Seasonal variations of CO_2 fluxes, C allocation and isotope fractionations of C and N along the soil-ectomycorrhiza-plant continuum in a beech forest

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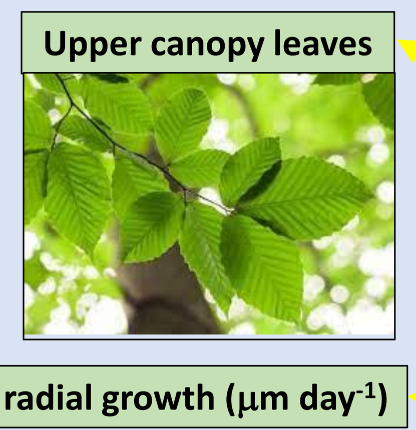
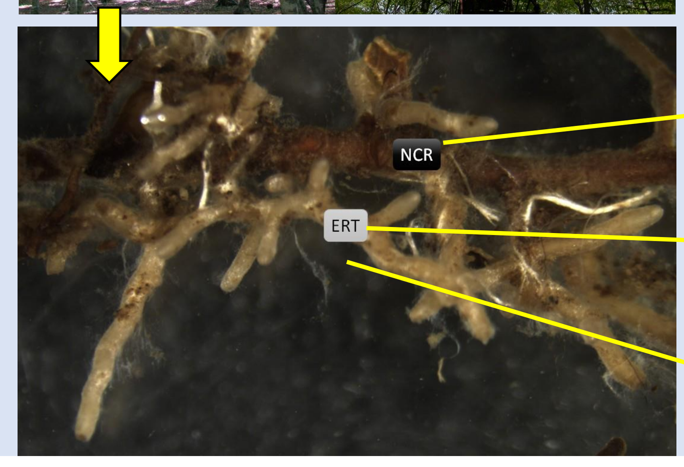
INTRODUCTION. In natural forest ecosystems, tree fine roots can establish symbiotic associations, mainly represented by ectomycorrhizas (ECM), with many species of soil fungi belonging to the phyla Ascomycota and Basydiomicota. ECM are mutualistic associations playing a key role in carbon (C) and nitrogen (N) regulatory dynamics in forest ecosystems, thus affecting tree nutrition, growth and health. This work evaluated the interplay between ECM development, C fluxes, stem radial growth, C and N exchange and isotope fractionations along soil-ECM-plant continuum in a Mediterranean beech forest. From bud break to leaf shedding, we monitored: net ecosystem exchange (NEE); leaf area index; stem radial growth; N concentration and isotope compositions of C and N ($\delta^{13}C$, $\delta^{15}N$) in rhizosphere soil, ectomycorrhizal root tips (ERT), ECM-free fine root portions (NCR) and leaves. **We hypothesized that coupling the isotopic measurements with phenology, ecosystem C uptake, leaf and wood production and ECM development may further improve our knowledge about the ecological role of ECM on ecosystem functionality and nutrient cycling in beech forests.**

AIM. The specific objectives of the present study were: i) to evaluate the seasonal interplay and trade-off between net ecosystem C uptake and C allocation to the canopy, stem growth and ECM during the different phenological stages; ii) to determine the relative isotopic fractionations along the soil-ECM-plant continuum.



The study was carried out in a beech forest in Central Apennine in the municipality of Collelongo (Abruzzo Region, Central Italy), where an experimental area for long term ecological research, actually included in LTER network, was established in 1991 (Selva Piana stand, 41°50'58" N, 13°35'17" E, 1,560 m elevation). Since 1993, fluxes of CO_2, H_2O and energy among forest and atmosphere have been measured using the eddy-covariance technique at the experimental site.



A synchronous seasonal pattern of ecosystem C uptake, stem radial growth and biomass accumulation in ectomycorrhizal root tips was recorded

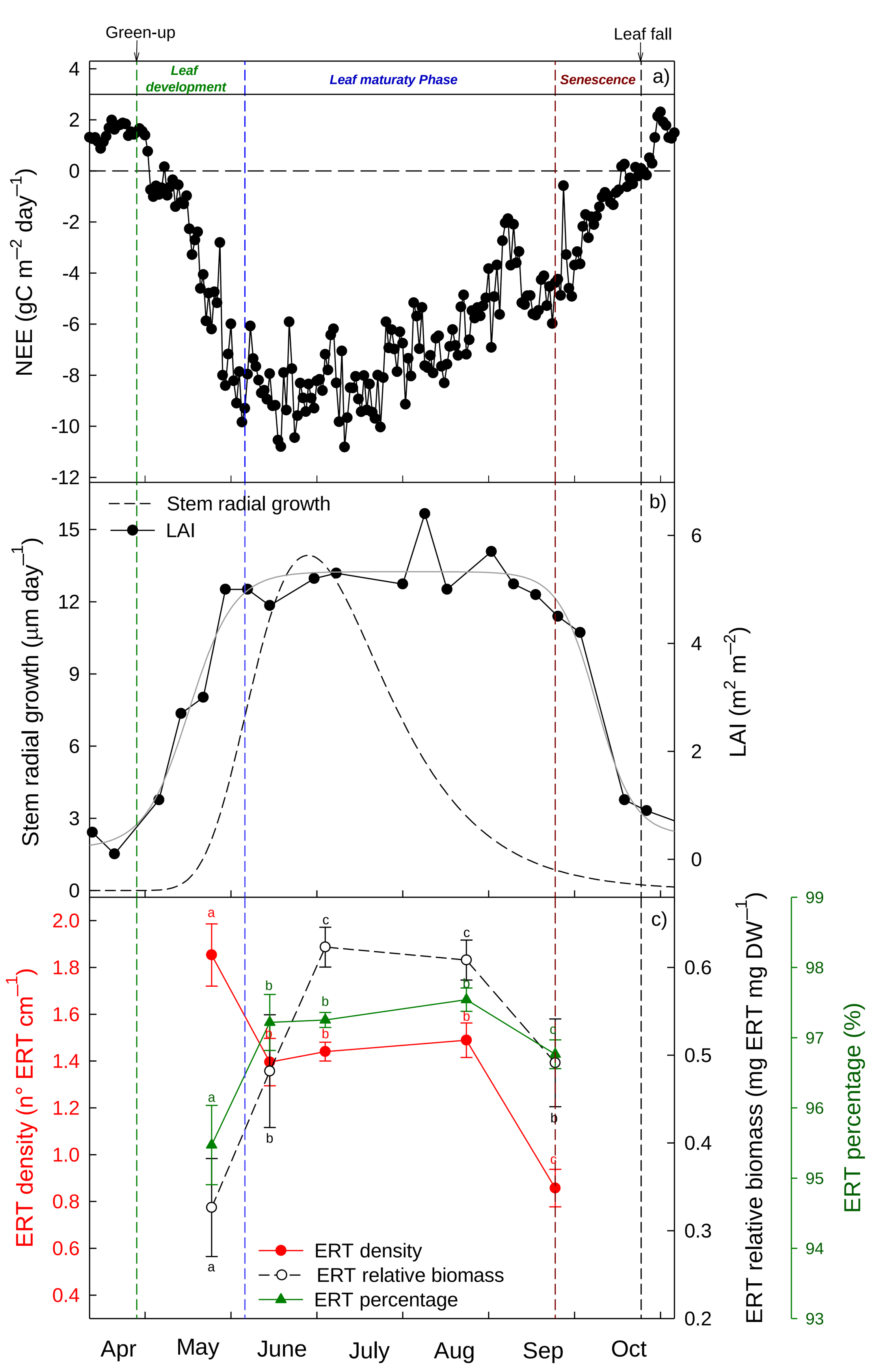


Figure 1. Seasonal variations for 2014 of: a) net ecosystem exchange (NEE, gC m⁻² day⁻¹), for convention negative NEE values indicate carbon absorption (C sink), while positive values indicate C release (C source).; b) leaf area index (LAI, m² m⁻²) and stem radial growth (µm day⁻¹), the green dashed line represents the green up, the blue dashed line is the maximum LAI, the brown dashed line is the onset of senescence, the black dashed line is the beginning of winter dormancy; c), ectomycorrhizal root tips (ERT) density (red), relative biomass (black) and percentage (green) in the Collelongo beech forest. Data for ERT density, relative biomass and percentage are means ± SE (n=5). Data with different letters are significantly different (P ≤ 0.05).

$\delta^{13}C$, $\delta^{15}N$ and N varied depending on both the season and the plant-ECM-soil component analysed

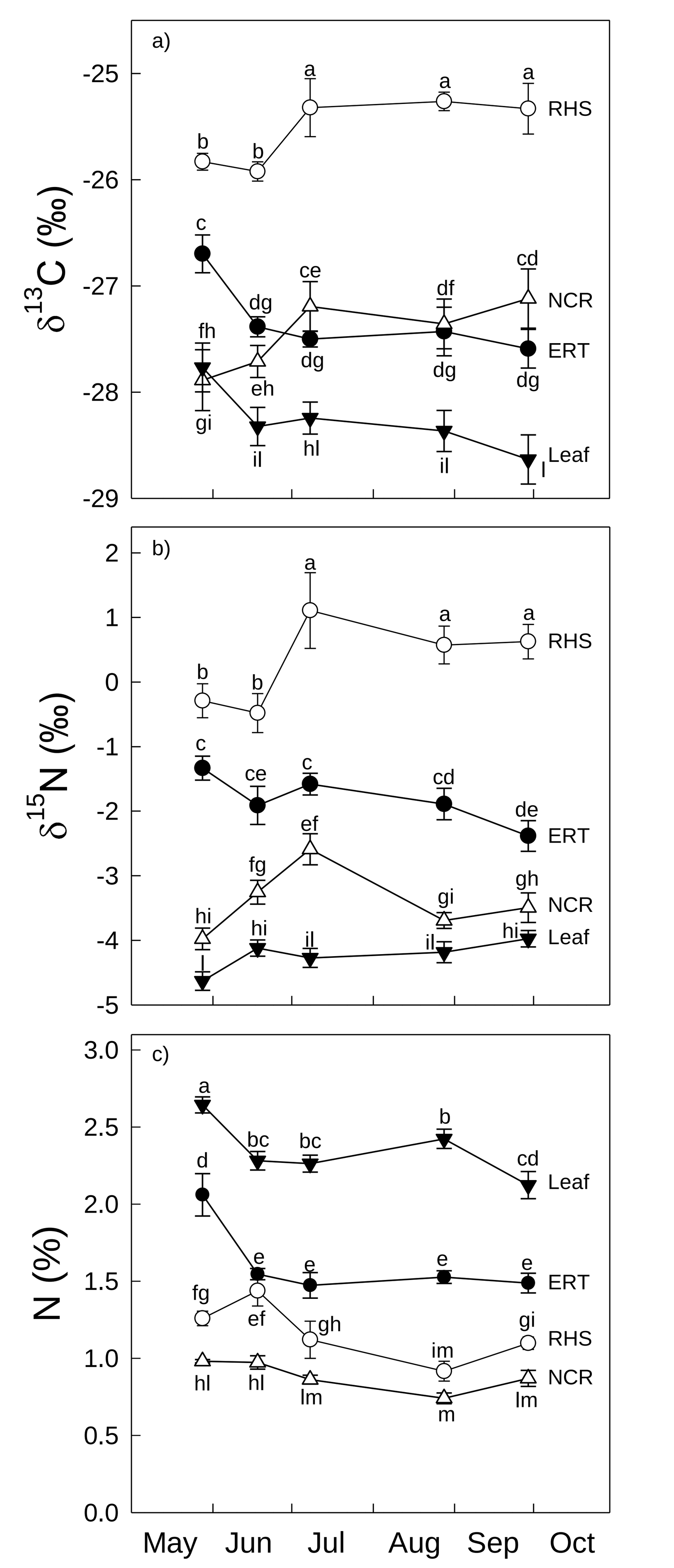


Figure 2. Seasonal variations of: a) carbon isotope composition ($\delta^{13}C$); b) nitrogen isotope composition ($\delta^{15}N$); c) nitrogen concentration (N, %) of rhizosphere soil (RHS), ectomycorrhizal root tips (ERT), non-colonized fine roots (NCR) and leaves in the Collelongo beech forest. Each point is the mean of five beech trees and bars are the SE. Data with different letters are significantly different (P ≤ 0.05).

The isotope composition of ERT showed a positive ($\delta^{13}C$) and negative ($\delta^{15}N$) correlation with that of leaves

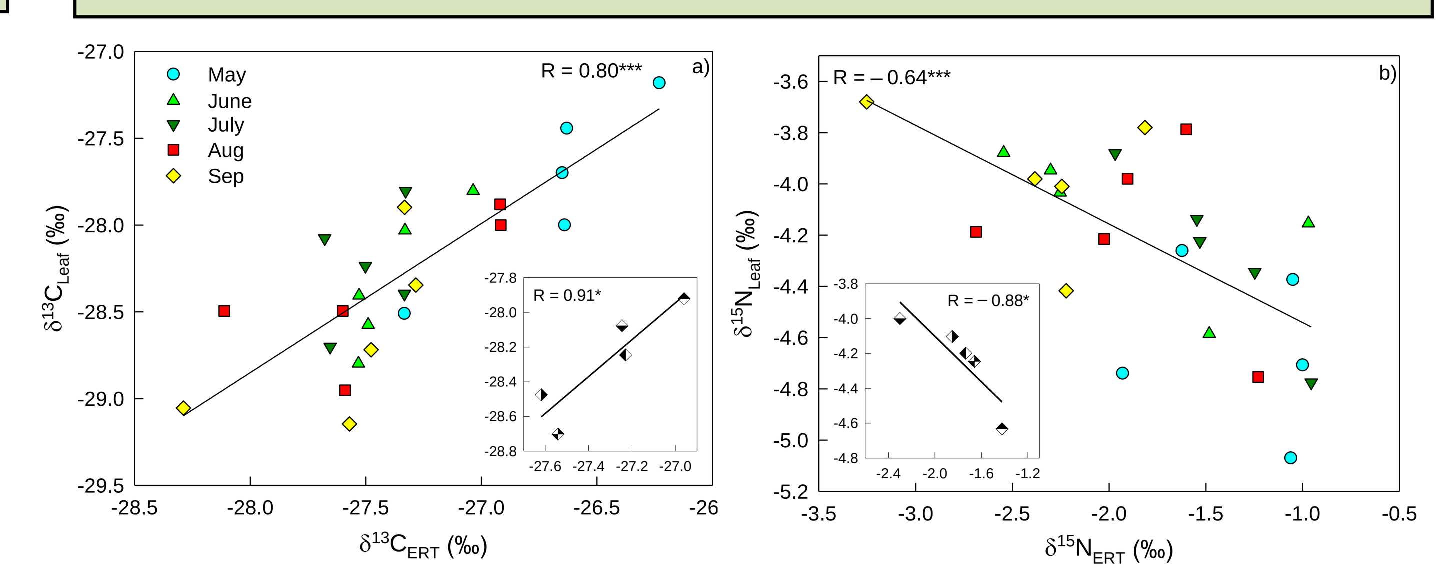


Figure 3. Linear relationships between: a) carbon isotope composition of ectomycorrhizal root tips ($\delta^{13}C_{ERT}$) and leaves ($\delta^{13}C_{leaf}$); b) nitrogen isotope composition of ERT ($\delta^{15}N_{ERT}$) and leaves ($\delta^{15}N_{leaf}$). Each point represents a single value and the shapes are referred to sampling date as reported in legend. The insert graphs represent the same relationships for the mean seasonal values of each trees (one point per tree). Correlation coefficient (R) and significance level (P) are reported (*P < 0.05; **P < 0.01; *** P < 0.001).

The isotopic fractionation between ERT and NCR ($\delta^{15}N_{ERT} - \delta^{15}N_{NCR}$) was positively related to ERT density and affected the $\delta^{15}N$ of leaves

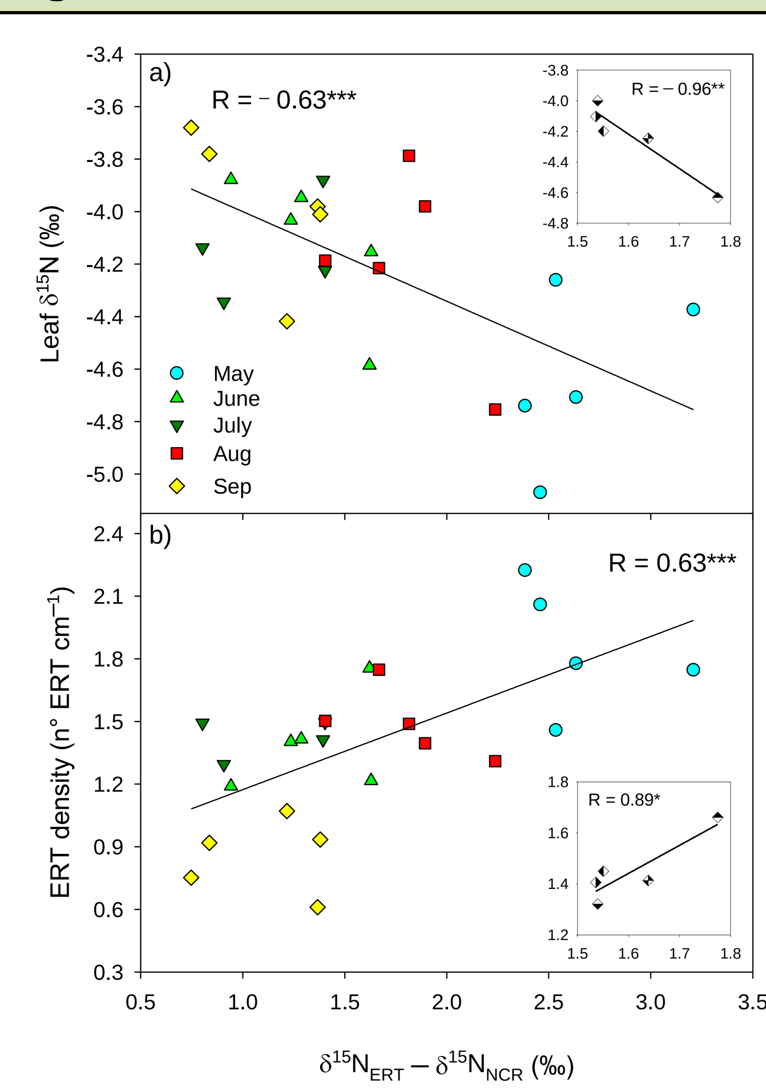


Figure 4. Linear relationships between ectomycorrhizal root tips (ERT) density and: leaf nitrogen isotope composition (a, $\delta^{15}N_{leaf}$) and $\delta^{15}N$ difference between ERT and non-colonized roots (b, $\delta^{15}N_{ERT}$-$\delta^{15}N_{NCR}$). The insert graphs represent the same relationships for the mean seasonal values of the individual trees (one point per tree). Correlation coefficient (R) and significance level (P) are reported (*P < 0.05; **P < 0.01; *** P < 0.001).

CONCLUSIONS

- The analysis of natural abundances of C and N stable isotopes along the soil-ECM-plant continuum on mature beech trees, revealed phenology-dependent exchanges and fractionations of these nutrients between ECM and host plant. Our results highlighted a synchronous seasonal pattern of ecosystem C uptake, stem radial growth and biomass accumulation in ectomycorrhizal root tips, which all reached a maximum around July. These data suggest that allocation of C towards stem growth and ECM development could represent a major C sink during spring-early summer period.
- The positive and highly significant correlation between $\delta^{13}C$ values of ERT and leaves suggested that these organs utilize the same C source and present a synchronous development.
- Mycorrhizal colonization induced a fractionation against ^{15}N between fungi and host plant, leading to a ^{15}N enrichment in ERT and a consequent ^{15}N dilution in NCR and leaf, leading to a negative correlation between ERT and leaves $\delta^{15}N$. It seems also noteworthy that the apparent fractionation between $\delta^{15}N$ ERT and $\delta^{15}N$ NCR largely explains the negative relationship linking $\delta^{15}N$ leaf and ERT density, thus revealing a crucial node of the intimate ecosystem dialogue between the two biogeochemical cycles of C and N.