

Assessing the influence of biogeographical region and phylogenetic history on chemical defences and herbivory in *Quercus* species



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ABSTRACT

Biogeographical factors and phylogenetic history are key determinants of inter-specific variation in plant defences. However, few studies have conducted broad-scale geographical comparisons of plant defences while controlling for phylogenetic relationships, and, in doing so, none have separated constitutive from induced defences. This gap has limited our understanding of how historical or large-scale processes mediate biogeographical patterns in plant defences since these may be contingent upon shared evolutionary history and phylogenetic constraints. We conducted a phylogenetically-controlled experiment testing for differences in constitutive leaf chemical defences and their inducibility between Palearctic and Nearctic oak species (*Quercus*, total 18 species). We induced defences in one-year old plants by inflicting damage by gypsy moth larvae (*Lymantria dispar*), estimated the amount of leaf area consumed, and quantified various groups of phenolic compounds. There was no detectable phylogenetic signal for constitutive or induced levels of most defensive traits except for constitutive condensed tannins, as well as no phylogenetic signal in leaf herbivory. We did, however, find marked differences in defence levels between oak species from each region: Palearctic species had higher levels of constitutive condensed tannins, but less constitutive lignins and less constitutive and induced hydrolysable tannins compared with Nearctic species. Additionally, Palearctic species had lower levels of leaf damage compared with Nearctic species. These differences in leaf damage, lignins and hydrolysable (but not condensed) tannins were lost after accounting for phylogeny, suggesting that geographical structuring of phylogenetic relationships mediated biogeographical differences in defences and herbivore resistance. Together, these findings suggest that historical processes and large-scale drivers have shaped differences in allocation to constitutive defences (and in turn resistance) between Palearctic and Nearctic oaks. Moreover, although evidence of phylogenetic conservatism in the studied traits is rather weak, shared evolutionary history appears to mediate some of these biogeographical patterns in allocation to chemical defences.

1. Introduction

The interactions between plants and phytophagous insects are more than 350 million years old (Labandeira, 2007), and have resulted in co-evolutionary arms races involving strong selection for increased plant defence and herbivore counter-defence (Ehrlich and Raven, 1964; Becerra, 1997; Berenbaum and Zangerl, 1998; Futuyama and Agrawal, 2009). The plant defensive arsenal against phytophagous insects includes a broad repertoire of structural barriers (e.g., spines, thorns, trichomes) and chemical compounds (e.g., phenolics, alkaloids, terpenoids) that kill, repel or reduce the performance of herbivores

(Agrawal, 2007; Núñez-Farfán et al., 2007). These physical and chemical traits exhibit enormous variation among plant species, even within a single genus (Agrawal, 2011), and elucidating the mechanisms and processes that originate and maintain such diversity represents a central challenge in evolutionary ecology (Becerra, 1997; Berenbaum and Zangerl, 1998; Agrawal, 2007, 2011).

The influence of historical processes on the evolution of plant defences can be inferred from analysing differences in allocation patterns among plant taxa belonging to different biogeographical regions (Bryant et al., 1994; Marquis et al., 2012; Ricklefs and He, 2016; Grutters et al., 2017). In cases where geographical differences have

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been observed, further investigations based on historical data and current observations on broad-scale drivers have served to point at the most probable processes or factors underlying contrasting trajectories of plant defence evolution (Bryant et al., 1994; Steinberg et al., 1995; Desurmont et al., 2011; Craft et al., 2013; Carrillo-Gavilán et al., 2015; Grutters et al., 2017). For example, comparisons of Nearctic (i.e., North America) and Palearctic (i.e., northern Eurasia) plant taxa have demonstrated that current differences in plant defensive investment between these regions have resulted from processes such as higher extinction rates and lower rates of recolonization of plant and herbivore species during the last glacial period in Palearctic regions compared with Nearctic regions (Archetti et al., 2009; Lev-Yadun and Holopainen, 2009).

In recent decades, with the advent of molecular techniques and phylogenetic comparative analyses, ecologists have been able to address the influence of phylogenetic non-independence on patterns of inter-specific variation in plant defence allocation (Becerra, 1997; Agrawal et al., 2009a; Kursar et al., 2009; Desurmont et al., 2011; Pearse and Hipp, 2012). Ehrlich and Raven (1964) predicted that more closely related plant species should share similar defensive chemistry, that closely related herbivores should feed on closely related plants, and that co-evolutionary arms races should lead to increased levels of plant defence and herbivore counter-defences (Agrawal et al., 2009a,b,c; Pearse and Hipp, 2009; Craft et al., 2013). Nonetheless, some studies have reported weak or lacking phylogenetic signals in plant defensive traits (e.g., Kursar et al., 2009; Rasmann and Agrawal, 2011; Endara et al., 2017), questioning the influence of shared evolutionary history on patterns of inter-specific variation in plant defences as proposed by classic theory. This latter group of studies suggests alternative processes influencing macro-evolutionary patterns in plant defence such as resource-tracking by herbivores following plant diversification (Endara et al., 2017) or convergent evolution (Kursar and Coley, 2003; Agrawal, 2007).

To address interspecific variation in plant defences, one key aspect is distinguishing between constitutive (i.e., basal levels expressed at any given time) and induced (i.e., those activated, increased, or synthesized only following herbivory) levels of defensive traits (Karban, 2011). Each strategy is favored over the other depending on the ecological context in which plants are embedded and studies have found that these defensive strategies in some cases trade off, i.e. increases in one strategy frequently lead to reductions in the other (Rasmann et al., 2011; Moreira et al., 2014). Although previous work has analysed these two modes of plant defence within a macro-evolutionary framework (e.g., Kempel et al., 2011; Rasmann and Agrawal, 2011; Moreira et al., 2014; Pellissier et al., 2016), few studies have compared allocation to constitutive and induced defensive strategies among geographically isolated taxa at the regional or continental level (but see Carrillo-Gavilán et al., 2015), therefore limiting our understanding of how historical process have contributed to shape plant defence evolution. In conducting these broad-scale comparisons, a key aspect to consider are the evolutionary relationships among the studied taxa; groups of closely related species may exhibit more similar patterns of allocation and such species could be geographically constrained to a given region (e.g., Fabaceae; Seigler et al., 1989). Accordingly, assessing the influence of evolutionary relationships while conducting biogeographical comparisons represents a robust approach for understanding how historical processes shape large-scale patterns of inter-specific variation in plant defensive traits (Agrawal et al., 2009a; Pearse and Hipp, 2012).

In this study, we assessed the production of chemical defences in oak species (*Quercus* spp.) from two disjointed biogeographical regions while controlling for the evolutionary relationships among these species. Phylogenetic and paleobotanical data suggest that the center of diversification for *Quercus* spp. is at middle latitudes of America; some species subsequently migrated to the Old World prior to the break-up of land bridges linking the northern continents, whereas others (e.g., red oaks) evolved too late to cross (Nixon, 1993; Manos et al., 1999). In

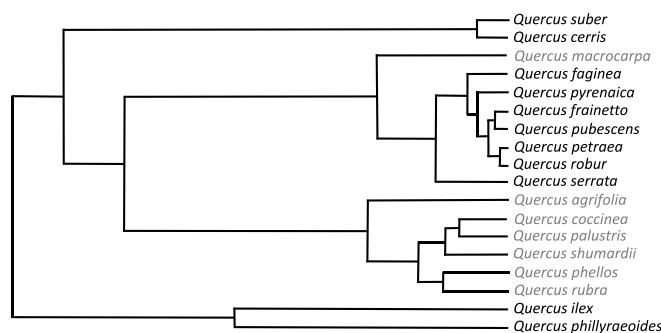


Fig. 1. Phylogenetic tree of the studied *Quercus* species based on Single Nucleotide Polymorphism matrices by ddRAD sequencing. Nearctic species are shown in grey font and Palearctic species are shown in black font.

addition, previous studies have held the existence of lower extinction rates of temperate tree species and higher rates of recolonization of plant and herbivore species since the last glacial period in Nearctic regions compared with Palearctic ones (Archetti et al., 2009; Lev-Yadun and Holopainen, 2009). According to these studies, Nearctic oak species would be better chemically defended than Palearctic ones. To test this, we performed a greenhouse experiment using one-year-old plants belonging to 18 oak species, 11 from the Palearctic region and seven from the Nearctic region (Fig. 1), and quantified the concentration of constitutive phenolic compounds in leaves as well as their induced levels. Defence induction was measured after damage inflicted by gypsy moth larvae (*Lymantria dispar*, Lepidoptera), a generalist herbivore that is native to the Old World but was introduced in North America and feeds on leaves of oak species from both biogeographical regions. After inducing plants, we also estimated the amount of leaf area consumed by the larvae to assess herbivore resistance in these species. In doing so, we sought to (i) assess the influence of shared evolutionary history (i.e., relatedness) on patterns of inter-specific variation chemical defences and herbivory by estimating the phylogenetic signal in these traits for the studied oak species, and (ii) test for differences between Nearctic and Palearctic oak species in allocation patterns to constitutive and induced chemical defences and herbivore resistance. In addition, we determined whether any such difference between regions is influenced by the shared evolutionary history of the studied species. This may occur if closely related basal vs. more derived species differ in their patterns of defence allocation and are represented differently in each biogeographical region. Overall, this study provides a unique assessment of the independent influences of long-term isolation (accounted for biogeographical region) and genetic relatedness (modelled by shared evolutionary history) on patterns of inter-specific variation in oak defences.

2. Results

2.1. Phylogenetic signal in plant chemical defences and herbivory

We found a significant phylogenetic signal for the concentration of constitutive condensed tannins, but not for any of the other classes of phenolic compounds (Table 1a). Likewise, we found no evidence of a phylogenetic signal in the inducibility for any of group of phenolic compounds (Table 1b) or in the amount of leaf herbivory (Table 1c).

2.2. Effects of biogeographical region and shared evolutionary history on leaf defences

Oak species significantly differed in their concentrations of constitutive leaf lignins and condensed and hydrolysable tannins, but not flavonoids (Fig. SMI in the Supplementary Material). Statistical models indicated a significant effect of biogeographical region on constitutive

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