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Effects of phylogeny and climate on seed oil fatty acid composition across 747 plant species in China

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ABSTRACT

Seed oil has long been recognized as an important source of food, industry and biodiesel. In biological aspect, seed oil fatty acid composition (FAC) affects lipid fluidity and cellular metabolism, depending on temperature. Hence, the variation of FAC in seeds may reflect adaptive strategies for seed survival and seedling establishment under contrasting climate conditions. In this study, we investigated the relative effects of phylogeny and climate on seed oil FAC, testing the hypothesis that the degree of fatty acid unsaturation increases in colder climates. A large seed oil FAC dataset representing 747 species from 207 sites across China was compiled and a general linear model was used to partition total variance in FAC into taxonomic ranks (family, genus and species) and environmental components. Multiple regression analysis was conducted to examine the relative effects of mean annual temperature (MAT) and mean annual precipitation (MAP). Phylogenetically independent contrast (PIC) analysis was used to test the evolutionary association of FAC with climate at the family level. The results showed that seed oil FAC varied considerably across plant species, with phylogeny explaining a greater proportion of variance than environment; however, FAC showed obvious large-scale spatial patterns. Total unsaturated fatty acid (UFA) content increased with increasing latitude. The degree of fatty acid unsaturation, as indicated by the ratio of UFA to saturated fatty acids and iodine value, was negatively correlated with MAT and to a lesser extent with MAP. The PIC results indicated that at the family level, nearly all significant phenotypic correlations of FAC with spatial and climatic variables were evolutionarily convergent. These results indicate that despite strong phylogenetic constraints on FAC, fatty acid unsaturation in seed oil appears to evolve as an adaptive strategy in colder climates. The affiliation of phylogenetic and climate in seed oil FAC may assist in the search of potential oil plants with particular FAC for food and fuel needs.

1. Introduction

The seeds of many plant species accumulate high concentrations of lipids, presumably because compared to carbohydrates, lipids contain approximately two times the amount of energy per unit dry mass, and a higher lipid contents thus increases the energy available for developing seedlings without sacrificing the dispersal advantage associated with small seed size (Baskin and Baskin, 1998). Seed lipids are also significant from an ethnobotanical perspective, because humans have utilized oil-rich seeds as source of food and oil throughout history (e.g. Yang et al., 2012). Because the degree of seed oil fatty acid unsaturation affects its fluidity, biological organisms are known to adjust fatty acid composition according to temperature to maintain ideal membrane fluidity (Guschina and Harwood, 2006). Lipids stored in seeds, which are presumably under evolutionary selection to maximize survival and germination success of seeds, may also be under natural selection by climatic conditions (e.g. Daws et al., 2007; Linder, 2000). However, little is known about the large-scale spatial (latitudinal) patterns of seed oil fatty acids along with their ecological significance.

Seed oils vary substantially in fatty acid composition across different taxonomic levels (Mayer and Poljakoff-Mayber, 1989; Trelease and Doman, 1984). For instance, studies on the fatty acid compositions of seed oils from Ranunculaceae (Aitzetmüller et al., 1999) and Boraginaceae (Özcan, 2008) have indicated that their fatty acid compositions differ notably at generic and infrageneric levels. Many studies have reported strong phylogenetic patterns in the fatty acid profiles of the seed oils (Aitzetmüller, 1995; Velasco

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and Goffman, 1999), such that it may be a useful trait for the characterization and delineation of taxa at different hierarchical levels (Mayworm and Salatino, 2002). To date, the relative contributions of taxonomy and climate to the variance in fatty acid compositions across diverse plants remain unclear.

The maintenance of membrane fluidity and stability by regulating seed oil fatty acid composition may allow plants to adapt to abiotic stresses, particularly chilling stress (Guschina and Harwood, 2006; Nishida and Murata, 1996; Upchurch, 2008). Many studies have shown that acclimation to colder temperature involves the homeostatic control of membrane fluidity through increasing unsaturated fatty acids relative to saturated fatty acids (Dornbos and Mullen, 1992; Linder, 2000; Nishida and Murata, 1996; Yoshida, 1984). In contrast, the role of fatty acid composition in drought tolerance remains unclear. The response of seed oil fatty acid composition to drought is negligible in some crop cultivars (e.g. Manavalan et al., 2009), whereas drought causes a reduction in seed oil saturated fatty acids in some species (Ashrafi and Razmjoo, 2010). However, these studies on the associations of fatty acid composition with environmental factors have been restricted to a few species or cultivars along a small range of environmental gradients (e.g. Ashrafi and Razmjoo, 2010; Ayerza, 2011; Boschin et al., 2008; Stevenson et al., 2007; Yang et al., 2012). Furthermore, no previous studies have been conducted to examine the general relationships between fatty acid composition and environmental factors such as temperature and precipitation across a large number of plants and a wide range of environments at a large scale. We predict that plants native to colder and/or drier climates tend to have seed oils with higher ratios of unsaturated to saturated fatty acids.

The extremely high diversity of plant species in China encompasses many plants that can serve as sources of renewable energy and food (Yang et al., 2012). With growing concerns over the gradual depletion of world petroleum reserves and environmental pollution associated with exhaust emissions, seed oil is viewed as a promising alternative energy resource (e.g. biodiesel) that is renewable, environmentally friendly, safe and biodegradable (e.g. Yang et al., 2012). Because of these economic utilities, fatty acid compositions, which affect the physicochemical characteristics and nutritional value of seed oil, have been extensively investigated (e.g. Thomas, 2000; Trelease and Doman, 1984). Herein, we analyzed the fatty acid composition of seed oils from the literature for 747 terrestrial plant species from 207 sites that encompass almost all ecosystems and climate regions in China. The two objectives of this study were to: (1) investigate the relative effects of taxonomic affiliations and climate on interspecific variation in seed oil fatty acid composition, and (2) test the hypothesis that the degree of seed oil fatty acid unsaturation increases as the climate becomes colder and/or drier with and without the consideration of phylogeny.

2. Materials and methods

2.1. Data compilation

Data on seed oil fatty acid composition (FAC) were compiled from the literature (Jia and Zhou, 1987; Wang et al., 1982). The total dataset represented 207 sites from a wide range of ecosystems across China (Fig. 1) and contained 1183 species-at-site combinations consisting of 747 species or varieties from 95 families (see Table S1 in Supplementary material).

Supplementary Table S1 related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.indcrop.2014.10.045.

Six variables were used to characterize seed oil FAC: content of total unsaturated fatty acids (UFA), the two main UFAs, oleic acid ((9Z)-9-Octadecenoic acid) and linoleic acid ((9Z, 12Z)-9,12-Octadecadienoic acid), total saturated fatty acids (SFA), the two main SFAs, palmitic acid (hexadecanoic acid) and stearic acid (octadecanoic acid). Seeds of 2–5 g were ground and extracted with petroleum ether in a Soxhlet apparatus for 14 h. The oil extract was evaporated by distillation until the solvent was totally removed. The contents of different seed oil fatty acids were determined using a gas chromatograph (Shimadzu GC-5A, Kyoto, Japan) equipped with a flame ionization detector and capillary column (1.5–2 m × 3–4 mm i.d. packed with 10–20% DEGS/Chromosorb W, 60–80 mesh). Approximately 0.5 g oil was converted to methyl ester using 10 ml of 2% (v/v) H_2SO_4 in methanol before being injected into the gas chromatograph, which was operated under the following conditions: the column temperature was usually 180–200 °C (for some complicated samples such as the oil from Lauraceae, the column temperature was programmed from 130 to 200 °C at a rate of 8 °C min^{-1}); the injector and detector temperatures were 250–300 and 250 °C, respectively; and the carrier gas was nitrogen at a flow rate of 40–50 ml min^{-1}. Peaks were denitrified using retention times by means of comparing them with

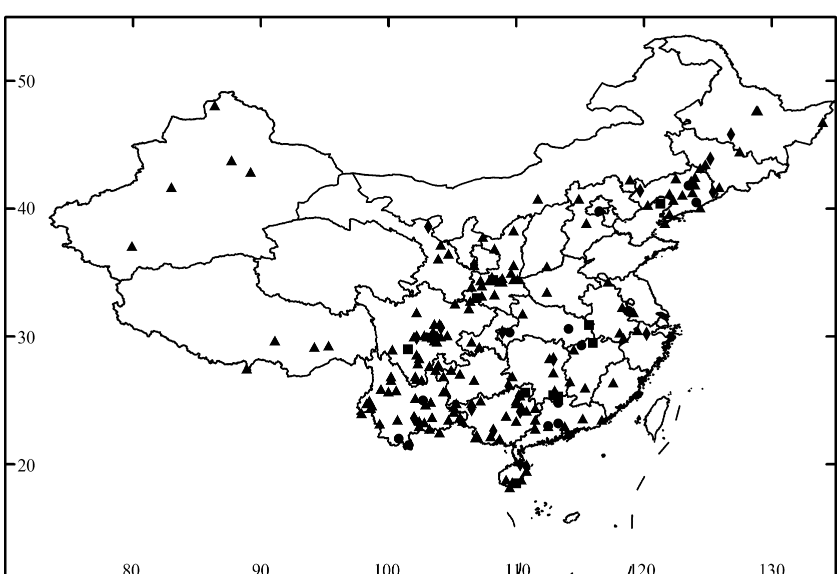

Fig. 1. Map of the study sites. ▲, ≤5 species sampled; ♦, 6–10 species sampled; ■, 11–20 species sampled; ●, > 20 species sampled.