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SPECIAL REVIEW

# Dissolved humic substances – ecological driving forces from the individual to the ecosystem level?

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## SUMMARY

1. This review focuses on direct and indirect interactions between dissolved humic substances (HS) and freshwater organisms and presents novel opinions and hypotheses on their ecological significance. Despite their abundance in freshwaters, the role of HS is still inadequately understood. These substances have been considered too large to be taken up by freshwater organisms. On the contrary, here we present evidence that dissolved HS are indeed taken up and interact directly and/or indirectly with freshwater organisms.
2. We show that dissolved HS exert a mild chemical stress upon aquatic organisms in many ways; they induce molecular chaperones (stress shock proteins), induce and modulate biotransformation enzymes and modulate (mainly inhibiting) the photosynthetic release of oxygen by freshwater plants. Furthermore, they produce an oxidative stress, which may lead to membrane oxidation. HS modulate the multixenobiotic resistance activity and probably other membrane-bound pumps. This property may lead to the increased bioaccumulation of xenobiotic chemicals. Furthermore, they can modulate the numbers of offspring in a nematode and feminise fish and amphibians. The ecological consequences of this potential remain obscure at present. HS also have the potential to act as chemical attractants (as shown with a nematode).
3. In some macrophytes and algae we show that HS interfere with photosynthesis and growth. For instance, the presence of HS suppresses cyanobacteria more than eukaryotic algae. By applying a quantitative structure activity relationship approach, we show that quinones in the HS interfere with photosynthetic electron transport. We show that even *Phragmites* leachate can act as a kind of phytotoxin. HS also have the potential to suppress fungal growth, as shown with the water mould *Saprolegnia parasitica* and force the fungus to respond by spore production.
4. In very soft, humic freshwaters, such as the Rio Negro, Brazil, HS stimulate the uptake of essential ions, such as Na and Ca, at extremely low pH (3.5–4.0) and prevent the ionoregulatory disturbance induced by acid waters, thereby enabling fish to survive in these environments.
5. We discuss whether or not HS are directly utilised by aquatic microorganisms or via exoenzymes, which may be washed in from the terrestrial catchment. There is accumulating evidence that the quality of the HS controls microbial growth. In total, net-heterotrophy may result from HS-mediated suppression of primary production by the quinone structures and/or from HS-mediated support of microbial growth. As there is also evidence that HS have the potential to support photoautotrophic growth and suppress microbial growth, the opposite community effect could result. Consequently, dissolved organic carbon (DOC) has to be chemically characterised, rather than simply measuring bulk DOC concentration.
6. In sum, dissolved HS interact with freshwater organisms in a variety of ways in unenriched humic lakes. In addition to the well known effects of HS on light regime, for example, and the direct and indirect supply with carbon (energy), other interactions may be much more subtle. For instance, HS may induce internal biochemical stress defence systems and have the potential to cause acclimatisation and even adaptation. We are just at the beginning of understanding these interactions between dissolved HS and freshwater organisms.

*Keywords*: chemical stress defence, dissolved humic substances, feminisation, membrane irritation, natural herbicides

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We dedicate this paper to the memory of Profs. Robert G. Wetzel and Richard C. Playle, great pioneers in the field of humic substances ecology and physiology, and personal friends who died much too young.