

# No seed size-number trade-off in European beech: climate governs investment per seed

K. Kondrat<sup>1\*</sup>, J. Szymkowiak<sup>1,2</sup>, A. Hacket-Pain<sup>3</sup>, J.J. Foest<sup>1</sup>, M. Bogdziewicz<sup>1</sup>

<sup>1</sup>Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland, \*katarzyna.kondrat@amu.edu.pl

<sup>2</sup>Population Ecology Research Unit, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland

<sup>3</sup>Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Roxby Building, Liverpool, L69 7ZT, UK

Keywords: *Fagus sylvatica*, mast seeding, size-number trade-off, reproductive allocation, climatic gradients, nitrogen limitation, seed provisioning

Mast-seeding trees can vary seed output by orders of magnitude among years, but it remains unclear whether high seed production reduces per-seed investment, as predicted by fixed-budget allocation models. We quantified individual seed production together with seed mass in European beech across 2,792 trees and 123 populations spanning the species' range, and seed protein and lipid content in 35 populations. Seed mass increased with seed production, with seeds from high-seeding years being 14% heavier than those from low-seeding years, providing no evidence of a seed size-number trade-off and instead supporting variable reproductive allocation. In contrast, protein content decreased by 31% with increasing seed production, whereas lipid content increased by 14%, indicating that nitrogen becomes constraining at high reproductive output while carbon-based provisioning is maintained. Climate further influenced provisioning: seed mass and protein content were lowest at the climatic range margins, being 28% and 32% lower, respectively, than at the center of the climatic range. These results show that European beech can increase seed output without reducing per-seed biomass, but that nitrogen limitation and climatic constraints may strengthen regeneration bottlenecks at both trailing and leading margins, especially as climate warming intensifies.