

Dominant trees alter growing conditions in their surroundings

P. Weber^{1,2} & R.D. Bardgett¹

¹Department of Biological Sciences, Lancaster University, Lancaster, LA1 4YQ, United Kingdom

²Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

E-mail: pascale.weber@alumni.ethz.ch

Introduction

Tree growth is, besides endogenous factors, influenced by various exogenous factors such as light and nutrient availability. Whereas competition for light has been regarded as a main driver for forest development, as expressed in many forest succession simulation models, belowground processes have been considered as less important for competitive interactions. This is probably partly due to the fact that processes in the soil are in general difficult to study and for this reason are still poorly understood. However, similar to changes in light availability, changing patterns of soil nutrient availability can be expected to play an important role in forest succession. Over time, single trees will alter the conditions in their surroundings in many ways. As the trees grow, light availability at the forest floor decreases. Litter accumulation and the actions of roots are influencing the decomposer community composition, which will consist of differing portions of fungal and bacterial biomass, depending on litter characteristics and abiotic conditions. As a consequence, patterns of light and nutrient availability in forests are typically heterogeneous. A better knowledge of these patterns and their influence on tree growth and regeneration will help to enhance our understanding of competitive and mutual interactions in forests, which can play a crucial role in the way forests will respond to future natural and anthropogenic changes.

Our aim here is to give a first estimate of the importance of belowground factors for tree growth and regeneration. We combine dendroecological with soil ecological methods to investigate how single freestanding trees influence soil properties and thereby the growth of regenerating trees in their neighbourhood zone. We test the hypothesis that soil properties affect the radial growth of the regeneration besides light availability and browsing pressure.

Material and Methods

In a remnant of the old Caledonian forests in Scotland, 16 old and freestanding Scots pine (*Pinus sylvestris* L.) trees were chosen. These trees can be described as making up patches in the forest and causing gradients in light and soil conditions from their stems to their outer crowns. To analyse differences in above and belowground conditions related to the distance to the centre of the large trees, we defined three zones of influence around each tree: the inner zone (I), comprising the area from the stem to the middle of the crown projection, the middle zone (M), comprising the area from the middle to the full crown projection and the outer zone (O) including the adjacent area outside of the crown projection (Fig. 1).

In each of these three zones around the 16 large trees, 5 topsoil samples were added up to one bulk sample per zone and tree. Increment cores of both the old dominant and the adjacent regenerating trees (up to five per plot) were extracted to measure the age and the

radial growth of each tree. If possible, at least one regenerating tree in each of the three zones of influence per large tree was chosen.

A light index for each of the regenerating trees was calculated based on its position relative to the crown (categories: <50cm distance from stem, I, M, O) and its orientation (categories: S, SE/SW, W/E, N) relative to the stem of the large tree. Furthermore, this index was modified by the height of the start of the crown of the large old tree.

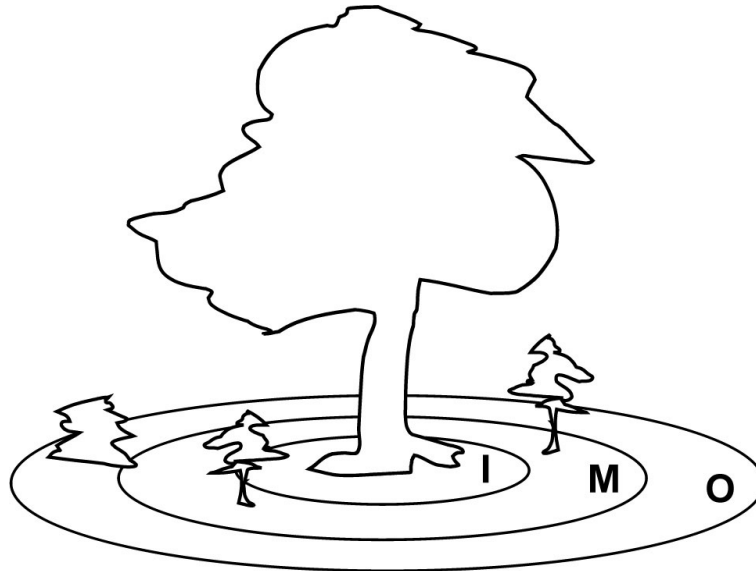


Figure 1: Sampling design. Each of the 16 plots includes one large and several regenerating Scots pine trees. On each plot, bulk soil samples were taken in each of the three zones of influence: I = inner, M = middle, O = outer zone.

Tree-rings of both the large and regenerating trees were measured and crossdated on a Lintab3 measuring system (F. Rinn S.A., Heidelberg, Germany) with a resolution of 0.01 mm and the TSAP tree-ring software (Rinn 1996). As a measure of the individual growth rate, mean annual growth of the last 10 years was calculated for each regenerating tree.

Soil samples were analysed for moisture content, pH, extractable inorganic N (NO_3^- , NH_4^+), dissolved organic N (DON) and C (DOC), microbial C and N, and microbial activity measured as basal respiration (for details cf. Harrison & Bardgett 2004).

First statistical analyses of the data included (1) testing for differences in the soil parameters between the three zones of influence and (2) linear regressions between the growth of the small trees and aboveground (light index) and belowground (soil property parameters) growing factors.

Results and Discussion

Soil properties, such as moisture content and availability of different nutrient forms, were found to differ among the three zones. First of all, soil moisture was significantly lower in the middle and in particular in the inner zone (close to the stem) than in the outer zone of influence (results not shown). These differences can be expected as a result of the trees'

water uptake and transpiration. Moisture availability itself is known to be an important parameter in influencing the microbial activity and rate of decomposition (Bardgett 2005). Second, among all measured nutrient compounds, availability of nitrate (NO_3^-) and dissolved organic C (DOC) showed also significant differences between the three zones (Fig. 2). Whereas NO_3^- was significantly lower underneath the crown (zones I and M), DOC was strongly decreasing with increasing distance from the stem.

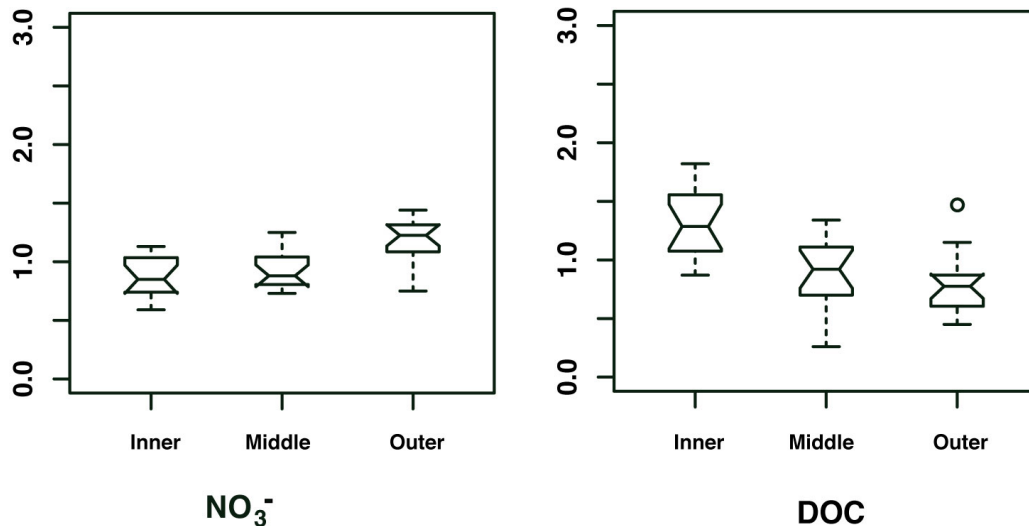


Figure 2: Notched boxplots of NO_3^- (left) and DOC (right) from the inner to the outer zone of influence (standardised on the plot). $N=16$. If the notches are not overlapping, the zones are significantly different at the 5%-significance level.

Low nitrate availability in the rooting area can result from the direct or indirect (via mycorrhizae) uptake of nitrate by the tree. Additionally, nitrate availability may also be low due to low mineralization rates (Bardgett 2005).

Our analyses of microbial biomass C and N support this second interpretation. Although the C:N ratio of the microbial biomass did not change between the three zones, microbial C was significantly higher in zone O (Fig. 3). At the same time, microbial C was strongly related to total extractable nitrogen (Fig. 3), indicating that microbial biomass was limited by nitrogen availability. Therefore, we can assume that available inorganic nitrogen is immobilized rather efficiently leading to a low net mineralization.

The comparatively high DOC values in the inner zone of influence can be interpreted as being the result of (1) high litter input from leaves and roots, which usually contains high amounts of carbon-based secondary compounds (Hättenschwiler & Vitousek 2000, Northup *et al.* 1998), and (2) root exudates, which typically have a higher C:N ratio than microbial biomass (Grayston *et al.* 1997). These high DOC values as well suggest that the availability of inorganic nutrients limits the incorporation of carbon into biomass, which goes well together with the above-described dependency of microbial C on total extractable nitrogen (Fig. 3).

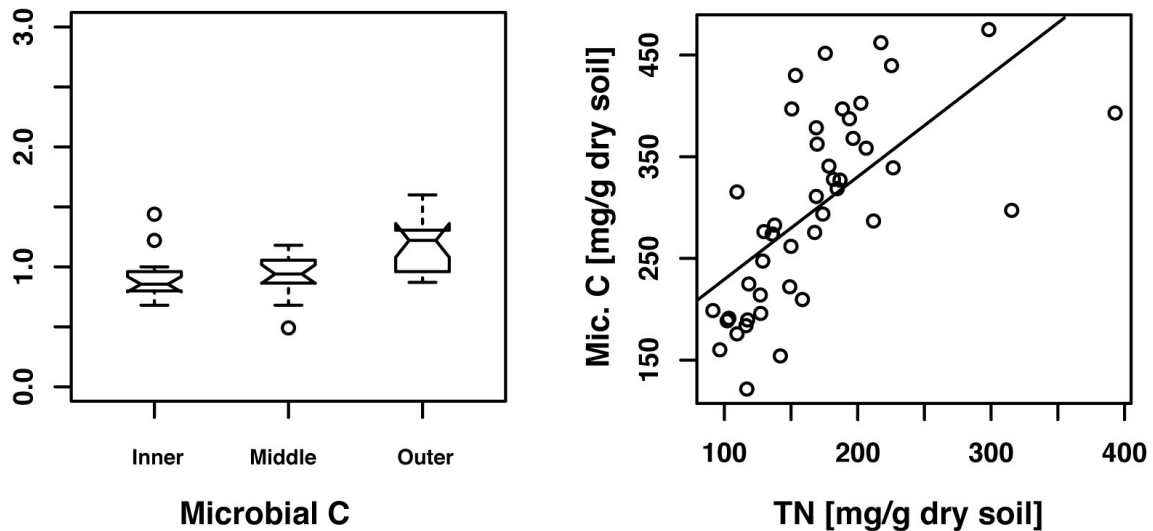


Figure 3: Notched boxplot (left) of microbial C from the inner to the outer zone of influence (standardized on the plot). $N=16$. Microbial C is linearly related ($p<0.001$) to total extractable N (right).

Conclusions

From these first results, we conclude that old large trees have a significant influence on soil conditions in a zone where litter fall and roots are acting. In this zone, they alter soil moisture content, nutrient forms and availability by affecting microbial community composition and activity. At this stage of the project it's too early to make a statement about how the here analysed gradients in soil and light conditions control radial growth of regenerating trees in the neighbourhood of the large old trees. However, first analyses suggest that the patterns of nutrient availability described here will also have an influence on tree-ring width of young trees.

Acknowledgements

The authors would like to thank H. Quirk and H. Gordon for helping with soil analyses, G. De Deyn, W. Mallott and M. Aira Viera for assisting in the field, S. Blackhall and A. McGregor from Rothiemurchus forest estate for providing information on the study site and Scottish Natural Heritage for the permission to conduct research in the Scots pine forests. The project was funded by Swiss National Science Foundation, Grant No. PBEZA—11073.

References

- Bardgett, R.D. (2005): *The Biology of Soils: A Community and Ecosystem Approach* Oxford University Press, Oxford.
- Grayston, S.J., Vaughan, D., Jones, D. (1997): Rhizosphere carbon flow in trees, in comparison with annual plants: The importance of root exudation and its impact on microbial activity and nutrient availability. *Applied Soil Ecology* 5: 29-56.
- Harrison, K.A., Bardgett, R.D. (2004): Browsing by red deer negatively impacts on soil nitrogen availability in regenerating native forest. *Soil Biology & Biochemistry* 36: 115-126.

- Hättenschwiler, S., Vitousek, P.M. (2000): The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology & Evolution* 15: 238-243.
- Northup, R.R., Dahlgren, R.A., McColl, J.G. (1998): Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: A positive feedback? *Biogeochemistry* 42: 189-220.
- Rinn, F. (1996): TSAP - Reference manual. Version 3.5 Rinntech, Heidelberg, Germany.