



Phosphorus storage and resorption in riparian tree species: Environmental applications of poplar and willow

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ABSTRACT

Phosphorus is a contaminant of major concern in agricultural systems, as increased concentrations in runoff have led to escalating incidents of eutrophication. A potential solution involves planting buffer strips of high biomass-producing tree species along riparian zones. Trees belonging to the family *Salicaceae* inhabit a diverse geographical range and display highly variable growth traits, allowing for their use in a wide range of environmental applications, including their use in agroforestry to prevent soil erosion, for reclamation of marginal lands, and acting as vegetative filters. Characterization of differences in nutrient allocation and storage in these tree species is needed to assess their effectiveness as buffer strips. For several willow and poplar varieties, phenotypic differences were quantified using ICP-AES and HPLC. Poplar varieties such as *Tristis* and *Northwest* demonstrated the highest capacity for luxury uptake, with an estimated 3.7–3.9 mgP g⁻¹ when 2.2 mM soluble phosphate (100N:70P) was applied. However, the majority of phosphorus was stored in the leaves and was returned to the environment as autumnal senescence progressed. Hybrid willows, such as *AAFC-5*, are excellent alternatives as the highest proportion of biomass was allocated to the stem, to be retained for long-term storage or coppiced and removed from the site. *AAFC-5* accumulated approximately 2.1 mgP g⁻¹ and had the lowest concentration of phosphorus in senescent leaves, resulting in higher resorption efficiencies than hybrid poplar. The observed variation in phenotypic plasticity among genotypes suggests a complex response to nutrient conditions that likely exists in many species beyond those presented in this study. Differences between closely related species can in turn, be used to investigate the genetic and biochemical controls of nutrient allocation and resorption. Should higher resorption rates be achievable in the phosphorus accumulating poplar hybrids, optimal recovery from phosphorus heavy soils could be attained through coppicing.

1. Introduction

Phosphorus, unlike other essential elements such as a carbon and nitrogen, does not form a stable gas phase, and as such its transport is heavily reliant on the weathering of insoluble calcium phosphate salts and subsequent aqueous transfer. Once in solution, phosphate is immediately bioavailable and ready for uptake by plants and other primary producers (Emsley, 1980, Filippelli, 2008). As plant roots remove the dissolved phosphate from the soil solution, the areas directly surrounding the roots become devoid of phosphate, creating a zone of depletion in which the release of soil phosphate from local mineral stores occurs too slowly to maintain the concentrations required to support rapid and sustained plant growth (Schachtman et al., 1998). To counter this effect, soluble phosphate fertilizer is routinely applied on agricultural lands to maintain high soil solution phosphate

concentrations. It's estimated that once in the soil, mineral phosphate fertilizers are fixed in as little as three hours (Chang and Chu, 1961). Furthermore, increasing phosphate supply above sufficient levels does not equate to higher phosphate uptake by plants, resulting in excess levels in the soil and increased leaching (Turtola and Yli-Halla, 1999). Increased phosphate loading into surface and sub-surface runoff from high production areas is the largest annual contributor of diffuse source nutrient pollutants. The accumulation of phosphate from diffuse sources results in decreased water quality and eutrophication downstream, yet is the most difficult to reduce and regulate (Ongley, 1996) with lengthy dissipation times for internal phosphorus loads from water catchments (Boesch et al., 2006).

Phosphorus was first identified as a contaminant of concern in the 1980s and was found to be the primary cause of eutrophication through the multi-year experiments conducted at the Experimental Lakes Area

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in Ontario (Findlay and Kasian, 1987). In recent years, phosphorus concentrations above the biological low limitation for algae production (0.03 mg/L) (Hamilton, 2012) continue to plague freshwater catchments, such as the Baltic Sea (Andersen et al., 2017), the Great Lakes region (International Joint Commission, 2014; Environment and Climate Change Canada, 2016) and the Mediterranean Sea (Spiteri et al., 2016). Worldwide, only the Netherlands and Australasia have set national water quality standards for phosphorus, with regional guidelines in place in areas of North America and input reduction targets set within the European Economic Community (Government of Canada, 2004). With the knowledge that control of point source pollution has not been satisfactory in reducing freshwater phosphorus levels, whole system ecological approaches within watershed areas are required to find economically feasible site dependent solutions capable of safeguarding the multiple entry points into aquatic systems. We propose the planting of *Salicaceae*, hybrid poplar (*Populus* spp.) and willow (*Salix* spp.) genotypes, around fields and riparian areas to act as vegetative water filtration systems for surface and sub-surface flow prior to its entry into water catchments. *Salicaceae* are ubiquitous across North America and are known for their high levels of genetic diversity, rapid and extensive growth rates and productivity, ease of propagation, and for their ability to be coppiced. Current uses for poplar and willow hybrids include fibre production for tissue and paper manufacturing, as windbreaks/shelterbelts in agricultural applications, and for biomass production as potential energy crops (Isebrands and Richardson, 2014).

Generally, under phosphate sufficient conditions, accumulation occurs primarily in plant leaves with 85–95% of total phosphate being stored within vacuoles as inorganic phosphate, suggesting that leaf mesophyll cells have a relatively high capacity for phosphate import and compartmentalization (Mimura et al., 1990; Marschner, 2012). The optimal total phosphorus concentration per gram dry weight in crop photosynthetic tissues is considered to be $< 4 \text{ mgP g}^{-1}$, but under high phosphate conditions concentrations can reach $> 5 \text{ mgP g}^{-1}$ (Veneklaas et al., 2012). Although phosphorus accumulation has been previously observed in poplar and willow (Teng and Timmer, 1990; Fillion et al., 2011), it is assumed that these species are able to control internal concentrations by increasing the rate of P efflux from roots, similar to what has been observed in water plants (Bielecki and Ferguson, 1983). Given the perennial nature of these tree species, it is imperative that nutrient resorption also be considered to accurately assess their phosphate filtration and removal capacity. Poplar phosphorus resorption efficiency has been reported to vary between 23 and 60% (Brown and van den Driessche, 2005), while the reported effects of leaf nutrient status on resorption have been conflicting (Aerts, 1996; Kobe et al., 2005; Vergutz et al., 2012). We aimed to quantify the effects of external phosphate concentrations on phosphorus storage before and after senescence, and identify what leaf phosphorus concentration ranges are indicative of luxury consumption in perennial tree species. This allows us to suggest which commercially available poplar and willow genotypes are optimal for phosphate phytoremediation, while concurrently building a foundation for further research into the genetic and biochemical controls of phosphorus resorption.

2. Materials and methods

2.1. Greenhouse trials

Two trials were conducted between July 2013 and January 2015 at the University of British Columbia Horticulture Greenhouse (49.26°N 123.25°W; elevation 82 m). Cuttings were taken from field-grown trees at the Agriculture and Agri-Food Canada (AAFC) Agroforestry Development Centre in Indian Head, Saskatchewan. The first trial consisted of six willow and four poplar genotypes (Table 1) arranged in a randomized block design and subjected to three different phosphorus treatments with eight to ten trees per genotype in a greenhouse experiment that ran from July 2013–March 2014. Trees were watered

once a week using nutrient solutions containing one of the following nutrient ratios; 100N:11P:70 K, 100N:28P:70 K, 100N:70P:70 K (355 μM –2260 μM P). Nitrogen to phosphorus ratios were chosen based on observed levels of excess phosphorus in the Canadian prairie province, Manitoba (Manitoba Phosphorus Expert Committee, 2006). In a second experiment that ran from July 2014 to January 2015, the number of poplar genotypes was expanded to eight (Table 1), due to their observed propensity for luxury uptake of phosphorus. Genotypes were subjected to one of the five following nutrient ratios; 100N:13P:64 K, 100N:70P:70 K, 100N:100P:150 K, 100N:130P:198 K, 100N:195P:291 K (420 μM –6300 μM P). The remaining nutrients were held constant across all treatments, and were as follows (mg/L); 10S, 7Mg, 0.7Fe, 0.03Cu, 0.2B, 0.4Mn, 0.06Zn, 0.007Mo, 0.03Cl, and 0.58Na (Ericsson, 1981).

All trees were grown from 15 to 21 cm cuttings received from AAFC for 12–14 weeks under 18 h supplemental lighting using high-pressure sodium lamps, which provided at least 600 Wm^2 until natural leaf senescence was to be induced. Senescence was induced by moving the trees to a growing environment consisting only of natural lighting at 10 °C for several weeks in late September for temperature adjustment before placing them outdoors. For the senescence evaluation, each block had paired trees of which one was harvested after 12 weeks and the other after the leaves had dropped from all trees. For the mature leaf tissue in both trials, all leaves from each tree were harvested and pooled at the 12-week harvest. Senescent leaves either involved pooling all leaves once the 9th leaf (Plastochron Index 9) was visually assessed to be 60% yellow (2013 trial) or by collecting all leaves only after they had naturally abscised from the tree (2014 trial). Resorption efficiencies were calculated by taking the difference between total leaf phosphorus content of mature leaves and senescent leaves divided by the total content of the mature leaves. At harvest, each tree was partitioned into leaves, bark, xylem and roots for biomass measurements and chemical analyses.

2.2. Chemical analysis

Three individuals displaying total biomass closest to the median for every genotype were air-dried and ground for nutrient analysis. All petioles and leaves from each tree were combined, and the entire root system was pooled before being ground. From the bottom 10 cm of the stem, xylem and bark were taken and processed individually. All material was ground using a 2010 Geno/Grinder® tissue homogenizer (SPEX® SamplePrep) at 1600 rpm for 30–60 s depending on the tissue. Samples were sent to SGS Laboratories in Guelph Ontario where inductively coupled plasma atomic emission spectroscopy (ICP-AES) was used for the determination of N, P, K, Ca, and Mg, according to the Association of Official Analytical Chemists (AOAC) protocol 985.01 (Helrich, 1990). The 9th leaf from the first fully unfurled leaf was collected from every tree at harvest and immediately placed into liquid nitrogen for inorganic phosphate determination using high performance liquid chromatography (HPLC). Inorganic phosphate was extracted by boiling 10 mg of dried tissue in 0.5 mL of 0.5 M HCl for 15 min. Samples were then centrifuged for 10 min at 17 000g to remove the supernatant and diluted four times with nanopure water. 20 μL of sample was separated on an IonPac AS-11 (4 × 250 mm) column at 30 °C. The elution profile ran from 0 to 3 min isocratic at 5 mM of NaOH followed by 3–15 min at a linear gradient of NaOH increasing from 5 to 100 mM. At the end of each run, the column was washed with 0.5 M NaOH for 20 min followed by a 20 min equilibration at 5 mM NaOH. The flow rate was held constant at 1 mL min^{-1} with anion concentrations determined on a conductivity detector. Background conductivity was decreased using an anion self-regenerating suppressor (Bentsink et al., 2002; Zhao et al., 2008).

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