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Tree roots in canopy soils of old European beech trees—An ecological reassessment of a forgotten phenomenon

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ABSTRACT

The formation of adventitious roots in humus accumulations in tree canopies is widely acknowledged from tropical and temperate rainforests, while the occurrence of those canopy roots in temperate tree species under mesic climates has been largely disregarded for ca. 100 years. Moreover, almost nothing is yet known of the ecological growth conditions or the structure or morphology of such canopy root systems. This study reports on the occurrence of tree fine roots in crown humus pockets of old European beech (*Fagus sylvatica* L.) trees. The aim was to compare these canopy roots with the fine roots in the terrestrial organic layer soil in terms of fine root biomass density, root morphological traits, ectomycorrhizal colonisation and chemical composition of the root tissue, and to relate these root traits to the chemical properties of the respective soils. Fine root biomass density in crown humus pockets was ca. 7 times higher than in the terrestrial organic layer, even though soil chemical properties of both rooting media were similar. Fine roots in the canopy differed from terrestrial fine roots by lower specific root tip abundance, specific root length, and specific root surface area, all of which points to a longer lifespan of the fine roots in the canopy. Moreover, canopy roots revealed a lower percentage of root tips colonised by ectomycorrhizal fungi than terrestrial roots (87% vs. 93%). Chemical composition of the root tissue in canopy and terrestrial soils was similar for most elements, but canopy roots showed lower P, Fe, and Al concentrations and a higher N/P ratio than terrestrial roots. Root P concentrations of both canopy and terrestrial fine roots were closely related to soil P concentration, but not to soil C/P or N/P ratios. On the other hand, tissue N of canopy roots, but not of terrestrial roots, revealed a clear dependence on soil N and C/N values, suggesting a more limited N availability in the canopy soil compared to the terrestrial organic layer. However, the overall small differences in soil chemical properties between canopy and terrestrial organic layer soil cannot explain the markedly higher volumetric root density in the crown humus and the differences in ecomorphological traits between canopy and terrestrial soil. Instead, it is speculated that these differences are more likely a result of temporarily high water availability in crown humus pockets due to high water flow along the surface of branches to the central crown parts of the beech trees.

Introduction

Although the formation of adventitious roots from above-ground tree organs under natural conditions has always been observed only incidentally, there are several reports of the phenomenon in the literature. Anatomically, the majority of adventitious root formations can be attributed to callus tissue resulting from damages or injuries of above-ground tree organs, or represent 'aerial roots' built by adventitious root primordia under particularly humid environmental conditions (Gill 1969; Jeník 1973, 1994; Fink 1982, 1983; Herwitz 1991). Less frequently, adventitious root formation has been reported as a response to the accumulation of organic material in the form of 'crown humus pockets' in the canopies of trees (e.g. Nadkarni 1981; Vance and Nadkarni 1992; Sillett and Bailey 2003; Perez et al. 2005; Hertel and Köhler 2010). The occurrence of tree roots in such humus accumulations in the canopy has recently been more widely reported, particularly from tropical or temperate rainforests (Jeník 1978; Nadkarni 1981; Nadkarni and Primack 1989; Herwitz 1991; Sillett and Bailey 2003; Leary et al. 2004; Perez et al. 2005). Moreover, these observations have been interpreted as a convergent evolution to enhance the nutrient uptake of the host trees in tropical and temperate rainforests (Nadkarni 1981; Sanford 1987; Moore 1989). However, the quantitative contribution of those canopy roots to the trees' nutrient uptake has been recently estimated to be marginal (Hertel and Köhler 2010).

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While the occurrence of tree roots in canopy soils of tropical and temperate rainforests is well documented in more recent literature, the existence of this phenomenon in temperate trees under less humid climate conditions has been almost entirely forgotten during the past centuries. This is surprising since a survey of available older literature reveals that adventitious root formation in temperate tree species was frequently described ca. 100–150 years ago. For example, Vogtherr (1910) lists more than 25 temperate European tree species that were recognized for their capability of forming adventitious roots. Some of the cited sources even date back to reports from the mid 19th century or earlier (e.g. Loudon 1844; Ratzeburg 1859). At least for Europe, the obvious discontinuity in the knowledge of the phenomenon could be due to the intensive exploitation of wood during the two world wars along with the subsequent onset of modern commercial forestry, both of which impeded the existence of old and senescent tree individuals that are most suited to adventitious root formation (Koop 1987). The majority of observations of adventitious root formation in temperate tree species refer to root initiation by layering of branches on the ground soil, or as a result of branch or stem damage (Vogtherr 1910; Cooper 1911; Day 1938; Wardle 1980; Koop 1987; Jeník 1994; Pierik et al. 1997). In contrast, root formation in crown humus accumulations of temperate trees has seldom been studied (von Alten 1882; Conventz 1900; Wedding 1904; Vogtherr 1910). The vast majority of reports on canopy roots, either in temperate or tropical forests, are of more anecdotal character and none attempted to provide more insight into the prevailing ecological conditions of tree roots in the canopy humus compared to the growth conditions of roots in the terrestrial soil.

The occurrence of adventitious roots in the canopy of old European beech trees (*Fagus sylvatica* L.) in an old-growth forest in (mesic) Central Germany was coincidentally discovered by the author during a visit to the stand after a strong storm had wind-thrown some of the old beech trees. The roots were found in canopy humus pockets accumulated in forks of major branches from the stem in the central part of the tree crown. A systematic survey of the stand revealed the presence of several old, wind-thrown beech trees with crown humus accumulations that were sampled for both crown humus samples and samples from the terrestrial organic layer soil adjacent to the respective tree stem. By comparing the canopy roots with the fine roots in the terrestrial organic layer soil in terms of fine root biomass density, root morphological traits, ectomycorrhizal colonisation and chemical composition of the root tissue, the hypotheses shall be tested that (1) soil chemical properties in crown humus samples of old beech trees are different from those in the terrestrial soil organic layer due to the different substrates and climate conditions for pedogenesis; and (2) these differences lead to differences in fine root abundance and in the ecomorphology of the tree fine roots in the canopy soil compared to the terrestrial fine roots. The aim of the study was to gain a better understanding of the ecological growth conditions of tree fine roots in canopy soils and to assess the plasticity of fine root formation of tree individuals in response to prevailing environmental conditions in two spatially explicitly different rooting media.

Materials and methods

Study site description

The studied forest stand was located in the Reinhard Forest situated in the south-western part of the Weser Mountains in Central Germany at ca. 300 m asl (51°32′N, 9°30′E). The stand represents a continuous old-growth deciduous forest containing a large number of particularly old tree individuals of several tree species, among them several old-growth (200–300 years-old) individuals of European beech (*Fagus sylvatica* L.). The annual air temperature is ca. 7.7 °C and the annual precipitation amounts to ca. 805 mm (data recorded at the nearby weather station 'Beberbeck', Deutscher Wetterdienst 1995).

The forest stand grows on moderately steep slopes (inclination < 10°) with a westerly aspect. The soils are moderately nutrient-poor cambisols and luvisols developed from Tertiary sandstone bedrock ('middle bunter') and Quaternary loess cover. A several centimetres thick organic layer has accumulated atop the mineral soil.

Soil and root sampling in the field

The occurrence of tree roots of beech trees in canopy humus pockets was discovered in an old tree individual wind-thrown during strong storms in autumn and winter. A systematic survey in November 2009 revealed that the majority of recently fallen or broken old beech trees (ca. 6 individuals in total) harboured humus pockets in their crowns. The crown humus accumulations were mainly found in the forks of major branches from the stem in the lower crown positions with a few being found in open knotholes from old branches broken from the tree stem. Most humus accumulations in forks continued into cracks of the stemwood beneath the forks.

In order to survey the biomass density of tree roots in the canopy soils of beech trees and to compare root ecomorphological traits between fine roots in the terrestrial soil and the canopy humus, soil samples were taken with a soil corer (5.5 cm in diameter, 65 mL volume) from crown humus pockets of four randomly selected beech individuals with crown humus accumulations. The minimum distance between the tree individuals was ca. 50 m. Three of the four beech trees were wind-thrown 200–300-year-old trees, within which crown humus accumulations were found in forks from the stem at approximately 3, 8, and 9 m above the ground. The trees did not show any signs of any particular disease and therefore may have been wind-thrown due to their large size and maybe senescent stem tissues. The fourth beech tree was a much younger (ca. 50 years old), living individual that showed crown humus pockets in open knotholes from old, broken branches. Three canopy soil samples were taken from each of the four beech individuals, transferred into plastic bags and stored at 4 °C in the laboratory, where further processing was conducted. In addition, three soil samples were taken with the soil corer from the terrestrial organic layer in the direct vicinity of each of the four beech trees (in ca. 1–2 m distance to the stem) and processed as described for the canopy soil samples.

Fine root inventory

In the laboratory, all visible tree roots were extracted by hand from the canopy and terrestrial soil samples and cleaned from adherent soil particles in water using a sieve with a mesh size of 0.25 mm. The soil residues were stored for analysis of chemical properties. All extracted roots were fine roots (roots < 2 mm in diameter). Living (biomass) and dead roots (necromass) were distinguished under the stereo-microscope by inspecting colour, root elasticity, and cohesion of the cortex, periderm and stele (e.g. Persson 1978; Hertel and Leuschner 2002). The fine root biomass and necromass of each sample were dried at 70 °C for 48 h and weighed. The data were expressed as fine root dry mass per unit soil dry weight (in mg g^{-1}) and per unit soil volume (in g L^{-1}).

Ten living rootlets per soil sample were randomly selected in order to analyse mean fine root diameter, specific root surface area (SRA, in cm^2 g^{-1}) and specific root length (SRL, in m g^{-1}) using a WhinRhizo (Régent Instruments Inc., Quebec, Canada) visual analysis system with a scanner. The abundance of fine root tips in