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Amino acids for parasitic weed management.

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Amino acids are the building blocks of proteins for all biota in agricultural systems. They are intermediaries in the soil nitrogen cycle between degradation of decaying organic matter and the mineralized nitrogen forms ammonium and nitrate. In addition, amino acids appear in the rhizosphere as a result of lysis and active efflux from microbial and plant root cells. While plants and microbes prefer to uptake inorganic nitrogen, they also present the capacity for taking up amino acids using different transport processes that present increased molecular complexity (Owen and Jones, 2001; Nasholm *et al.*, 2009). An increased crop ability to uptake amino acids from the rhizosphere is an interesting trait to select for low nitrogen-input agronomic systems that rely on organic matter (Reeve *et al.*, 2009; Moe 2013). Besides their role as a nitrogen source, the abundance and content of amino acids in the rhizosphere affect microbial phenotypes relevant for rhizosphere function. Microbial motility, colony development or sporulation are known to be influenced by amino acids (reviewed in Moe 2013). On the other hand, certain amino acids toxic to the microbial community are deposited in the soil by some particular species of rhizospheric biota which do not succumb themselves to their own delivered toxicity suggesting a function in ecological niche colonization (Valle *et al.*, 2008). Microbial-derived efflux of amino acids can also be toxic for plants. As an example, Frenching disease is a crop physiological disorder caused by high levels of isoleucine efflux by saprophytic rhizobacteria. In Frenching soils, susceptible crops develop symptoms of chlorosis, wilting and stunting (Steinberg 1946).

Plant growth inhibition observed by abundance of certain amino acids is usually the result of the activation of negative feedback during amino acid biosynthesis. This is the case with branched enzyme networks such as the biosynthesis of aromatic, branched-chain or aspartate-derived amino acids. This regulatory mechanism maximizes efficient exploitation of resources preventing too much of a specific product to be made in detriment of other products that the cell needs as well. Too much of a specific end-product shuts off its production by deactivating an enzyme participating in its synthesis. In some cases, the deactivation of the enzyme induces starvation for other amino acids produced in parallel. For example, in the above-mentioned Frenching disease, high levels of isoleucine efflux by saprophytic bacteria causes the inhibition of acetolactate synthase (ALS) an enzyme in the branched-chain pathway causing valine and leucine starvation. Similarly, key enzymes in the aspartate pathway of amino acid synthesis can be deactivated by abundance of lysine or threonine or their combination causing methionine starvation. On occasions, such inhibition phenomena limit protein synthesis and growth and can be abolished by exogenous provision of the offended amino acid (Piryns *et al.*, 1988; Henke *et al.*, 1974).

The patterns of amino acid inhibition and rescue depend on a variety of factors including plant species, plant growth stage and amino acid concentration (Henke *et al.*, 1974) which are exploitable in crop protection in order to differentially target pests without detrimental inhibition for the crop species. In fact, several crop protection methods are inspired by the natural process of amino acid inhibition. For example, herbicides such as imidazolinones and sulfonylureas inhibit the enzyme ALS, slowly killing the weed by starving it of branched-chain amino acids (Duggleby *et al.* 2008). Another example is the use of mycoherbicides with enhanced efficacy against weeds through increased efflux of amino acids toxic to the target weed. Such is the case of the 45- to 65-% enhancement of mortality observed in wild hemp treated with valine-overproducing variants of the mycoherbicide *Fusarium oxysporum* f. sp. *cannabis* in comparison to the weed control obtained with the wildtype *F. oxysporum* f. sp. *cannabis* strain (Tiourebaev 1999; Tiourebaev *et al.* 2001). Another alternative is based on the innate ability of allelopathic crops to naturally compete against weeds. Plants deposit through root exudation a complex collection of chemicals with amino acids being the second most abundant class of compounds exuded (Jaeger *et al.*, 1999) which in some cases include amino acids acting as natural herbicidal weapons. Such is the case of roots of festuca grasses that exude a potent herbicidal amino acid m-tyrosine whose weed killing action is probably caused by negative feedback for phenylalanine biosynthesis in weeds growing around them (Bertin *et al.*, 2007). Finally, the direct application of inhibitory amino acids to agricultural soils has

been effective not only for the control of weeds such as Canada thristle, red bromegrass, kudzu and cannabis (Sands and Pilgeram 2009) but also other pests such as plant parasitic nematodes (Zhang *et al.*, 2010).

Broomrapes (*Orobanche* and *Phelipanche* species) are holoparasitic weeds that attack crops withdrawing nutritive resources from their roots via haustorial connections (Parker 2013). They are very difficult to control because once seedlings of broomrape weeds attach to the crop root they merge as a whole organism. It becomes very difficult to inhibit the development of broomrape without damaging the crop. Although broomrapes depend on the crop for essential inorganic and organic resources, they possess their autonomous amino acid biosynthesis pathways which are targeted by the amino acid-inhibiting herbicides glyphosate, imidazolinones and sulfonylureas (Dor *et al.*, 2017). Those herbicides are delivered on the foliage of an herbicide-tolerant crop and transported downwards to the underground parasite across the haustorium (Eizenberg *et al.*, 2013). Those herbicides exert the inhibitory action on the aromatic and branched-chain amino acid-biosynthesis pathways locally in the parasite by inhibiting the parasite encoded EPSPS and ALS without affecting amino acid synthesis in the crop which has been selected to resist the herbicide (Dor *et al.*, 2017). A biotechnological alternative to amino acid-inhibiting herbicides could be engineering future transgenic crops harbouring silencing constructs against the broomrape-encoded ALS or EPSPS genes. Silencing signals that specifically target the expression of parasitic weed-encoded genes have been proved to translocate across the haustorium (Tomilov et al 2008, Aly *et al.*, 2009).

Parasitic weed growth is inhibited by exogenous application of specific amino acids but their mode of action has not been revealed (Vurro *et al.*, 2006; Nzioki *et al.*, 2016; Fernandez- Aparicio *et al.*, 2017). The lack of identification of amino acids that abolish the inhibition renders uncertain whether the inhibitory action observed is caused by specific antimetabolite effect in which negative feedback triggered by the inhibitory amino acid causes starvation for another amino acid essential for parasitic weed growth or, by a separate phenomenon of general amino acid toxicity, of yet unknown molecular basis. Anyway, the effect of amino acids in weed parasitism is considered valuable for developing alternative control strategies because it has the potential to develop species-specific pesticides due to the differential inhibition patterns between parasitic weed species and also between parasitic weed species and their crop hosts. This strategy also has the potential to develop pesticides with low persistence in the soil as the applied amino acids is expected to be rapidly depleted by soil-dwelling microbes (Jones and Kielland, 2012). Preliminary steps towards including amino acids in sustainable management strategies have been taken. For example, the germination of *Phelipanche ramosa* and *Orobanche minor* is inhibited by amino acids such as methionine at concentrations that are not inhibitory to their respective hosts tomato and red clover. Leucine and tyrosine are toxic to *Striga hermonthica* but innocuous to its host maize. The effects of these amino acids at field scale have been investigated in crops of red clover and maize respectively using strategies of direct soil application of methionine or using bioherbicides with high levels of leucine and tyrosine efflux. Both techniques showed significant reduction levels of parasitic weed infection (Nzioki *et al.*, 2016; Fernandez-Aparicio *et al.*, 2017). In addition to amino acid application via direct delivery or microbial efflux, the potential of root exudates containing orobanchicidal amino acids can be investigated in strategies of cover crops or intercrops. For example, root exudates of clover, a host crop for *O. minor* but not for *P. ramosa* are rich in glycine (Lesuffleur *et al.*, 2007). Interestingly, glycine is reported to be a strong inhibitor of *P. ramosa* (Vurro *et al.*, 2006), while it does not inhibit *O. minor* germination (Fernandez- Aparicio *et al.*, 2017). Deploying such an approach opens the way to the design of sustainable alternatives finely crafted against the specific local weed problem. Another possibility could be selecting crops with altered amino acid exudation. In rhizotron experiments performed in our lab, *Phelipanche* seeds showed reduced capability to infect roots of tomato plants with increased efflux of lysine. This preliminary information warrants further investigations towards putting amino acid-based techniques into commercial practice for parasitic weed control.

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