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Research Paper

Phosphate starvation during the transition phase increases the sex ratio and 12-*oxo*-phytodienoic acid contents in females of *Urtica dioica*☆

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ABSTRACT

The transition phase in plants, which is marked by the onset of flowering and seed production, is very sensitive to the physical environment. Moreover, dimorphic plant species can show important sex-related differences in the response to nutrient availability. How availability of inorganic phosphate (Pi) during the transition phase influences sex ratios and whether or not male and female plants respond differently to nutrient stress is still however very poorly understood. Here, we examined whether contrasting Pi availability during the transition phase may influence sexual differentiation in stinging nettle (*U. dioica* L.) plants. We also evaluated to what extent males and females respond differently to varying Pi concentrations in terms of nutrient accumulation, C and N isotopic composition, photo-oxidative stress and hormone profiling. Results showed that reduced Pi availability delays plant maturation in males, causing as well an increase in the sex ratio towards females. Females showed enhanced lipid peroxidation (as indicated by higher lipid hydroperoxide contents) compared to males under Pi starvation, but sexes did not differ in photosystem II efficiency. Furthermore, reduced Pi availability led to enhanced 12-*oxo*-phytodienoic acid contents, the immediate precursor of jasmonic acid, particularly in females. This increase was, however, not accompanied by increases in other jasmonates, neither free nor conjugated jasmonic acid, thus suggesting a specific role for 12-*oxo*-phytodienoic acid in chemical defense in females under Pi starvation. Sex biased ratios in favour of females over males and enhanced 12-*oxo*-phytodienoic acid contents in the former under Pi starvation illustrate the great adaptive capacity of dimorphic species to reduced nutrient availability.

1. Introduction

Plants are exposed to varying degrees of stress factors during their lifetime. Stress can be biotic, imposed by other organisms, or abiotic, arising from an excess or deficit of a given stress factor (e.g. water, nutrients, light, temperature, etc) in the physical environment (Levitt, 1986). Many factors can affect plant response to abiotic stress, including the duration of the stress, its severity, previous exposure to stress, the part of the plant being examined, and the phase of plant growth or development when it is occurring (Bray, 1997). How a stress factor can influence sex lability in dimorphic species has been studied previously (reviewed by Korpelainen, 1998; Sakai and Weller, 1999; Barrett, 2002), but it is still poorly understood. In general, environmental stresses caused by less-than-optimal light, nutrition, weather or water conditions often favour maleness (Korpelainen, 1998; Munné-Bosch, 2015). However, this topic is still insufficiently explored considering the high diversity of dimorphic species and stress factors. For instance, to our knowledge the influence of Pi starvation during the transition phase on sex determination in dioecious perennial plants has not been explored thus far.

It is generally assumed that plant maturity, which is marked by the onset of flowering and seed production, has drastic effects on the capacity of plants to respond to stress (Bond, 2000). For example, it has been generally accepted that females often show higher proportional investments in reproduction than males in dioecious plant species (Hancock and Bringhurst, 1980). However, the theory that females grow less than males as a consequence of higher investment in reproduction appears to be true for some woody perennials, but it is not so clear or not generally applicable in herbaceous perennials (Obeso, 2002; Barrett and Hough, 2013; Juvany and Munné-Bosch, 2015). Indeed, recent in-depth analyses at the physiological level suggest that sex-related differences observed in dioecious species are highly species-specific (Juvany and Munné-Bosch, 2015) and may well respond to long-term compensatory mechanisms (Obeso, 2002). Therefore, it is

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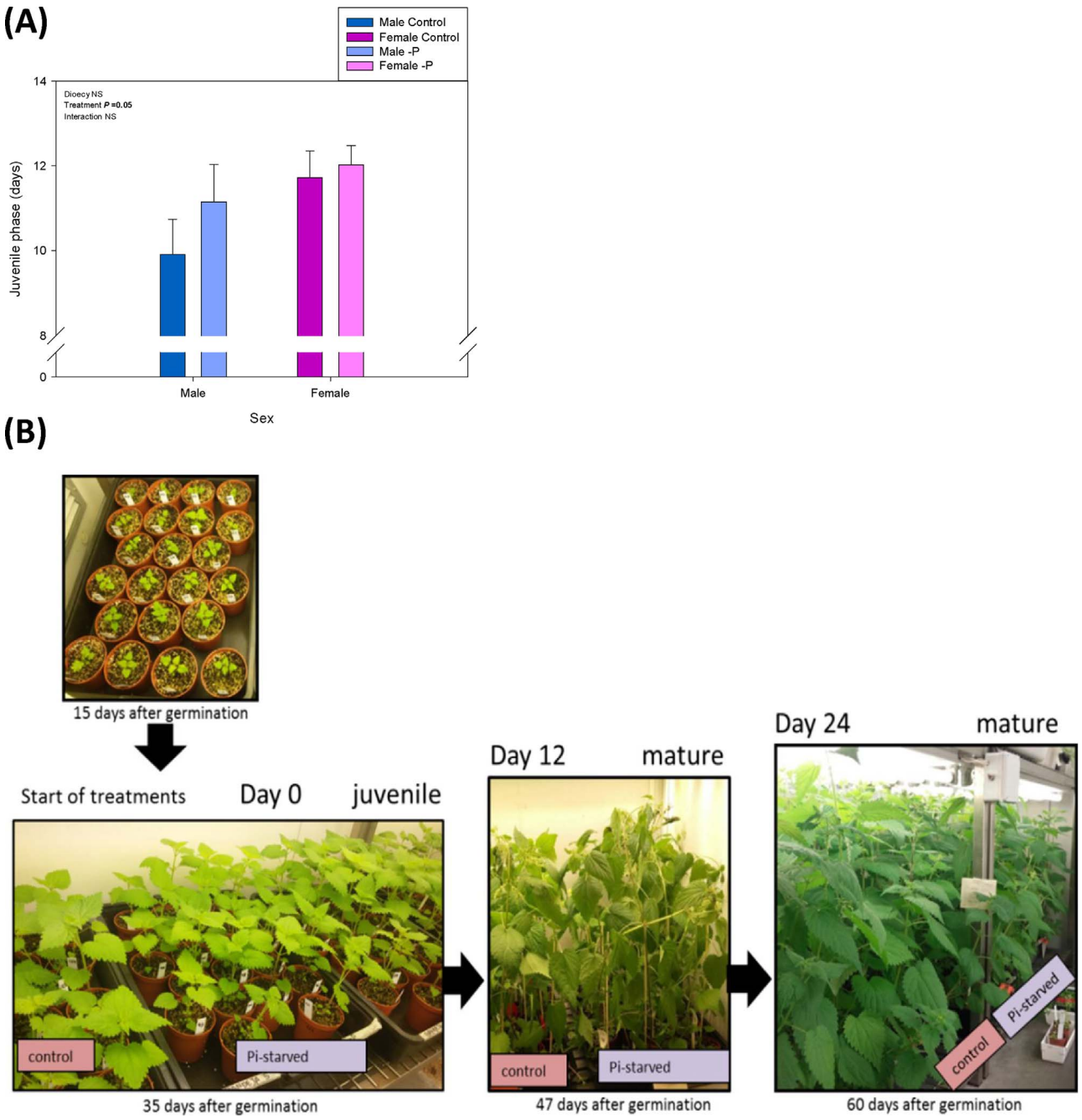

Fig. 1. (A) Length of the juvenile phase, estimated as days from germination to flowering in *U. dioica* either under Pi starvation or control conditions. The sex ratio in Pi-starved and control plants was 2.0 and 1.6, respectively. Data represent the mean ± S.E. of n = 20 males and 35 females. Significant differences between sexes (dioecy), treatments and its interaction were examined through two-way factorial analyses of variance (ANOVA, $P \leq 0.05$). NS, not significant. (B) Phenotype of plants during the sampling dates at 0, 12 and 24 days after the start of treatments (Pi-starved *vs.* control plants).

essential to get further insight into our current knowledge on plant response to abiotic stress in dimorphic species, considering not only the differences caused by sex, but also integrating a better knowledge of what are the causes of biased sex ratios found in nature, an aspect that requires special attention in the frame of climate change (Munné-Bosch, 2015).

Phosphorus (P) is one the most abundant macronutrients in plant tissues, but the low availability of this element in the soil is often the limiting factor for plant growth and development. P is essential for the storage of genetic information (is necessary for forming nucleic acids and other essential cellular components), it plays a crucial role in cell membranes (such as the formation of membrane phospholipids), as well as in practically all energy transactions through ATP, and it is both a substrate and a regulatory factor in photosynthesis and oxidative metabolism, among others. The chemical form of P taken up by plants is inorganic phosphate (Pi), mostly in the form of orthophosphate ($H_2PO_4^-$) under physiological pH (Ullrich-Eberius et al., 1984; Furihata et al., 1992). Due to its chemical properties, Pi is easily immobilized in the soil by forming insoluble complexes or precipitates with metals (Al or Fe in acidic soils and Mg or Ca in calcareous soils, Manning, 2008). Thus, Pi is one of the most important mineral nutrients limiting plant growth and development (Marschner, 2012).

Urtica dioica, often called common nettle or stinging nettle, is a dioecious, herbaceous and perennial plant distributed widely in many parts of the world (Taylor, 2009). Nettles have a strong association with human activity. In some cases, human and animal waste may be