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Research paper

Water availability influences accumulation and allocation of nutrients and metals in short-rotation poplar plantation

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ABSTRACT

We analyzed the effect of manipulated water availability on an accumulation of nutrients and metals, their stoichiometry, and allocation to roots or leaves in a short rotation coppice (SRC) poplar plantation. The aim of this study was also to clarify how these changes are related to the effects of drought on growth parameters. This study was conducted in Domanínek, Czech Republic in an SRC poplar clone J-105 (*Populus nigra* L. × *P. Maximowiczii* H.). This plantation was established as an uncoppiced (single stem) and later on converted into multi-stem (coppice).

A rain-out shelter experiment (reduced throughfall) was established in the second year of coppice and the drought stress (DS) applied for 3 years. Water availability altered the accumulation and allocation of nutrients and metals in above and belowground biomass. Reduced water availability led, in particular, to the significantly lower accumulation of potassium (K) in both leaves and roots and a higher carbon (C) to potassium (K) ratio (C:K) in leaves. The significant decline of zinc (Zn) was also found in roots under reduced throughfall. Reduced water availability led to increased accumulation of cadmium (Cd) in leaves and decreased accumulation in roots. This resulted in significantly lower root:leaf ratio for Cd content. An opposite response was found for the allocation of copper (Cu). We also demonstrated that major changes in accumulation and allocation are associated with changes in growth. The results indicated that such knowledge may contribute to understanding the role of nutrient uptake and translocation in acclimation to DS and it may help in developing phytoextraction methods on contaminated soils.

1. Introduction

Climate change is altering the patterns of weather conditions such as temperature and precipitation amount, distribution and incidence of drought events [1]. The species used for bioenergy purposes, and poplar , in particular, are highly influenced by soil moisture, water holding capacity of soil or water table level [2–4], and their productivity and economy can be greatly affected by increasing frequency of drought events under ongoing climate change [5–7]. Drought may influence the growth parameters such as leaf area, leaf area index (LAI), the diameter of the plants, structure, and contents of nutrients and other elements in both leaves and roots [8].

The functions of ecosystems, organism's structure, and its life dynamics are strongly influenced by the carbon:nitrogen:phosphorus (C:N:P) stoichiometric ratios in the environment and organisms as well [9–11]. Changes in elemental composition and stoichiometry in plants under conditions of climate change have been at the forefront of work by plant biologists and ecologists in recent decades. Knowledge regarding changes in elemental composition and allocation within plants may help in understanding the biochemical responses, acclimation, and adaptation to such expected conditions as elevated CO_2 concentration, high temperatures, or drought periods (reviewed by Sardans et al. [9]).

The elemental composition of plants could be determined, in part, by long-term adaptation to a particular abiotic environmental condition and by specific ecological processes such as the optimal successional stage. Plant species require some degree of flexibility for the success and allow abiotic and biotic shifts. Sistla and Schimel [12] have reported that stoichiometric flexibility enables an organism to adjust their elemental ratios while maintaining a constant function. Rivas-Ubach et al. [13] have reported an orchestrated response to drought and warming in plant stoichiometry and metabolism, which indicates a key role of elemental composition in acclimation. In leaves, an increase in

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C: nutrient ratios due to increases in C-rich components linked to the preventing of water stress is well known stoichiometric responses to reduced water availability [14,15].

Drought stress (DS) generally decreases growth and net photosynthesis as well as the capacity to uptake N, P and potassium (K) from soil [16–18]. Drought may affect soil microbial activity and fertility as a direct effect of low soil water potential and related changes in plants. The most common effect of drought is a reduction in soil enzyme activity resulting in reduced soil biological activity [19–22]. As the main nutrients N, P, and K are involved in various mechanisms of drought tolerance such as osmotic adjustment, root elongation or enhanced antioxidative capacity [23], reduced availability of nutrients under DS can result in synergistic response to DS both directly through their reduced uptake and indirectly through reduced tolerance. Moreover, Gargallo-Garriga et al. [24] documented that allocation of nutrients and metabolites between above- and belowground biomass is a crucially important aspect of acclimation to DS. Plant elemental stoichiometry also can be associated with such important ecological processes as species diversity [25,26] and litter decomposition [27,28].

Within this study, we tested the hypothesis that reduced water (throughfall) availability in an SRC poplar alters the uptake and translocation of some nutrients and heavy metals, thereby resulting in changed stoichiometric ratios and allocation of elements between below- and aboveground biomass (roots and leaves). Expected in particular were changes in P and K content along with corresponding changes in stoichiometric ratios. An additional aim was to clarify how these changes are associated with the effects of DS on growth parameters.

2. Materials and methods

2.1. Experimental site and plantation

The study was carried out in Domanínek, Czech Republic (49°521′N; 16°235′E, at an altitude of 578 m above the sea level), near the town of Bystřice nad Pernštejnem. Climate at the site is cool and wet, with the mean annual precipitation in period 2001–2013 of 610 mm and mean annual air temperature 7.5 °C. The plantation was established in April 2001 within a total area of 1.5 ha to test performance of the hybrid poplar clone J-105 (*P. nigra* L. × *P. maximowiczii* H.). To establish the plantation, unrooted 25 cm long stem cuttings were planted in a double row design with inter-row distances of 2.5 m and spacing of 0.7 m within rows, thereby aiming to achieve a theoretical density of 9216 trees ha^{-1}. This plantation (uncoppiced, single-stem) was harvested at about 15–20 cm above ground in winter 2008/2009 and converted into multi-stem coppice. Details of this experimental site and plantation have been described by Fischer et al. [29].

2.2. Soil analysis

Soil sampling and analyses were carried out prior (in 2001) to establishment of the plantation and that was described in earlier study by Trnka et al. [30]. In 2009, basic physical and chemical soil analyses were carried out (Table 1). Soil samples for physical and chemical analyses were collected using soil sampling rings. Bulk density was determined as per methodology suggested by Zbíral et al. [31]. Particle size analyses were conducted by pipette method followed by Van Reeuwijk [32]. For chemical analyses, samples were air-dried and passed through 2 mm sieve. Soil pH/KCl was determined in 1:2.5 (soil:1 M KCl) suspension using a combined reference glass electrode and pH meter. Organic C content was analyzed by oxidometric titration method according to Nelson and Sommers [33]. Total N amount was determined by dry combustion “elemental analysis” according to ISO 13878:1998. Available P was quantified by SKALAR auto-analyzer (Breda, The Netherlands) and available K, magnesium (Mg), and calcium (Ca) was determined by atomic absorption spectrophotometry (AAS: ContrAA 700, AnalytikJena, Jena, Germany).

Table 1
Soil chemical and physical properties determined at the beginning of the experiment (2009) within three basic soil horizons.

	Unit	Depth (cm)		
		0–27	27–60	60–80
Silt	%	43.0	40.0	26.1
Clay	%	19.8	27.8	19.4
Water holding capacity	%	36.3	41.1	35.7
Bulk density	$g.cm^{-3}$	1.5	1.37	2.72
Organic matter content	%	1.33	0.35	0.27
Cation exchange capacity	$meq.kg^{-1}$	120	102	118
Total nitrogen content	%	0.22	0.16	0.09
pH (KCl)		4.86	4.39	3.78
Available P	$mg.kg^{-1}$	42	3	2
Available K	$mg.kg^{-1}$	134	160	70
Available Mg	$mg.kg^{-1}$	180	558	263
Available Ca	$mg.kg^{-1}$	2463	3561	1451

2.3. Experimental design

In June 2011, a rain-out shelter experiment was established (detail experimental design was published by Orság et al. [34]) in the coppiced plantation (age of coppice at the time of rain-out shelters establishment was 2 years and the overall age of plantation was 10 years). Square plots, with an area of 25 m^2 (5 m × 5 m), were randomized in three blocks (replicates). Within each block, the control (ambient throughfall) and DS (throughfall reduction by rain-out shelters) plots were established (Fig. 1A). Throughfall was reduced by 40% from mid-June 2011 to mid-June 2013 and to 70% from mid-June 2013. To avoid horizontal root growth to neighboring plots and lateral water flow, trenches (0.5–0.8 m deep) were established around each plot with reduced water availability. Each plot had 20 stumps with several shoots/stems (for experimental details see Fig. 1).

From 2011 to 2013, we measured soil moisture water content using a PR1/PR2 profile probe (Delta-T Devices, Cambridge, UK). We installed 18 access soil moisture measurement tubes in total for all three blocks. Each block had six access tubes, three for DS and three for control treatments (Fig. 1C). The soil moisture tubes were installed diagonally across each plot (i.e., one tube in the lower middle row, one in the center double row, and another in the upper middle row (Fig. 1C). The soil moisture measurements with profile probe PR1/PR2 were taken usually weekly and biweekly, each year from March to the end of November.

2.4. Meteorological measurements

In an open area close to the plantation, we measured daily mean air temperature using an EMS 33 sensor (EMS Brno, Czech Republic) and total precipitation using a MetOne 370 tipping bucket rain gauge (MetOne Instruments, Grants Pass, OR, USA). Monthly mean air temperature and monthly total precipitation from 2011 to 2013 and long-term mean (2001–2013) air temperature and total precipitation are shown in Table 2.

2.5. Growth parameters

During the growing season, we measured weekly and biweekly LAI and diameter at breast height (DBH) in DS and control treatments, respectively. The LAI was measured within rows and inter-rows for each plot using SunScan instrument (Delta-T Devices, Cambridge, UK, details are mentioned by Tripathi et al. [35]). For DBH measurement, we randomly selected 10 stumps from each plot and measured all shoots/stems belonging to these stumps. The DBH was measured by a digital