frosts begin to pose a threat to tree species. This threat continues to augment as species approach temperate and boreal habitats. Various tree species have evolved to counteract these threats, first by becoming deciduous and integrating a dormancy phase, and then through phenological, morphological, and genetic strategies. In tropical environments, temperatures and precipitation are quite consistent, especially in comparison to temperate systems. This consistency permits a wealth of floral and fauna to grow and thrive, rendering most tropical systems biodiversity hotspots. As soon as habitats begin forming polewards, there is less competition, however environmental and abiotic stressors are heightened. Temperate forests experience larger variations in temperature and precipitation, thus amplifying the risks of drought and frosts. Tree species have been able to fill these temperate ecological niches through adaptive radiation. By shifting their phenologies, and utilizing chilling, spring warming, and photoperiodic cues, trees across the latitudinal gradient have been able to occupy more habitat types with a decreased risk of damage. In order to adequately and efficiently access resources in the spring and summer, due to the far shorter growing season in comparison to the tropics, different species use different cold-adapted traits. Some of the most common strategies are through winter bud morphology, with the integration of protectant bud scales, trichomes, abscidic acid and antifreeze proteins, and leaf serrations. The adaptability of tree species is essential, especially as the threats of global climate change continue to amplify. Species must be able to maintain continuous ranges with ample gene flow so that varying regional threats can be diminished.

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