Study on the mechanisms of rhizosphere priming effects induced by root exudates in a temperate broad-leaved forest

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The primary production of terrestrial ecosystems is commonly constrained by nitrogen (N) availability , and rhizosphere priming effect (RPE) plays an important role in stimulating soil N cycling (Phillips et al. 2011; Cheng et al. 2014; Finzi et al. 2015). Although the quality and quantity of root exudates are thought to be key plant traits controlling RPE, few studies actually explain the variation of RPE among different species with root exudates. Moreover, most studies focused on non-woody species or tree seedlings under laboratory conditions. We are far from understanding the influences of RPE on soil C and N cycling in forest ecosystems. My main research aims were to investigate the amount and the chemical composition of root exudates among four canopy species co-existing in a warm-temperate forest, explain the among-species variations of root exudates with tree-species functional traits, investigate the mechanisms of RPE induced by root exudates, and then to discuss the consequences of RPE on N cycling in the rhizosphere soils of the four canopy species in this forest.

Based on the fact that root exudates related with photosynthetic capacity and N demand within a species, I investigated whether the flux rate of root exudates varied among co-existing canopy species in relation to their species-specific functional traits and N demands in Chapter 2. I conducted an *in situ* experiment to investigate these questions in a warm temperate forest on two dominant species, *Quercus serrata* and *Ilex pedunculosa*, and two of their congeneric species, *Quercus glauca* and *Ilex macropoda*, respectively. During the growing season from June 2013 to May 2014, the flux rates of root exudates for *Q. serrata* and *I. macropoda* (both deciduous species) were consistently greater than those of their congeneric evergreen species on a root-length, a root-weight, and an individual-tree basis. The annual N demands of these species correlated with mean flux rates of root exudates per species. Within a species, flux rates of root exudates correlated positively with leaf N contents, suggesting a physiological linkage between photosynthetic capacities and belowground carbon allocation. These results further suggested that root-exudate fluxes relate to species-specific aboveground functional traits. However, this possibility needs to be substantiated with more species.

In chapter 3, I investigated the interaction between root exudates and rhizosphere microbes to reveal the mechanisms of rhizosphere priming effect induced by root exudates. I used the same tree species as in Chapter 2 because the variation of the flux rates of root exudates seemed to be species-specific but not random. I investigated the interaction between root-exudate fluxes with the biomass C/N ratio and community structure (F:B ratio) of soil microbes. Subsequently, I investigated how N-degrading enzyme activity and net N-mineralization rate were affected by microbial C/N ratio and community structure. I found that both microbial C/N ratio and community structure in the rhizosphere soils remained similar with those in the bulk soils. Microbial biomass C was much greater in the rhizosphere soils than in the bulk soils, probably reflecting the occurrence of flushes of root exudates in the rhizosphere soils. Because the microbes maintained their C/N ratio in spite of greater biomass C, there would be a greater demand for N in the rhizosphere soils. In line with this, the activity of an N-degrading enzyme, i.e. NAG also positively related with microbial biomass C in the soils. Indeed, net N-mineralization rates were

significantly and positively related to root-exudation flux rates among the four target species in my experimental forest, probably because root exudates raised the microbial N demand and enzymatic activity.

In Chapter 4, I further investigated two groups of the most frequently detected organic compounds in root exudates, namely monosaccharides and organic acids, among four target species. I investigated these compounds because they are readily-usable substrates to soil microbes. The proportion of monosaccharides and two types of organic acids (citric and fumaric acid) to total C in the root exudates exhibited no significant difference among species, while the proportion of oxalic acid was different among species. The flux rates of monosaccharides and citric acid related positively with total C in the root exudates. Using a PCA analysis on the monosaccharides and all organic acids that I had detected, I found that chemical composition of root exudates was similar among the four species. This might be another reason why the amount of root exudates was important to explain the variation of net N-mineralization rates among the four species in this forest.

Collectively, the results of Chapter 2, Chapter 3 and Chapter 4 showed a consistent pattern that aboveground N demands functionally related to N-acquisition strategy through C investment to root exudates among the four target species. Two deciduous species, *Quercus serrata* and *Ilex macropoda*, had higher root-exudation rates than their congeneric species *Q. glauca* and *I. pedunculosa* through a whole growing season, which matched the pattern of aboveground N demand in Chapter 2. In Chapter 3, net N-mineralization rates in the rhizosphere soils positively related with flux rates of root exudates among the four species, indicating that the species of higher root-exudate rates are capable to acquire more N. Root exudates can be an efficient C investment to acquire N and the C investment to belowground mirrors the demand of aboveground vegetation for N. The amount of total C in root exudates quantitatively explained the magnitude of rhizosphere priming effects well, probably because the chemical composition of root exudates was similar among the target species.

Lastly, in Chapter 5, I investigated the relationship of fine-root exudation with the fine-root respiration, and fine-root morphological/chemical traits in the dominant species *Quercus serrata* and its congeneric species *Quercus glauca*. How root respiration relates to other root traits (e.g. morphological and chemical traits) has been well established. However, our knowledge of how root exudation relates to those traits is rather limited. In my study site, root-exudation rates positively related to N concentrations of fine-root tissue and mycorrhizal colonization ratios as also seen in root respiration. Root-exudation rates and respiration rates were positively correlated with each other. On average, the rates of fine-root respiration were 8.7 and 10.5 times greater than those of exudation in terms of C flux on a root-length basis and a root-weight basis, respectively. This result indicated a constant C-allocation balance between fine-root exudation and fine-root respiration; this possibility needs to be tested in the future with more species including different ecosystems.

In the present doctoral study, I showed that the processes of aboveground and belowground subsystems are functionally and physiologically linked by root exudates at the plant-soil interface. Root exudates of the four target species reflected both above- and belowground plant functional traits and explained the magnitude of the microbial N mining. The available N derived from microbial mining actually reflected the demands for N among the four target species in my study.