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Beyond Mean Reaction Norms: Trait Plasticity and Growth of Trees under Interspecific Competition Above and Below Ground

Boris Rewald[1], Hans Sandén[2], Douglas L. Godbold[1,2], and Ramona Werner[2,3]
[1]Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic
[2]Institute of Forest Ecology, BOKU University, Vienna, Austria
[3]School of Integrative Plant Science, Cornell University, Ithaca, United States

Mixed-species forests have the potential to enhance ecosystem resilience and productivity in the context of global change. While plant traits are increasingly being used to extend the scope of Earth observations to the organismal level and to link them to ecosystem functioning, intraspecific trait variability and plasticity are often neglected - models often rely on species-level means from databases. Furthermore, studies of species interactions and trait dynamics often overlook belowground plasticity. We investigated how competitive interactions influence growth and functional traits of four temperate deciduous tree species. We hypothesized that (1) growth effects in mixtures occur not only at the level of wood biomass, but also at the level of leaves and fine roots, resulting in overyielding effects at the stand level, (2) competitive interactions in mixed-species communities increase trait dissimilarity at the community level, and (3) species acclimation to intra vs. interspecific competition follows different types of reaction norms, including changes in trait mean and/or variability, depending on competitive status.

A forest inventory was conducted in planted monocultures, 2-species and 4-species mixtures of European *Acer*, *Tilia*, *Quercus* and *Carpinus*, representing a spectrum from acquisitive to conservative tree species. Competition effects were assessed with linear mixed effects models at the level of biomass and space acquisition, including leaf, canopy, stem and fine root traits. Using monocultures and 4-species mixtures, we analysed trait dissimilarity, means and variability of traits related to resource acquisition and use, including an extended ectomycorrhizal trait space, using kernel density-based metrics and generalised linear mixed models.

Most diverse stands, especially those with acquisitive *Acer*, exhibited aboveground overyielding, 1.5 to 1.9 times higher than monocultures. Fine roots showed significant overyielding in 4-species stands. Biomass allocation were highly species-specific and varied significantly at the diversity level. At the community level, aboveground traits other than specific leaf area showed limited plasticity, but belowground there was a marked difference between competitive superior and inferior species. Reaction norms of aboveground traits were dominated by shifts in mean and variability, whereas root traits were dominated by increases in variability in mixture. Trait dissimilarities, as a measure of plasticity across diversity levels, differed markedly between species, competitive dominance, and above and below ground. Overall, dominant *Acer* acclimated

least to interspecific competition, whereas inferior *Tilia* and *Carpinus* showed variability-driven plasticity above and below ground. *Quercus* showed mean-driven reaction norms below ground, with minimal changes in trait variability in the mixture.

Our data highlights the need to increasingly consider effects at the whole-plant level, as both above- and belowground components contribute significantly to overyielding in mixed-species environments. Our results further underscore how species mixing and competitive hierarchies drive trait plasticity at the level of mean and/or variability, highlighting distinct above- and belowground strategies (i.e. reaction norms) that may drive resource complementarity and thus govern longer-term coexistence and biogeochemical cycling in mixed-species stands.