Root nodulation: the twelfth hypothesis

by
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In designing agroforestry systems with direct tree/crop interaction, such as in hedgerow intercropping, conventional wisdom says that tree roots should be in deeper layers of the soil than crop roots. This arrangement should achieve the best overall efficiency of nutrient uptake.

However, interaction between tree and crop roots may be greater than is commonly supposed. During a recent workshop in Nairobi, organized by ICRAF and the International Board for Soil Research and Management (IBSRAM), we found that sufficient evidence exists to put forward a hypothesis that can be tested by critical observations on various sites.

Hypothesis: Roots of nitrogen-fixing trees have more nodules, where nitrogen fixation takes place, when they are in close contact with roots of non-nitrogen-fixing plants. This increased nodulation may lead to the direct transfer of nitrogen to the non-nodulating plant.

Supporting observations

In several cases, improved nodulation has been observed on tree roots in close contact with roots of non-nodulating trees and shrubs. The association can be so close as to cause confusion concerning which species is nodulated.

In southeastern China, abundant nodules were found under *Eucalyptus* roots in a mixed *Eucalyptus-Casuarina* plantation (Dommergues, 1987). On closer inspection, the nodules were found to be attached to the *Casuarina* roots.

In another instance, nodulation was reported for *Rubus ellipticus* in a botanical garden in Indonesia; the actinomycete (fungus-bacterium that stimulates nodule formation in certain tree species) *Frankia* was isolated from the nodules and nitrogen fixation was established (Becking, 1984). However, in subsequent work on this unexpected symbiotic association, it turned out that the nodules belonged to *Myrica rubra* trees (Stowers, 1985).

Roskoski (1981) studied nodulation and nitrogen fixation by the leguminous tree *Inga jinicuil* in a coffee plantation. She found that nodules and fine roots of this species were not randomly distributed throughout the area studied, but were concentrated around the trunks of coffee trees, within or just below the litter layer.

Finally, in southern Sumatra, Indonesia, we tested hedgerow intercropping as one option in a project aimed at improving nitrogen management for food crops on acid upland soils. As most of the trees on the site were shallow rooted, we included a local deep-rooted, leguminous tree—*Peltophorum pterocarpum*—as a hedgerow species (van Noordwijk et al., in press). One of the drawbacks of this tree is that it is non-nodulated, as far as we know. However, on excavating root systems in 1989, when the trees were three years old, we were surprised to find nodulated tree roots close to maize plants adjacent to the *Peltophorum* hedge. It turned out that the nodules belonged to a *Gliricidia* hedgerow, 3.5 metres away.

During subsequent root excavations in an experiment to test the effect of stem pruning height on root distribution, we were again misled initially by intense nodulation close to *Peltophorum* stems. In this instance, the nodulated roots could be traced to the *Gliricidia* hedgerows in the neighbouring plot, more than 6 metres from the observation point.

Reports of increased nodulation of tree roots in association with annual crops are more scarce. An indication that this may occur was obtained in 1985 at a high-rainfall substation of the International Institute of Tropical Agriculture (IITA) in Onne, southeastern Nigeria. In a hedgerow-intercropping experiment on a strongly acid soil (pH(KCL) 3.6, pH(H_2O) 4.7), *Leucaena leucocephala* formed a shallow root system, occupying the same soil layer as the cassava crop grown in the alleys.

Leucaena roots were observed in direct contact with cassava roots, at about 2 metres from the *Leucaena* hedge (Hairiah and van Noordwijk, 1986). Nodulation was not quantified in the different zones in this experiment, but the direct contact of tree nodules with food-crop roots suggests that direct transfer of nitrogen is possible.

In research conducted by the French Office de la recherche scientifique et technique d'outre-mer (ORSTOM) at Dakar, Senegal, large (5–8 centimetres in diameter) nodules of an *Albizia lebbeck* tree were so intertwined with sorghum roots 15 metres away that the observer thought he had discovered a nodulated sorghum (Gaetano Germani, personal communication).

Discussion

Except for the work of Roskoski (1981), none of the observations quoted here is sufficiently quantitative to refute or support the hypothesis. Yet, we hope to raise interest in the matter and stimulate further observations under a wide range of condi-

LEFT: Nodulated root of Gliricidia sepium *more than 6 metres from its stem base, close to the stem of a* Peltophorum pterocarpum *hedgerow. Roots were excavated from the top 20 centimetres. Many fine roots with nodules were lost during this operation.*

RIGHT: Close association of nodulated Leucaena *roots and cassava tuberous roots in the topsoil in a hedgerow-intercropping experiment on an acid soil in southeastern Nigeria (Onne).*

tions. To test the hypothesis, root observations should be made perpendicular to the hedgerows and nodulation should be observed at increasing distances from the hedgerow, either per unit of tree root length, or per unit volume of soil.

If the hypothesis is confirmed, it could have consequences for the balance of positive and negative tree/crop root interactions, at least for nodulating trees mixed with non-nodulating crops. Fixed nitrogen might be transferred directly to crops, avoiding the pathway of uptake by the tree and return to the soil via prunings. This would be similar to the much-disputed case of grass/legume mixtures (Johansen and Kerridge, 1979) or to maize/legume intercropping (Eaglesham et al., 1981).

The fact that all roots leak nutrients means that closely neighbouring roots containing little nitrogen could utilize nitrogen exuded from roots of high nitrogen content. And because a large part of the fine tree roots, including nodules, can be expected to die after the tree's shoot/root balance is disturbed by pruning, transfer is even more likely in a hedgerow-intercropping system.

As a mechanism underlying this hypothetical stimulation of nodulation, we may mention two possibilities. The simplest is connected with the usual inhibition of nodulation in soils of high mineral nitrogen content. Underneath food crops or in any other well-rooted zone, we may expect depletion of mineral nitrogen, and thus stimulation of nodule formation. A more complex explanation would involve a role for root exudates of the accompanying non-nitrogen-fixing plant. Host infection by rhizobia associated with *Frankia* might be positively (or negatively) affected by non-symbiotic bacteria thriving in the rhizosphere of the non-nodulating plant. Schmidt (1978) has established that rhizobia in certain cases can thrive in the rhizosphere of non-nodulating plants and thus increase the potential of the soil to stimulate nodule formation in the vicinity of their roots.

The 'Ten hypotheses for soil-agroforestry research' proposed by Young (1989a; 1989b, p. 218) are of a broad nature, referring to overall effects of processes. Wilson (1990) put forward a more specific hypothesis—that the shading effect of a tree canopy improves nitrogen fixation. Our own hypothesis also relates to a more specific process, linked to Young's hypotheses 4 (nitrogen fixation) and 10 (importance of roots). We hope that this proposal will stimulate further study of root nodulation in agroforestry and the possible mechanisms involved.

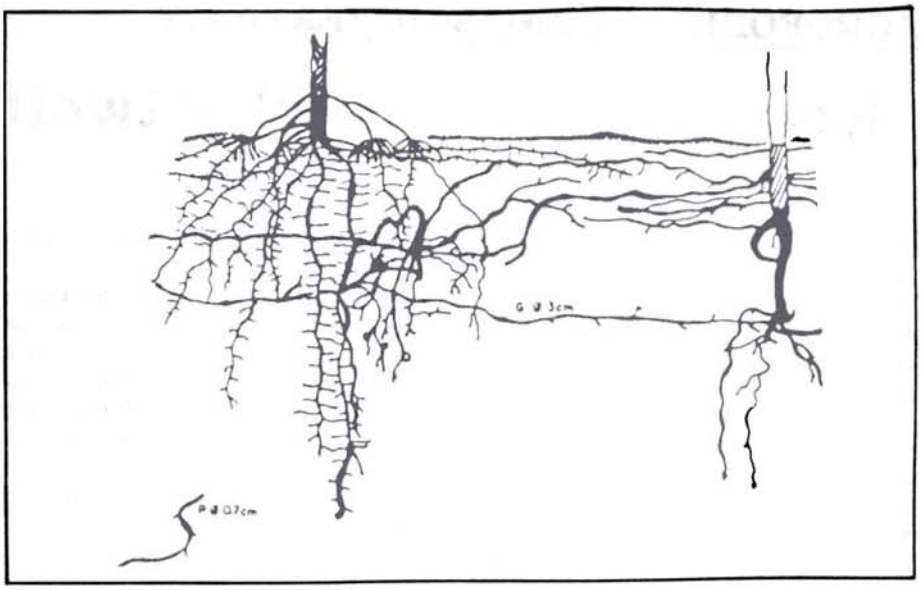

Diagram of maize roots in a hedgerow-intercropping experiment in southern Sumatra with Peltophorum pterocarpum *trees and a* Gliricidia sepium *hedgerow. The nodulated roots belong to the* Gliricidia *hedgerow 3.5 metres from the maize row. The roots in deeper layers belong to the* Peltophorum.

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