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Differences in resistance to nitrogen and phosphorus deficiencies explain male-biased populations of poplar in nutrient-deficient habitats

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ABSTRACT

In most forest soils, the availability of nitrogen (N) and phosphorus (P) nutrients is low and unable to meet the requirement of tree growth. In the past decades, sex-based differences in poplar have been investigated in morphology and physiology. Proteomic techniques provide new insights into sex-specific differences at the molecular level. This review gives a comparative overview of the effects of N and P deficiencies on poplar physiological and proteomic characteristics. Male poplars are more efficient at photosynthesis and nutrient usage than females. Proteins related to carbohydrate metabolism, defence responses and transcription and translation processes are changed to adapt diversely in males and females. These results provide evidence that male poplar have better resistance to nutrient-limiting conditions than females, which may be reasonable for the male-biased sex ratio in nutrient-deficient habitats. Furthermore, this review also discusses the potential growth-defence trade-offs in male and female poplar coping with nutrient limitations.

Biological significance: In the past decades, the physiological and molecular responses of individual trees exposed to nutrient deficiency have been well studied. An important model woody plant, *Populus*, is dioecious and shows a male-biased sex ratio in nutrient-deficient habitats. Individually, different responses to nutrient limitation between the sexes determine the bias of population sex ratios. Proteomic techniques provide new insights into sex-based differences in the molecular mechanisms underlying nutrient deficiency. This review gives a comparative overview of the identification of nitrogen and phosphorus deficiency effects on physiological and proteomic characteristics. Male poplars are more resistant and have a smaller range of protein changes than females in response to N and P deficiency, which explains the observed male-biased sex ratios to a certain extent. Furthermore, this review also discusses the possible growth-defense trade-offs in male and female poplars coping with nutrient deficiency.

1. Introduction

Among approximately 240,000 angiosperm species, there are at least 14,620 dioecious species [1]. The sex ratios of most dioecious plants are not the equilibrium expectation of 1:1, but rather, species typically show male-biased sex ratios of nearly twice the frequency of female-biased ratios [2]. Several studies have reported that the male-biased sex ratio is linked to sex-based differential reproductive costs [3]. Female plants allocate more resources (water, nutrients and carbohydrates) to reproduction (e.g., flowers, seeds and fruits) than males [4] during their life cycle. Sexually differential responses to environmental conditions show a strong relationship with the sex ratio of a given population [5] and have even been observed in premature young plants [4]. A previous study reported that sex-based differences in growth-defence trade-offs influence reproduction-growth trade-offs [6]. Resource allocation between defence and growth can be greatly affected by soil nutrient conditions, particularly nitrogen (N) and phosphorus (P). N plays a crucial role in forest productivity and is often limited in the young soils of temperate zones, whereas P deficiency consistently, but not exclusively, occurs in many older and tropical soils [7,8]. The total amount of N and P taken up by plants is related to ecosystem productivity and N and P supply. In highly productive agroecosystems, total N uptake by crops may be as high as 450 $kg \cdot ha^{-1} \cdot year^{-1}$ for irrigated wheat under ideal conditions [9,10]. The concentration of N in the plant dry matter of herbaceous plants is typically 10–20 $g\ kg^{-1}$ for grasses and 20–30 $g\ kg^{-1}$ for legumes and is even higher in younger tissues. For woody plants, the concentration of N varies with plant tissues, with typical concentrations of $\leq 5\ g\ kg^{-1}$

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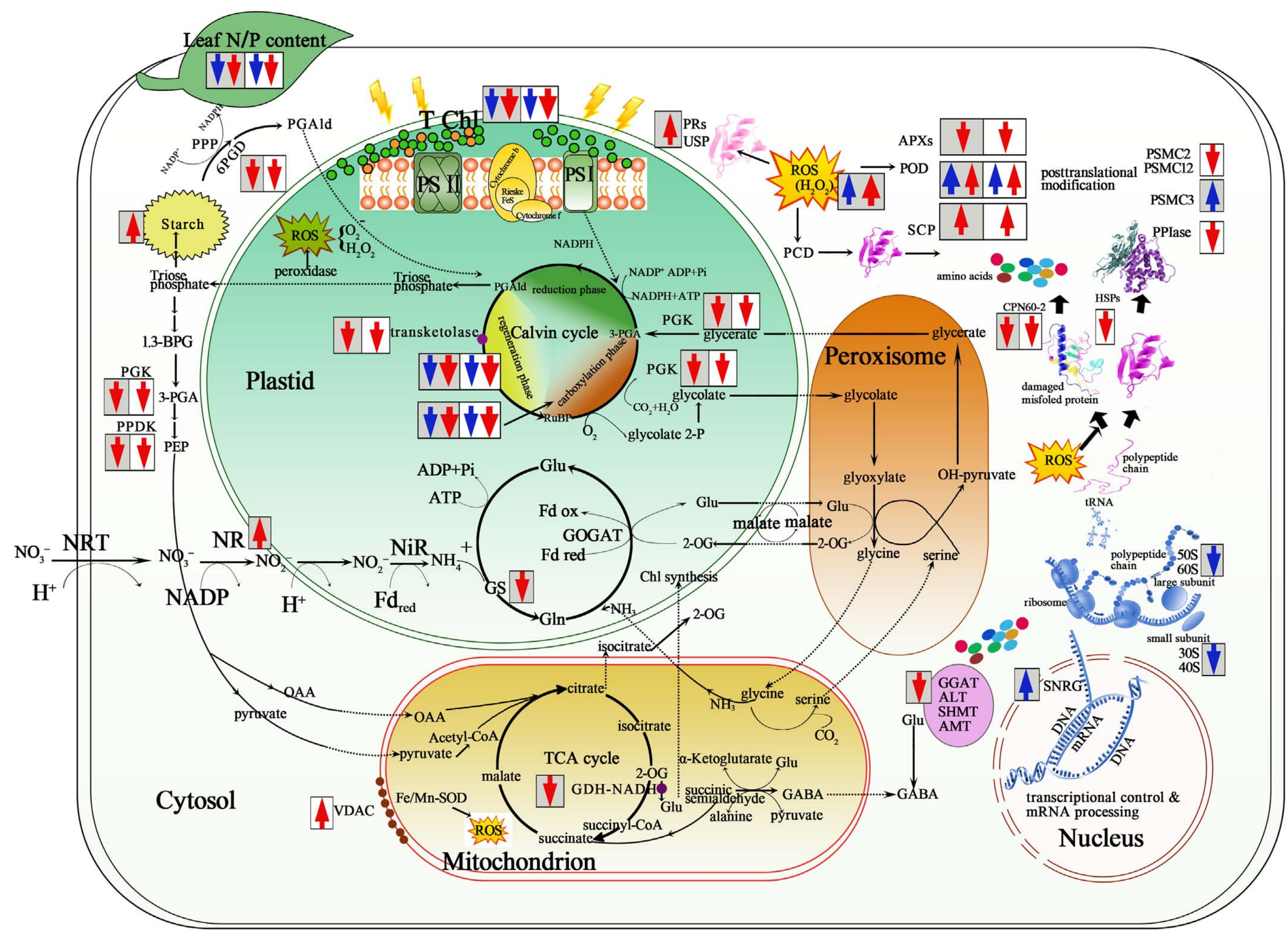

Fig. 1. Hypothetical cellular pathways and processes in N- and P-deficient *P. cathayana* males and females [30,54,55]. Grey boxes indicate changes caused by N deficiency and white boxes indicate change caused by P deficiency. Red (female) and blue (male) arrows indicate the up- or down-regulation of substances in various directions. The thickness of the arrows indicates greater changes in males or females. Proteins or metabolites are shown as abbreviations: ALT, alanine amino transferase; AMT, amino methyl transferase; APX, ascorbate peroxidase; 1.3-BPG, 1,3-diphosphoglycerate; Fdred, ferredoxin; GOGAT, glutamate synthase; GDH-NADH, glutamate dehydrogenase-NADH; GABA, γ-aminobutyrate; GGAT, glutamate-glyoxylate amino transferase 2; GS, glutamine synthetase; Glu, glutamate; Gln, glutamine; NRT, nitrogen transporter; NR, nitrate reductase; NiR, nitrite reductase; OAA, oxaloacetic acid; 2-OG, 2-oxoglutarate; PGAld, glyceraldehyde 3-phosphate; PPP, pentose-phosphate pathway; 6PGD, 6-phosphogluconate dehydrogenase; PGK, phosphoglycerate kinase; 3-PGA, 3-phosphoglycerate; PPDK, pyruvate phosphate dikinase; PEP, phosphoenol pyruvic acid; PCD, programmed cell death; POD, peroxidase; PPIase, peptidyl-prolyl cis-trans isomerase; PRs, pathogenesis-related proteins; PSMC, 26S protease regulatory subunit; ROS, reactive oxygen species; RuBp, ribulose-1,5-bisphosphate; SNRG, small nuclear ribonucleoprotein G; SHMT, serine hydroxymethyl transferase; SCP, Serine carboxypeptidase; USP, universal stress proteins. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

for xylem and ≤ 20 g kg^{-1} for leaves [10]. For perennial woody shrubs or tree agriculture, biological N fixation of 550–600 kg ha^{-1} $year^{-1}$ has been recorded [11], although 100–200 kg ha^{-1} $year^{-1}$ is typical [12]. The concentrations of P in plant biomass are typically 1–5 g kg^{-1} dry matter, and aboveground P is approximately 10–100 kg ha^{-1} in most ecosystems. However, the P concentration in natural soils ranges from 100 to 1000 mg kg^{-1} [10]. In poplar under different nutrient conditions, the foliar N and P concentrations ranged from 2.50–35.7 and 1.05–2.98 mg g^{-1} dry weight, respectively. Root N and P concentrations were approximately 1.05–2.98 and 0.83–3.50 mg g^{-1} dry weight, respectively (Supplemental Table 1). Therefore, N and P are often limited in temperate forests and cannot meet the requirements for the growth and development of trees [13]. The lower availability of N and P may be an important driving factor for the biased sex ratio [14]. However, the mechanisms underlying this phenomenon are not clear.

Populus, a model tree with fast growth and small genome, is a male-biased genus. In the past decades, sex-specific responses regarding growth and physiological processes have been demonstrated in young poplar under stressed conditions, e.g., elevated temperature, chilling and drought [15–18]. These studies have provided evidence that sex-related trade-offs occur in growth and resistance. Soil nutrient deficiency can greatly limit poplar growth and affect physiological processes and gene expression pathways (Supplemental Table 2). Proteomics (e.g., iTRAQ) as a powerful tool has been used to shed light on the molecular mechanisms underlying plant adaptations to mineral nutrient deficiency. Here, we discuss recent studies on sex-specific physiological and proteomic changes in *Populus* caused by N and P deficiencies to exemplify the potential endopathic driving forces for male-biased sex ratios in nutrient-deficient habitats.

2. Sex-specific physiological responses to nitrogen and phosphorus deficiencies

In terrestrial ecosystems, the availability of N and P is consistently limited, reflecting the low input, slow immobilization and gaseous emissions of these soil nutrients [19,20]. N or P deficiency generally results in stunted trees with narrow and small leaves and even abscission. Supplemental Table 2 lists the recent studies on N or P deficiency in poplar. For young poplar, N or P deficiency significantly decreased plant height, total biomass and the root-stem ratio. However, female