



Commentary

Genetic vs. phenotypic responses of trees to altitude

Sean C. Thomas

Faculty of Forestry, University of Toronto, 33 Willcocks Street, Toronto, ON, Canada M5S 3B3; Corresponding author (sc.thomas@utoronto.ca)

Received August 24, 2011; accepted September 6, 2011; handling Editor Danielle Way

Trees in mountainous regions commonly exhibit dramatic changes in morphology and physiology along altitudinal gradients. Several environmental factors vary systematically with altitude as a result of fundamental physical processes: these include atmospheric pressure and partial pressures of constituent gases, air temperature and atmospheric turbidity. In addition, there are commonly regional or local patterns of variation in rainfall, wind exposure and other factors that can make altitudinal clines difficult to interpret (Körner 2007.) Nevertheless, declining temperature with increasing altitude (adiabatic lapse) is the most predictable pattern overall and generally has the largest direct impact on plant physiological processes. Unlike many small alpine herbaceous plants that occur in specialized thermal environments low in the boundary layer, leaf temperatures of trees tend to closely track altitudinal air temperature patterns (Körner 2007). Altitudinal clines thus represent an important and arguably underutilized tool in understanding the impacts of climatic change on trees.

Do commonly observed altitudinal clines in traits such as leaf size, leaf mass per area and photosynthetic parameters represent a purely phenotypic response or does genetic differentiation contribute substantially? In this issue Bresson et al. (2011) present results of a common garden experiment to address this issue for two common European tree species (European beech: *Fagus sylvatica*; and sessile oak: *Quercus petraea*), studied along replicated altitudinal transects in the French Pyrenees. Although similar studies are common for herbaceous plants, there have been relatively few common garden studies of this type for trees (e.g., Zhang and Marshall 1995, Oleksyn et al. 1998, Hovenden and Broadribb 2000, Vitasse et al. 2009), with a smaller subset directly comparing phenotypic to genetic patterns (Cordell et al. 1998, Hovenden and Vander Schoor 2003, Premoli and Brewer 2007).

Bresson et al. document strong phenotypic trends with altitude in most of the leaf parameters examined (Figure 1).

Light-saturated photosynthesis (A_{\max}), stomatal conductance (g_s), foliar N (N_a) and leaf mass per area (LMA) all increase substantially with increasing altitude, while leaf size decreases. Stomatal density showed a weak increase in oak and no trend for beech (a disappointing result from the perspective of paleontological reconstruction of altitude: Kouwenberg et al. 2007). However, in contrast to the strong phenotypic patterns, common garden experiments revealed a significant genetic signal only in the case of foliar N and (for beech) leaf mass per area (Figure 1). Even for traits showing a significant genetic pattern, the proportional change is consistently lower than that observed for the phenotypic pattern.

Several prior studies have emphasized the importance of genetic adaptation in determining altitudinal clines in foliar characteristics in trees (e.g., Oleksyn et al. 1998, Vitasse et al. 2009). Prior observations that altitudinal clines largely reflect phenotypic plasticity have been considered unusual, and were invoked to explain ecological dominance in the famously polymorphic Hawaiian tree *Metrosideros polymorpha* (Cordell et al. 1998). However, the results presented by Bresson et al. (and also Hovenden and Vander Schoor 2003 and Premoli and Brewer 2007) suggest that this pattern is in fact widespread among trees. Another contribution of Bresson et al. (2011) is to quantitatively evaluate the degree of genetic contribution to the observed altitudinal clines. Genetic differentiation among populations across altitudes, even in cases where significant clines were detected, was relatively low, ranging from undetectable to 28% (in the case of leaf size for *Q. petraea*) (Figure 1). Likewise, in the common garden experiment, intra-population variability in leaf functional traits substantially exceeded inter-population variability in every case (Bresson et al. 2011, Table 2).

Quantitative dominance of phenotypic plasticity in determining altitudinal clines in leaf functional traits of tree species has some important implications to understanding (and predicting) forest responses to climate change generally. Phenotypic

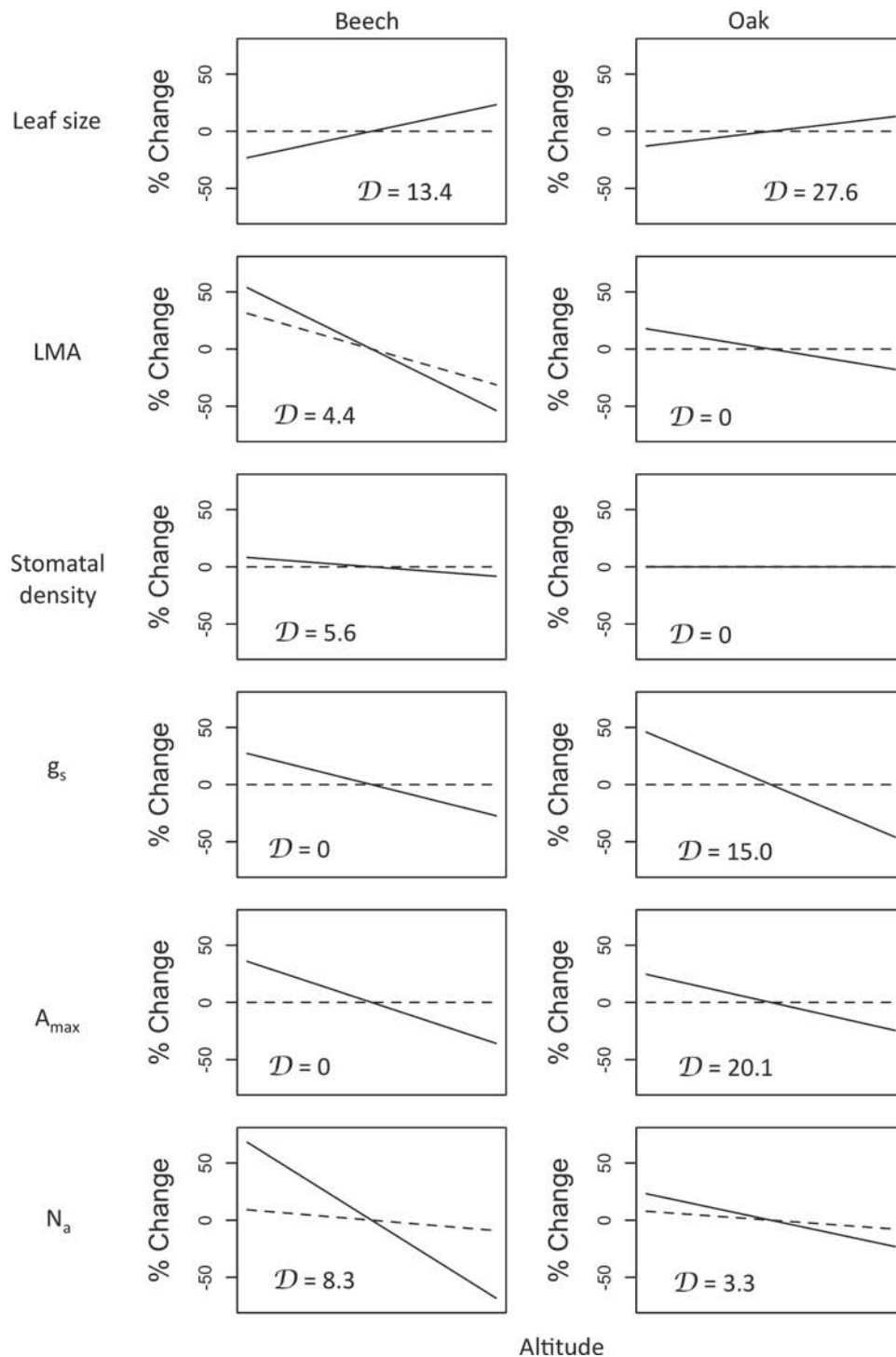


Figure 1. Relative changes in foliar traits with altitude described by Bresson et al. (2011). Solid lines represent phenotypic patterns; dashed lines represent genetic patterns determined by a common garden experiment. Values for each trait are scaled such that the x-axis spans the range of altitudes examined (150–1600 m), and the y-axis the percentage change in a given trait (recalculated from regressions presented by Bresson et al.). Non-significant relationships are represented by a flat line; values for D are the genetic differentiation among populations from different altitudes for the trait in question, expressed as a percent. LMA: leaf mass per area; g_s : stomatal conductance; A_{\max} : light-saturated photosynthesis; N_a : foliar N content.

plasticity is relatively easy to model: for example, temperature response functions generated by experimental studies (Way and Oren 2010) provide a tractable empirical approach to predicting tree growth and physiological responses to changing

temperature. In contrast, modeling of evolutionary responses requires information on population structure, gene flow, trait heritabilities and selection pressures. Long generation times in trees also greatly slow any selective response. These

considerations support an approach in which short-term phenotypically plastic responses of physiological processes are assumed to be the primary drivers of tree responses to a changing environment.

Adaptive responses to altitude are still, of course, of great interest. The capacity for adaptive change may ultimately be critical in determining tree species survival under climate change (Aitken et al. 2008). This is an acute issue in many alpine environments where small isolated tree populations frequently occur. However, the results of Bresson et al. and the handful of studies evaluating both phenotypic and genetic contributions to altitudinal clines in trees (Cordell et al. 1998, Hovenden and Vander Schoor 2003, Premoli and Brewer 2007) lend support to an approach to the modeling of physiological responses to temperature change (and their consequences to ecosystems) in which phenotypic plasticity can be assumed as the dominant underlying process. However, further studies along these lines—of altitudinal, latitudinal and other natural gradients—are needed to ensure that such a simplifying assumption is robust.

References

- Aitken, S.N., S. Yeaman, J.A. Holliday, T.L. Wang and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1:95–111.
- Bresson, C.C., Y. Vitasse, A. Kremer and S. Delzon. 2011. To what extent is altitudinal variation of functional traits driven by genetic adaptation in European oak and beech? *Tree Physiol.* 31:1164–1174.
- Cordell, S., G. Goldstein, D. Mueller-Dombois, D. Webb and P.M. Vitousek. 1998. Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* 113:188–196.
- Hovenden, M.J. and T. Broadribb. 2000. Altitude of origin influences stomatal conductance and therefore maximum assimilation rate in Southern Beech, *Nothofagus cunninghamii*. *Aust. J. Plant Physiol.* 27:451–456.
- Hovenden, M.J. and J.K. Vander Schoor. 2003. Nature vs nurture in the leaf morphology of Southern beech, *Nothofagus cunninghamii* (Nothofagaceae). *New Phytol.* 161:585–594.
- Körner, C. 2007. The use of 'altitude' in ecological research. *Trends Ecol. Evol.* 22:569–574.
- Kouwenberg, L.L.R., W.M. Kürschner and J.C. McElwain. 2007. Stomatal frequency change over altitudinal gradients: prospects for paleo-altimetry. *Rev. Mineral. Geochem.* 66:215–241.
- Oleksyn, J., J. Modrzynski, M.G. Tjoelker, R. Zytkowskiak, P.B. Reich and P. Karolewski. 1998. Growth and physiology of *Picea abies* populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Funct. Ecol.* 12:573–590.
- Premoli, A.C. and C.A. Brewer. 2007. Environmental vs genetically driven variation in ecophysiological traits of *Nothofagus pumilio* from contrasting elevations. *Aust. J. Bot.* 55:585–591.
- Vitasse, Y., S. Delzon, C.C. Bresson, R. Michalet and A. Kremer. 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can. J. For. Res.* 39:1259–1269.
- Way, D.A. and R. Oren. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiol.* 30:669–688.
- Zhang, J.W. and J.D. Marshall. 1995. Variation in carbon isotope discrimination and photosynthetic gas exchange among populations of *Pseudotsuga menziesii* and *Pinus ponderosa* in different environments. *Funct. Ecol.* 9:402–412.