



## Hypothetical framework integrating the main mechanisms involved in the promoting action of rhizospheric humic substances on plant root- and shoot-growth

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### ABSTRACT

The ability of rhizospheric humic substances to improve plant growth has been well established by many studies carried out using diverse plant species cultivated under many different conditions. These beneficial effects of humic substances on plant development are expressed in both root and shoot. However, the mechanisms responsible for this action of humic substances are only partially known and poorly integrated. In fact, although the studies focused on plant root development are numerous, those dealing with plant shoot development are scarce. Likewise, studies integrating humic effects on root and shoot are also few.

In this context, the main goal of this work is to summarize some of the results regarding the effects of humic substances on plant development within a hypothetical holistic framework that will allow us to interconnect these findings and disclose some features of the functional crosstalk between the effects on soil, root and shoot. Furthermore, the significance of all these mechanisms in plants growing in the field is also discussed.

### 1. Introduction

A number of studies have shown the strong positive correlation between soil fertility and the soil content of transformed (humified) organic matter, also known as natural organic matter (NOM) (Magdoff and Weil, 2004a). These relationships are mainly related to the significant presence of stable, brown-black, organic fractions in the soil horizons (mainly in the horizon A) where plant roots are developed (rhizosphere) (Pinton et al., 2001a). Moreover, the organic matter in the rhizosphere is highly influenced by and associated with great biodiversity in micro- and macro-organisms (Pinton et al., 2001a,b; Hinsinger et al., 2009).

Although the chemical nature of NOM is controversial, many studies have demonstrated that, in fact, organic fractions in the solid soil interface are chemically and physically linked to clays and other inorganic matrices (metal oxides, metal phosphates and so on...) and minerals (Weil and Magdoff, 2004b; Schumacher et al., 2005; Kinyangi

et al., 2006; Schaumann, 2006a; Lehmann et al., 2008). Moreover, organomineral soil layers contain organic molecules with very different degrees of transformation, from very simple organic molecules present in living matter (sugars, aminoacids, phyto regulators, organic acids, proteins, lignin and cellulosic fragments and so on) to organic fractions with diverse degree of chemically- and/or biologically- induced transformation that have traditionally been related to soil humus (Wershaw, 1993; Stevenson, 1995; Derenne and Largeau, 2001; Weil and Magdoff, 2004b; Piccolo, 2002). Therefore, NOM in soil horizons involves a heterogeneous ensemble of organic molecules with diverse degrees of transformation, with this heterogeneity depending on many soil factors that influence the transformation of fresh organic matter, such as microbiota, temperature, moisture, soil chemical composition and physical texture (Wershaw, 1993; Stevenson, 1995; Derenne and Largeau, 2001; Weil and Magdoff, 2004b; Piccolo, 2002). This molecular complexity is enhanced by the very diverse inorganic fractions that may be bound to organic fractions (Schumacher et al., 2005; Kinyangi et al.,

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Fig. 1. Meeting of the waters of Negro River and Solimoes River in Amazonia.

2006; Schaumann, 2006a; Lehmann et al., 2008).

However, when we focus our attention on one of the NOM fractions that directly interacts with living organisms (microorganisms, plant roots), the object of study is delimited to some extent and the molecular complexity of the system, though still high, might be modelled with greater accuracy. Thus, if we assume that one of the NOM fraction having higher bioactivity is that dissolved in the soil solution and aquatic reservoirs (dissolved organic matter, DOM), the study of the physico-chemical features of DOM fractions in solution will allow us to better understand their effects on plants and microorganisms.

In principle, we can assume that DOM is, to some extent, the product of a natural “extraction” of NOM present in soil resulting from the action of water in soil. This process would be affected by water pH, also related to soil pH. A good example of this “natural” extraction process is the “rio negro” in Amazonia (Fig. 1). As a result of NOM molecular complexity, DOM in soil solution and in aquatic ecosystems will include organic molecules with diverse degrees of chemical and/or biological transformation, from very simple organic molecules (amino acids, sugars, proteins, polysaccharides and so on ...) to highly transformed organic molecules (Herbert and Bertsch, 1995; Zsolnay, 1996; Kalbitz, 2001; Deb and Shukla, 2011). These organic molecules may associate with each other in solution, forming more stable molecular assemblies or aggregates, which, in turn, might have new chemical and biological activities. Some authors have concluded that these molecular entities, which traditionally have been named humic substances (HS), resulting from the self-assembly of organic molecules and minerals present in soil solution, can be defined as a type of natural supramolecules (Piccolo, 2002) (Fig. 2). However, this assertion deserves deeper discussion since there are no specific published studies showing that humic molecular aggregates in solution have chemical and biological features qualitatively different from those of their molecular components. In consequence, the question of whether HS are supramolecules or only molecular aggregates remains open and deserves more research. However, some results suggest that some chemical properties probably emerge when humic molecular aggregates are formed, such as amphiphilicity and biological recalcitrance, likely due to the presence of fatty acids and highly hydrophobic molecules in HS molecular aggregates (Chilom and Rice, 2009; Chilom et al., 2013; Khalaf et al., 2014; Nebbioso and Piccolo, 2011; Piccolo, 2002; Terashima et al., 2004). On the other hand, some studies indicate that HS molecular systems include both macromolecules and simpler molecules, which may form large molecular aggregates in solution, with the degree of aggregation depending on the pH, ionic strength and mineral composition of the solution (Garcia-Mina, 2007; Baigorri et al., 2007; Chilom et al., 2009; Esfahani

et al., 2015). In fact, HS molecular aggregates behave like macromolecules from a physico-chemical viewpoint (Garcia-Mina, 2007).

It is obvious that the molecular composition and structural conformation of DOM humic systems (or HS) in solution might be, and probably are, different from those of NOM in solid matrix, although DOM probably also contain significant inorganic residues such as clays, oxides, etc. (Schumacher et al., 2005; Kinyangi et al., 2006; Schaumann, 2006b). However, fluorescence-based studies focused on the molecular conformation in solution of HS extracted from either aquatic or soils ecosystems using various methodologies (reverse osmosis and alkaline extraction), presented very small differences between them (Alberts and Takacs, 2004). This fact indicates, at least, two relevant issues: (i) humic molecular aggregates in alkaline extracts have similar structural features and molecular conformation in solution to those naturally produced in aquatic environments; and (ii) extraction methods do not significantly alter DOM main conformational features. These two points are very important because they show that alkaline extraction is a valuable proxy to study not only DOM reactivity and bioactivity but also some NOM main properties. On the other hand, the fact that the conformational arrangements in solution for HS extracted from the same organic source through different methodologies are similar also indicates that the formation of humic molecular aggregates in solution is not a random process since it seems to be governed by energetically favoured weak molecular forces resulting from the chemical interaction of specific functional groups present in their structure (Piccolo, 2002; Chilom et al., 2013; Esfahani et al., 2015).

On the other hand, the beneficial action of HS treatment on the growth and physiology of plants cultivated in different soil types has been established by many studies (Chen et al., 2004a; Rose et al., 2014; and references therein). Most of these studies describe experiments with HS applied to the roots, but there are also studies involving the application of HS to the leaves (Chen et al., 2004a; Rose et al., 2014). However, the information regarding the specific molecular and physiological mechanisms involved in the plant growth promoting action of HS is rather fragmentary and poorly integrated into a more general overview (Chen et al., 2004a; Rose et al., 2014; Olaetxea et al., 2016).

One relevant point that has to be taken into account is that the beneficial action on plant growth caused by HS applied to the leaves is probably governed by mechanisms different from those involved in the beneficial action resulting from HS application to the roots. For instance, the mechanisms related to nutrient mobilization in soil resulting from the metal complexing ability of HS will not play important roles when HS are applied to the leaves. Likewise, the biochemical processes that may be affected by HS on the leaf surface are probably different, at

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