Enhancing plant defence: the role of mutualistic fungi in silicon-mediated pest resistance

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Grasses have primarily coevolved with large grazing herbivores, a relationship that has strongly shaped their defensive architecture. This evolutionary history has led to the development of traits such as basal meristems and prolific tillering, enabling rapid regrowth following grazing. Consequently, grasses typically lack a diverse arsenal of chemical defences and instead rely on alternative strategies, including rapid tissue turnover, physical barriers, and symbiotic associations with microorganisms to deter insect herbivores. Microbial symbionts may provide chemical protection, while structural defences, such as silicon accumulation, play a key role. Silicon serves as a major structural defence against both biotic and abiotic stress, comprising up to 10% of grass dry mass. Many temperate grasses associate with mutualistic fungi, such as *Epichloë* endophytes and arbuscular mycorrhizal fungi, and these symbiotic plants can exhibit altered host chemistry, subsequently influencing herbivore interactions. However, few studies have investigated how silicon-based physical defences interact with these fungal symbionts and their chemical defence mechanisms. This research addressed this knowledge gap by examining how silicon, *Epichloë*, and arbuscular mycorrhizal fungi interacted to affect plant resistance to insect herbivores. Two forage grasses (*Festuca arundinacea* and *Lolium perenne*) with contrasting leaf dynamics, were studied under factorial combinations of silicon supplementation, fungal inoculation (five novel grass-*Epichloë* associations [tall fescue: AR584 or common-toxic; perennial ryegrass: AR37, AR1, or common-toxic] or as *Epichloë*-free controls], and one arbuscular mycorrhizal fungal strain of *Rhizophagus irregularis*), and herbivore pressure from *Helicoverpa armigera* (a moth) and *Rhopalosiphum padi* (an aphid). Experiments showed that all *Epichloë* strains increased silicon concentrations in tall fescue on average to 31%. Of the five *Epichloë* strains in perennial ryegrass only strain AR37 had any effect increasing silicon concentrations. Silicon also enhanced *Epichloë* colonization (fungal mass) in tall fescue, but not in perennial ryegrass. In soil systems, silicon reduced the growth of *H. armigera* more effectively than any of the *Epichloë* strains, though both silicon and *Epichloë* contributed to plant defence in a compatible, non-antagonistic manner. In perennial ryegrass, silicon influenced *Epichloë*-derived alkaloid production, specifically epoxyjanthitrems. Scanning electron microscopy revealed that silicon and *Epichloë* could compatibly enhance surface defences and reduce insect feeding efficiency, while also compromising herbivore immunity. In a final experiment using only AR584 in tall grass fescue, tripartite interactions involving arbuscular mycorrhizal fungi, *Epichloë*, and silicon were explored under aphid attack. While endophytes suppressed aphid performance, arbuscular mycorrhizal fungi counteracted these effects, potentially through reduced alkaloid levels and increased foliar nitrogen. Silicon increased uptake in all symbiotic treatments but did not affect aphid performance. Overall, this

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research provided novel insights into the complex and context-dependent nature of grass defence systems. Silicon offered stronger protection against folivores, while endophyte-derived alkaloids were more effective against aphids. Interactions between fungal symbionts and silicon varied by plant species, fungal genotype, and herbivore type. These findings underscore the potential of harnessing natural plant–microbe–silicon interactions to enhance grass resilience against a range of biotic stressors, offering valuable insights for the development of more sustainable forage systems.