

Transgenerational trade-off: the hidden costs of maternal defoliation in grass–endophyte symbiosis

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Epichloë endophytes form systemic, vertically transmitted symbioses with cool-season grasses, providing chemical defence against herbivores through alkaloid production. While often described as a ‘defensive mutualism’, the fitness costs of this relationship for the host plant, particularly across generations, remain poorly understood. This study investigated whether repeated defoliation of *Festuca pratensis* (meadow fescue) mother plants alters seed production, seed viability, and the endophyte-conferred resistance of progeny plants.

A common-garden experiment was established using both endophyte-symbiotic (E+) and endophyte-free (E–) plants. Over one growing season, half of the plants were subjected to severe, repeated defoliation to simulate grazing stress. Plant biomass, inflorescence number, seed biomass, chlorophyll activity, and alkaloid concentrations in leaves and seeds were quantified. Seed viability and germination rates were tested, followed by a greenhouse experiment where progeny were challenged with the aphid *Rhopalosiphum padi* to assess resistance conferred by maternally induced alkaloids.

Results revealed a strong resource allocation trade-off. Defoliation reduced leaf alkaloid concentrations in E+ plants but increased alkaloid investment into seeds. This shift enhanced seed protection and provided seedlings with elevated alkaloid levels during the first six weeks of growth. Consequently, progeny of defoliated E+ plants exhibited reduced

aphid performance compared with progeny of non-defoliated E+ plants, confirming a transgenerational defensive effect. However, these benefits came at a reproductive cost: seeds from defoliated E+ plants had significantly lower germination rates than seeds from E+ non-defoliated or E– plants. Germination was negatively correlated with seed alkaloid concentrations, suggesting that endophyte-driven defence investment compromised reproductive success.

These findings highlight a context-dependent nature of the grass–endophyte relationship. Under intense foliar stress, the endophyte prioritizes transgenerational defence, allocating resources toward alkaloid-enriched seeds at the expense of seed viability. While this strategy enhances early-stage herbivore resistance in progeny, it reduces the number of viable offspring, suggesting a fitness trade-off between defence and reproduction. From an evolutionary perspective, this dual outcome may help explain the observed variability of endophyte frequencies in natural grass populations. In environments with high herbivory pressure, enhanced seed protection could outweigh reduced germination, whereas under low herbivory, the cost to reproductive output may favour endophyte-free grasses. Overall, the study demonstrates that *Epichloë*-conferred defensive mutualism does not fully bypass the growth–defence trade-off but instead redistributes it across generations, balancing survival advantages against reproductive costs.