

Abstract

How has frost tolerance evolved in temperate forest deciduous trees?

I will write a review paper that investigates the evolution of frost tolerance in deciduous tree species found in temperate forests. Temperate tree species are at risk of freezing and drought events in the spring and must exhibit plastic phenological responses in order to best avoid these risks. Over the winter months, leaf buds in northern regions have evolved to harden and tolerate very low temperatures. This tolerance is possible through various methods including the synthesis of particular proteins and hormones, such as antifreeze proteins and ABA (abscisic acid). However, in the spring, those proteins and hormones will need to diminish in order to allow buds to dehardening so that leaf primordia can be exposed and grow. The interplay of dehardening and frost-tolerance has evolved multiple times in many species. I will write a review that assesses the molecular and genetic evolution of temperate tree buds and frost tolerance across native species phylogenies occupying various ecological and climatic niches.

Additional notes

Endo-dormancy is the period of winter when temperate trees are inhibited from growing regardless of the outdoor environment. Eco-dormancy is the period of time when growth can occur but the external environment is not conducive to growth (e.g. too cold). Temperate trees require a certain number of chilling units in order to leave the endo-dormancy phase. This protects temperate and boreal trees from stochastic warm spells in winter.

Howe 2003 - From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees

1. Cold hardiness and fall phenology is genetically uncorrelated to cold hardiness and spring phenology.
2. Cold hardiness annual cycle:
 - (a) growth cessation and bud set
 - (b) cold acclimation begins
 - (c) endo-dormancy is developed
 - (d) and then is released via chilling
 - (e) "loss of cold hardiness"
 - (f) primary growth is initiated
3. spring frosts tend to present the most risk to frost damage, more so than the fall.
4. cold hardiness in winter is typically far harder than what the actual temperatures drop to, so damage in winter is generally due to drought, not frost damage (Fuchigami et al, 1971; Sakai and Larcher, 1987)
5. mitotic activity typically initiates much earlier than bud swelling or budburst (Fielder and Owens, 1989)
6. FALSE CLAIM TO INVESTIGATE: "Within species, there is relatively little variation in cold hardiness during the active growth period (e.g. *Pinus sylvestris*, Hurme et al. 1997; *Betula pendula*, Li et al., 2003b).
7. Growth cessation is typically in response to shorter photoperiod cues - more prominent in seedlings, early successional species, and species less susceptible to late summer droughts or frosts.
8. Bud set is typically "determined by the number of stem units in terminal buds and by the period required for their elongation and maturation, rather than by current environmental conditions (Chuine et al. 2001)."

9. Cold acclimation stages in woody plants:
 - (a) shorter photoperiods
 - (b) Exposure to cold temperatures and frosts
 - (c) In some: Exposure to extremely cold temperatures (i.e. -30°C to -50°C)
10. "The required threshold temperature and duration of warm temperatures varies both within and among species (Chuine et al. 2001)" - in regards to cold deacclimation in the spring.
11. not only photoperiod and temperature cues regulate the cold hardiness cycle; soil moisture and nutrient availability can affect the developmental cycle as well (Bigras, 2001 - **Can't find!**).
12. Regular low night temperatures may trigger a different pathway for cold acclimation than infrequent, short duration low temperatures throughout the winter or very long-term durations of low temperatures that may release buds from endo-dormancy earlier in the season.
13. High levels of genetic diversity for cold hardiness, chilling requirements, and spring forcing temperatures for spring budburst across temperate and boreal forest tree species
14. "The propensity for second flushing is genetic, but this trait is only expressed on some sites in some years (Schermann et al., 1997)."
15. "Once established, trees tend to complete elongation growth early in the season, thereby consistently avoiding damage when early frosts do occur."
16. Phytochromes: photoreceptor proteins that detect photoperiod
17. Transcription Factors for cold acclimation: CBF and DREB1
18. Studies have shown that there are strong relationships between genetic clines for cold adapted traits along environmental gradients. Cold adapted traits include growth initiation and cessation, endo- and eco-dormancy time periods, and cold hardiness over the winter. This provides strong evidence for natural selection (Morgenstern, 1996, Endler, 1977).

19. Genetic variation for cold adapted traits is additive
20. Variation in cold adapted traits across populations is strongly correlated to climatic and regional regimes
21. Common garden experiments have shown that individuals from a more northern or higher elevation provenance, tend to initiate budburst sooner, thus increasing its risk for late spring frosts. This could be due to lower chilling requirements or lower forcing requirements. **(So then maybe this why these species rely on photoperiod!!!)**
22. "There is less genetic variation for bud flush than for bud set (Aitken and Hannerz, 2001)." However, bud flush is different than bud dehardening, which is considered a cold adapted trait, and, therefore, there will be greater genetic variation in bud dehardening among geographically distinct populations rather than great variation in budburst timing.
23. There is evidence for certain species to demonstrate great sympatric variation within local climates for cold adapted traits, whereas other species show less variation among geographically explicit populations. Cold hardiness, bud set, and budburst tend to be strongly associated with provenance climatic regimes.
24. The association between climatic gradient and genetic cline for cold adapted traits supports evidence for natural selection acting on this relationship.
25. However, there is strong within population genetic variation in many tree species due to the composition and structure of a certain environment (e.g. topographical variation or variation in canopy cover).
26. Phenological genetic control is generally much stronger than genetic control for other types of traits such as size or growth pattern (Zobel and Talbert, 1984). "In general, bud flush is under slightly stronger genetic control than is bud set." - (Aitken and Hannerz, 2001; Howe et al, 2000)
27. "spring cold injury is under strong genetic control, whereas the genetic control of fall cold hardiness is both moderate and tissue specific." which depends on the temporal effects of acclimation and deacclimation to cold temperatures.

28. It is still being disputed whether the selection for growth initiation and cessation on cold adaption is due to pleiotropy or linkage disequilibrium, however it is more likely due to linkage disequilibrium. This is supported by the unpredictability of within population variation and relationships.

29. A greater understanding of the specific genes underlying cold adaptive traits is necessary in order to glean a better understanding of ecology and evolution of temperate and boreal forest ecosystems.

Regarding number 21 from the Howe 2003 list...

Studies indicate that species growing at more northern latitudes tend to respond greater to photoperiod than species growing further south (Caffarra & Donnelly, 2011; Vihera-aarnio *et al.*, 2006; Partanen, 2004).

Larcher 2005 - Climatic constraints drive the evolution of low temperature resistance in woody plants

1. The adaptation to frost resistance evolved in a stepwise progression.

Lechowicz 1984 - Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities

1. Variation in leaf out phenology across temperate forest trees can be attributed to three factors: phylogenetic effects, historical or epigenetic effects, or adaptive traits.
2. Historical effects - trees that dispersed to a new habitat may leaf out based on traits acquired from the provenance location.

Alberto 2013 - Potential for evolutionary response to climate change

- evidence from tree populations

1. Tree species with smaller ranges and fragmented distributions are more prone to genetic drift. The capacity for dispersal and propagation is crucial for local adaptation and to respond to changes in climate.
2. "Forst tree populations harbor considerable genetic variability in many quantitative traits (Cornelius, 1994; Morgenstern 1996; Howe 2003)." However, trees growing in the wild will generally have lower levels of heritabilities and greater environmental variation (Conner et al., 2003).
3. Individuals or species with many loci with small effects will respond to strong selection on cold adapted phenotypes.
4. Temperate and boreal trees must be phenotypically plastic in order to respond to the varying climate. With adaptive plasticity, trees will be more able to track with climate change. However, this will result in weaker selective pressures and, ultimately, slower changes in adaptation. Studies have found that plastic responses to large shifts in climate outweigh the decreased selection (Chevin and Lande, 2010; Lande, 2009).
5. 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. Although, some continuous populations may have greater genetic variation than their fragmented counterparts.

References

- Aitken, S.N. & Hannerz, M. (2001) Genecology and gene resource management strategies for conifer cold hardiness. *Conifer cold hardiness*, pp. 23–53, Springer.

- Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R. & et al. (2013) Potential for evolutionary responses to climate change - evidence from tree populations. *Global Change Biology* **19**, 1645–1661.
- BENEDICT, C., SKINNER, J.S., MENG, R., CHANG, Y., BHALERAO, R., HUNER, N.P.A., FINN, C.E., CHEN, T.H.H. & HURRY, V. (2006) The cbf1-dependent low temperature signalling pathway, regulon and increase in freeze tolerance are conserved in populus spp. *Plant, Cell and Environment* **29**, 1259–1272.
- Caffarra, A. & Donnelly, A. (2011) The ecological significance of phenology in four different tree species: Effects of light and temperature on bud burst. *International Journal of Biometeorology* **55**, 711–721.
- Cavender-Bares, J., González-Rodríguez, A., Eaton, D.A.R., Hipp, A.A.L., Beulke, A. & Manos, P.S. (2015) Phylogeny and biogeography of the american live oaks (quercussubsectionvirentes): a genomic and population genetics approach. *Molecular Ecology* **24**, 3668–3687.
- Chuine, I., Aitken, S.N. & Ying, C.C. (2001) Temperature thresholds of shoot elongation in provenances of *Pinus contorta*. *Canadian Journal of Forest Research* **31**, 1444–1455.
- Endler, J.A. (1977) *Geographic variation, speciation, and clines*. 10, Princeton University Press.
- Fielder, P. & Owens, John, N. (1989) A comparative study of shoot and root development of interior and coastal douglas-fir seedlings. *Canadian Journal of Forest Research* **19**, 539–549.
- Fuchigami, L., Evert, D. & Weiser, C. (1971) A translocatable cold hardiness promoter. *Plant Physiology* **47**, 164–167.
- Grime, J. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary time. *American Society of Naturalists* **111**, 1169–1194.
- Howe, G., Saruul, P., Davis, J. & Chen, T. (2000) Quantitative genetics of bud phenology, frost damage, and winter survival in an f 2 family of hybrid poplars. *TAG Theoretical and Applied Genetics* **101**, 632–642.

- Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany* **81**, 1247–1266.
- Koehler, K., Center, A. & Cavender-Bares, J. (2011) Evidence for a freezing tolerance-growth rate trade-off in the live oaks (*quercus* series *virentes*) across the tropical-temperate divide. *New Phytologist* **193**, 730–744.
- Larcher, W. (2005) Climatic constraints drive the evolution of low temperature resistance in woody plants. *Journal of Agricultural Meteorology* **61**, 189–202.
- Lechowicz, M. (1984) Why do temperate deciduous trees leaf out at different times? adaptation and ecology of forest communities. *American Society of Naturalists* **124**, 821–842.
- Morgenstern, M. (2011) *Geographic variation in forest trees: genetic basis and application of knowledge in silviculture*. UBC press.
- Niinemets, Ü. (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management* **260**, 1623–1639.
- Niinemets, Ü. & Valladares, F. (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* **76**, 521–547.
- Partanen, J. (2004) Dependence of photoperiodic response of growth cessation on the stage of development in *picea abies* and *betula pendula* seedlings. *Forest Ecology and Management* **188**, 137–148.
- Rodrigo, J. (2000) Spring frosts in deciduous fruit trees - morphological damage and flower hardiness. *Scientia Horticulturae* **85**, 155–173.
- Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants*. Springer-Verlag.
- Schermann, N., A.W.A.S. & Bastien, J. (1997) Genetic parameters of stem form traits in a 9-year-old coastal douglas-fir progeny test in washington. *Silvae Genetica* **46**, 166–170.

- Svenning, J.C. (2003) Deterministic plio-pleistocene extinctions in the european cool-temperate tree flora. *Ecology Letters* **6**, 646–653.
- Vihera-aarnio, A., Hakkinen, R. & Junttila, O. (2006) Critical night length for bud set and its variation in two photoperiodic ecotypes of *betula pendula*. *Tree Physiology* **26**, 1013–1018.