Ballhorn D.J., Kautz S., Lion U. & Heil, M. (2008) Trade-offs between direct and indirect defences of lima bean (*Phaseolus lunatus*). J. Ecol 96, 971-980

Abstract
Plant defence theory predicts trade-offs among defence traits as a result of resource limitation or pleiotropic effects. Although theoretically widely accepted, empirical demonstrations of such trade-offs are surprisingly scarce and mechanistic explanations are usually lacking.
We quantified cyanogenesis (the release of hydrogen cyanide (HCN)) as a direct defence and the emission of volatile organic compounds (VOCs) as an indirect defence against herbivores. To elucidate whether the trade-offs occur at the genetic or phenotypic level we investigated cultivated and wild-type accessions of lima bean (Fabaceae: Phaseolus lunatus L.) and compared different leaf developmental stages. Genetic relationships among the accessions were studied using amplified fragment length polymorphism (AFLP) analysis.
Cyanogenesis and the release of VOCs differed significantly among the accessions and were negatively correlated: high cyanogenic accessions released low amounts of VOCs and vice versa. The same remained true for the ontogenetic stages, since primary leaves of all accessions hardly ever produced HCN at all, yet regularly showed high release rates of VOCs.
Low and high cyanogenic accessions of lima bean formed distinct clades in an AFLP-based dendrogram, while wild-types and cultivars did not separate. The first pattern indicates that the underlying defensive syndromes are genetically conserved, while the latter is likely to be caused by a multiple origin of cultivated lima beans or an extensive gene flow among cultivated and wild plants.
Synthesis Trade-offs between cynogenesis and VOC release were obvious both between accessions and at the ontogenetic level, and thus cannot be explained by pleiotropy. We contend that allocation restrictions and/or adaptations to different enemy pressures are most likely to explain why lima bean can invest into cyanogenesis or VOCs, but not both.