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Growth enhancement of Norway spruce trees under long-term low-dose N addition is due to morphological rather than to physiological changes

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Human activities have drastically increased the input of nitrogen (N) to nearly natural terrestrial ecosystem in a way that nowadays critical loads are exceeded in many European regions. This atmospheric N deposition implies that forests are shifting from naturally N-limited to N-saturated. In trees, enhanced N availability can cause increased tissue N concentrations and thus higher leaf-level photosynthetic rates. Thereby, they may increase carbon (C) sequestration by increased growth. N addition experiments in temperate forests showed that chronic N deposition can either have a positive, negative or no effect on tree growth. Knowledge of underlying physiological mechanisms how trees respond to N addition especially in the long-term is still lacking. In this study we used tree ring growth patterns and a dual stable isotope approach (δ13C and δ18O) to investigate tree growth response and the underlying physiological reactions to a long-term low-dose N addition (+25 kg N / ha / a). This experiment is conducted since 14 years in a mountain Picea abies forest using a paired-catchment design in Alptal, Switzerland. Basal area increment (BAI) increased significantly by about one third, with a N use efficiency (C sequestration per kg N deposition) in tree stems of ca. 4 kg C per kg N. Neither earlywood nor latewood δ13C values changed significantly compared to the control, indicating that intrinsic water use efficiency (A/g) did not change due to these years of N addition. Further, the isotopic signal of δ18O in early- and latewood shows no significant response to the treatment indicating that neither stomatal conductance nor leaf-level photosynthesis changed. Foliar analyses showed that needle N concentration significantly increased in the fourth to seventh treatment year accompanied by increased needle dry mass, needle area, and by increased height growth. Later, N concentration and height growth returned to values close to the control while single needle dry mass and area remain high. Our results support the theory that enhanced stem growth caused by N addition is mainly due to increased leaf area index (LAI). Higher LAI implies that more photosynthetically active radiation is absorbed and therefore canopy-level photosynthesis is increased. Finally, we conclude that models assuming that N deposition increases tree growth through higher leaf-level photosynthesis might be mechanistically inaccurate.