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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

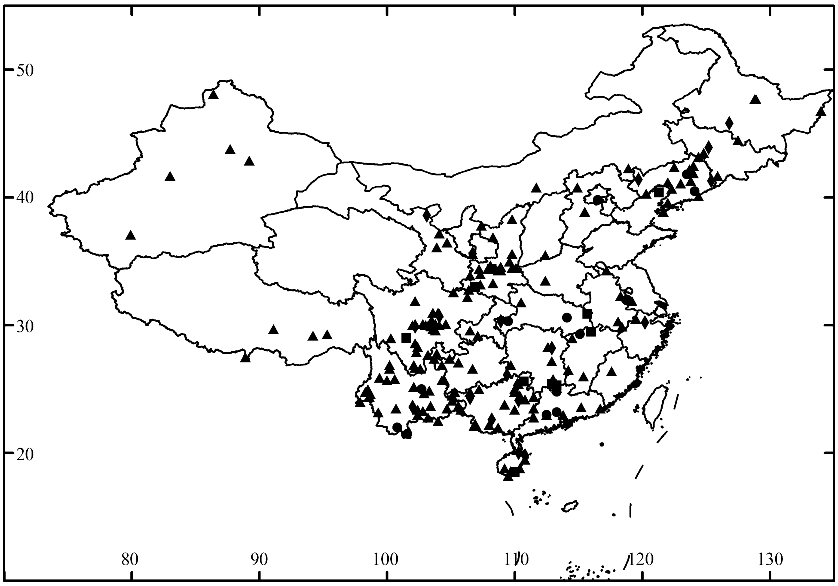

Fig. 1. Map of the study sites. ▲, ≤5 species sampled; ◆, 6–10 species sampled; ■, 11–20 species sampled; ●, > 20 species sampled.

Table 1
Summary of statistics for seed oil fatty acid composition.

	Unit	Number of observations	Minimum	Maximum	Mean	SD	Skewness
Total unsaturated fatty acid (UFA) content	%	1183	33.5	99.0	82.8	10.8	−1.26
Oleic acid content	%	1181	2.7	95.7	30.3	18.7	1.03
Linoleic acid content	%	1168	0.2	87.7	37.9	21.7	0.23
Total saturated fatty acid (SFA) content	%	1183	1.0	66.5	17.2	10.8	1.26
Palmitic acid content	%	1178	0.8	52.4	12.3	8.4	1.34
Stearic acid content	%	1083	0.1	59.8	3.6	4.1	6.03
UFA/SFA ratio		1183	0.5	99.0	8.2	8.2	3.68
Iodine value	$g\,100\,g^{-1}$	1183	41.1	245.7	117.6	30.1	0.52

authentic standards. For comparison, oil extraction and methyl ester preparation were conducted under the same conditions.

Two variables were used as indicators of the degree of fatty acid unsaturation: UFA/SFA ratio and iodine value. Iodine value is an integrated measure of the degree of fatty acid unsaturation, which is defined as the mass of iodine in grams that is consumed by 100 g of fatty acids (Knothe, 2002) and was determined according to Wijs (1929).

Site latitude was derived from Google Earth and spanned from 18.2 to 48.1° N latitude. Meteorological data (mean annual temperature, MAT, and mean annual precipitation, MAP) were taken from the China Meteorological Data Sharing Service System (CMDSSS; http://cdc.cma.gov.cn/); however, if MAT and MAP were not available from CMDSSS, they were obtained from the nearest local weather stations to the sampling sites and temperature was then extrapolated using an altitudinal lapse rate of 0.6 °C per 100 m. Among sites, MAT ranged from 1 to 26 °C, and MAP ranged from 16 to 2400 mm year^{-1}.

2.2. Data analysis

All statistical analyses were performed using R software version 3.0.1 (R Core Team, 2013). The Shapiro–Wilk normality test showed that all seed oil traits except content of total UFA exhibited right-skewed distributions (Table 1 and Fig. 2). Therefore, total UFA content was normalized by 'Blom' transformation that is available within the "Rank Cases' package of SPSS, and all other seed traits and climate variables were log$_{10}$-transformed to attain normality and homogeneity of residuals prior to analysis.

Using a restricted maximum likelihood method in the 'lme' function, we fitted a general linear model to the variance across four scales nested one into another (i.e. nested analysis of variance with random effects) in the increasing order of species, genus, family and site. Variance component analysis was performed using the 'varcomp' function. The 'ape' and 'nlme' packages are necessary to run the 'varcomp' and 'lme' commands. In our case the estimated components of variance can be roughly distinguished into a

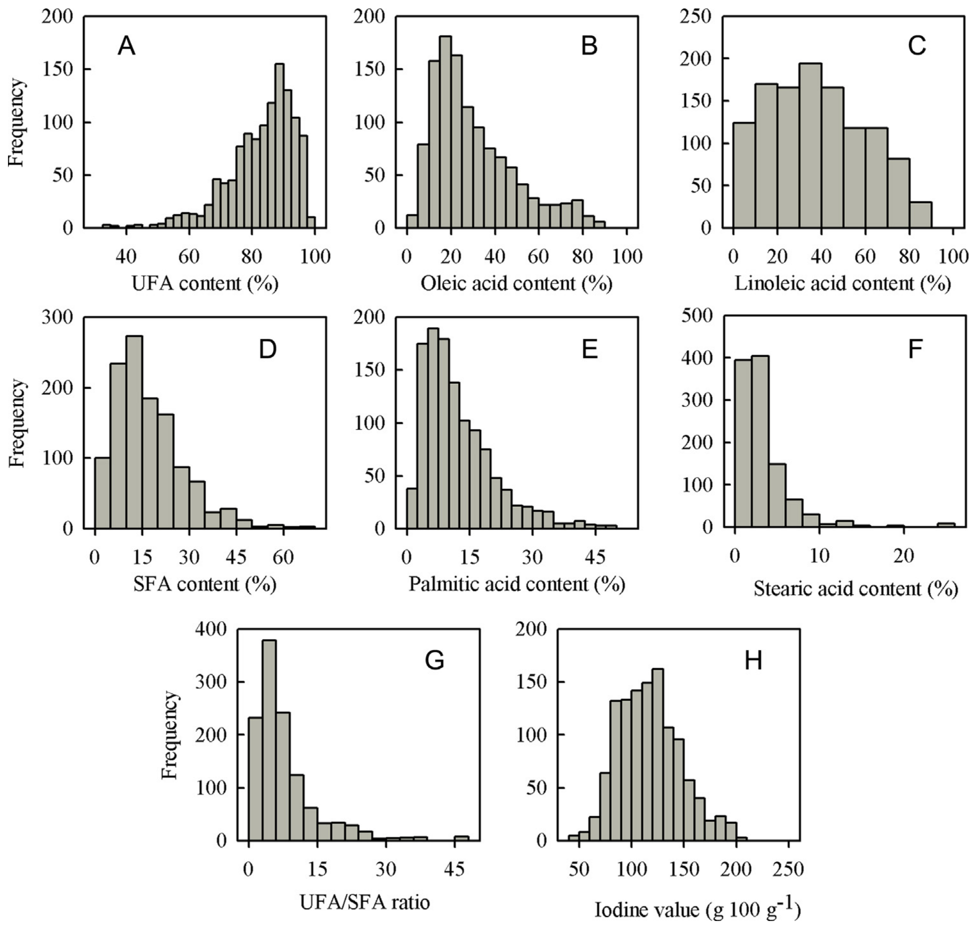

Fig. 2. Frequency distributions of fatty acid composition: (A) total unsaturated fatty acid (UFA), (B) oleic acid, (C) linoleic acid, (D) total unsaturated fatty acid (SFA), (E) palmitic acid, and (F) stearic acid contents, (G) UFA/SFA ratio, and (H) iodine value.

"site–environmental" and a "genetic" term. The genetic term (estimated here as the sum of the family, genus and species effects) represents the phylogenetic structure of the dataset. The remaining variance assigned to "site" is interpreted as the environmental term that reflects the combined influences of climate, soil and location. In addition, multiple regression analysis was conducted to examine the relative effects of MAT and MAP on seed oil FAC.

Because previous work has indicated that phylogeny may determine seed oil FAC (e.g. Aitzetmüller et al., 1999; Özcan, 2008), correlation analysis of FAC with site climate variables was complemented with phylogenetically informed analysis at the family level, using phylogenetically independent contrasts (Felsenstein, 1985). We built a phylogeny that was resolved up to the family level using phylomatic (http://phylodiversity.net/), which uses an APG III-derived megatree as the base tree (Angiosperm Phylogeny Group, 2009). The branch length adjuster (BLADJ) algorithm in phylocom (Webb et al., 2008) was used in combination with estimated family ages (Wikström et al., 2001) to assign branch lengths in this phylogeny. Our primary analysis showed that the phylogenetic signals (*K* value) for fatty acid profiles were between 0.214 and 0.370, indicating that FAC at the family level was less similar between phylogenetic branches than expected from a Brownian motion model of trait evolution (Felsenstein, 1985). Compared with the *K* values reported for other plant traits (e.g. Blomberg et al., 2003; Westbrook et al., 2011), the seed oil FAC evaluated here exhibited a moderate degree of phylogenetic signals. Contrasts for each variable were calculated using the "pic" function of the "picante" package, and phylogenetically-independent-contrasts correlation coefficients were then calculated using the 'lm' function.

3. Results

3.1. Seed oil fatty acid composition

Seed oil fatty acid composition varied considerably across plant species in China, with total unsaturated fatty acids (UFAs) ranging between 33.5 and 99.0% (mean = 82.8%; Table 1 and Fig. 2). The ratio of UFAs to saturated fatty acids (SFAs) ranged from 0.5 to 99% and the iodine value ranged between 41 and 246 g 100 g^{-1}. The two most abundant UFAs were oleic acid (1181 in 1183 species-at-site combinations) and linoleic acid (1168 in 1183), and the two most abundant SFAs were palmitic acid (1178 in 1183) and stearic acid (1083 in 1183). The two main UFAs, oleic acid and linoleic acid, were negatively correlated with each other ($r = -0.328$, $P < 0.001$), and UFA/SFA ratio was positively correlated with linoleic acid ($r = 0.155$, $P < 0.001$). The two main SFAs, palmitic acid and stearic acid, were positively correlated with each other ($r = 0.374$, $P < 0.001$), and both were negatively correlated with UFA/SFA ($r = -0.828$, $P < 0.001$ for palmitic and $r = -0.540$, $P < 0.001$ for stearic acid, respectively) and iodine value ($r = -0.361$, $P < 0.001$ for palmitic and $r = -0.094$, $P < 0.01$ for stearic acid, respectively).

3.2. Partitioning of the variance

The partitioning of the total variance into genetic and environmental components shows that a higher proportion of the variance was attributable to the nested taxonomic ranks (i.e. genetic component) than to the environmental component (Fig. 3). Specifically, >70% of the total variance was attributable to the genetic term for all traits in the dataset. On average, family, genus and species components for all traits accounted for 23, 33 and 26% of the total variance, respectively. However, the proportion of the variance attributable to the genetic component differed for different traits. For example, the genetic component accounted for 73% of the total variance in UFA/SFA ratio, and 93% of the total variance in stearic acid content.

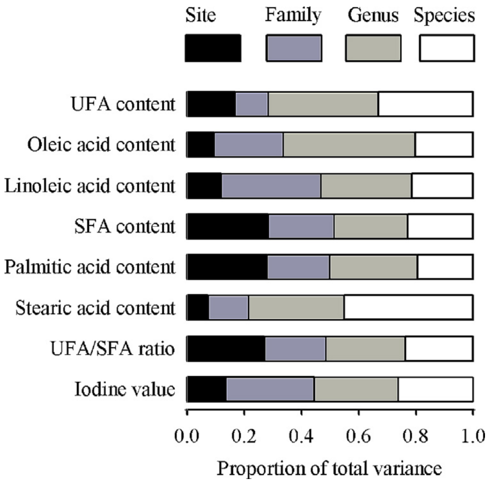

Fig. 3. Partitioning of the total variance for fatty acid composition into site, family, genus, and species plus error (residual) components. UFA, unsaturated fatty acid; SFA, saturated fatty acid.

3.3. Correlation of seed oil fatty acid composition with environment

Seed oil fatty acid composition showed an obvious large-scale spatial pattern. With increasing latitude, the total UFA and linoleic acid contents increased (Fig. 4), the contents of total SFAs and the two most abundant SFAs, palmitic acid and stearic acid, decreased (Fig. 5), and the degree of fatty acid unsaturation, as indicated by the UFA/SFA ratio and iodine value increased (Fig. 6). The MAT and MAP were negatively correlated with latitude across the study sites ($r = -0.869$, $P < 0.001$ for MAT and $r = -0.716$, $P < 0.001$ for MAP, respectively). With increasing MAT and MAP, the total UFA and linoleic acid contents along with the degree of fatty acid unsaturation decreased, while the contents of total SFAs and the two most abundant SFAs increased (Figs. 4–6). Multiple regression analysis showed that MAT and MAP together explained 2–23% of the total variance in individual FAC (R^2 values; Table 2). Total UFAs, SFAs, UFA/SFA ratio and iodine value were more strongly influenced by MAT than by MAP, as shown by the higher absolute values of partial correlation coefficients (Table 2). Analysis of phylogenetically independent contrasts showed convergent evolution; when seed oil fatty acid composition with spatial and climate was significant in non-phylogenetic analyses at the family level, in almost all cases it was also significant as PIC correlations (Table 3).

4. Discussion

Overall, the relative abundance of common fatty acids in seed oils varied widely across species from different sites in China (Table 1 and Fig. 2). The total unsaturated fatty acid content reported here ranged from 33.5 to 99.0% (Table 1), which covers nearly the whole range of unsaturated fatty acid content reported for wild and cultivated plants in the world (e.g. Aitzetmüller et al., 2003; Akbar et al., 2009; Ayerza, 2011; Camas et al., 2007; El-Beltagi et al., 2007; Minzangi et al., 2011; Özcan, 2007, 2008; Parashar et al., 2010). As an indicator of fatty acid unsaturation, iodine values ranged from 41 to 246 g 100 g^{-1} (Table 1), falling within the previously reported range (Thomas, 2000). The large variation in fatty acid composition indicates a large potential to select ideal plants for specific health, nutritional, and industrial usages.

We found that the relative abundance of common fatty acids in seed oils is more strongly explained by taxonomic affiliation than by climate (Fig. 3). The importance of genetics over plastic response to environment as determinants of fatty acid composition

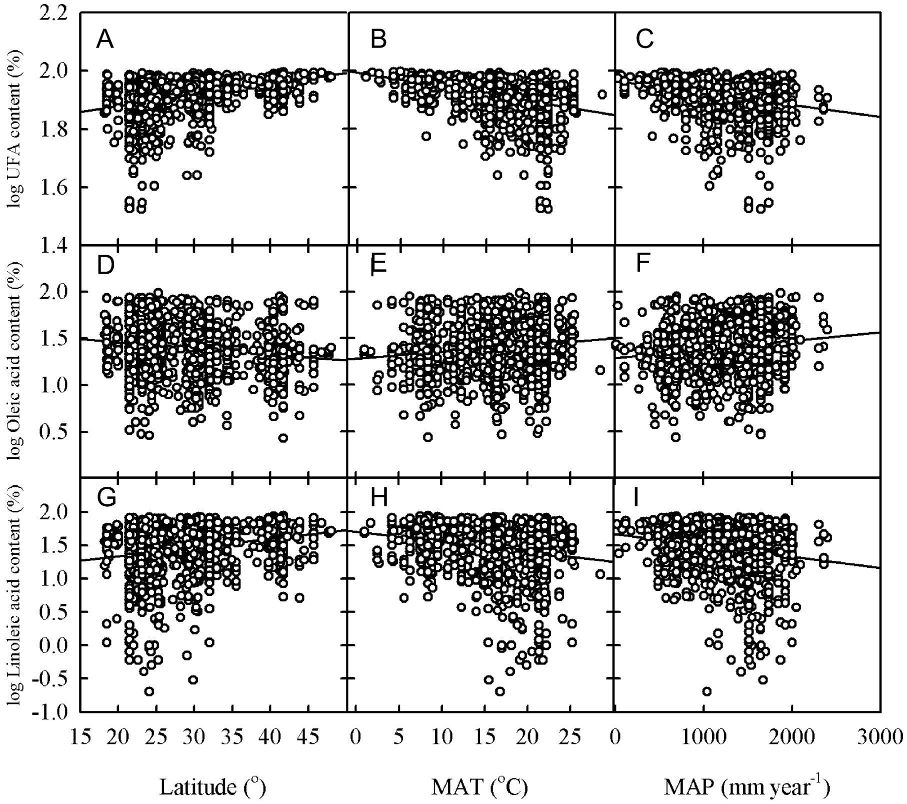

Fig. 4. Contents of total unsaturated fatty acid (UFA), oleic acid and linoleic acid in relation to latitude and climate variables: (A, D, G) latitude, (B, E, F) mean annual temperature (MAT), and (D, F, I) mean annual precipitation (MAP).

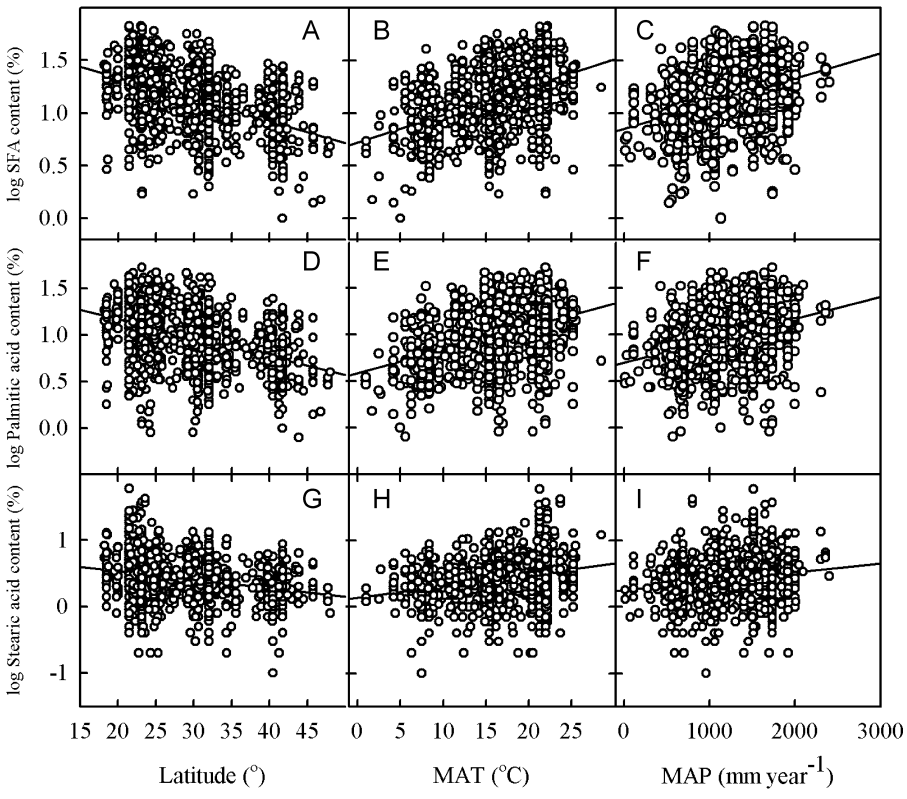

Fig. 5. Contents of total saturated fatty acid (SFA), palmitic acid and stearic acid in relation to latitude and climate variables: (A, D, G) latitude, (B, E, F) mean annual temperature (MAT), and (D, F, I) mean annual precipitation (MAP).

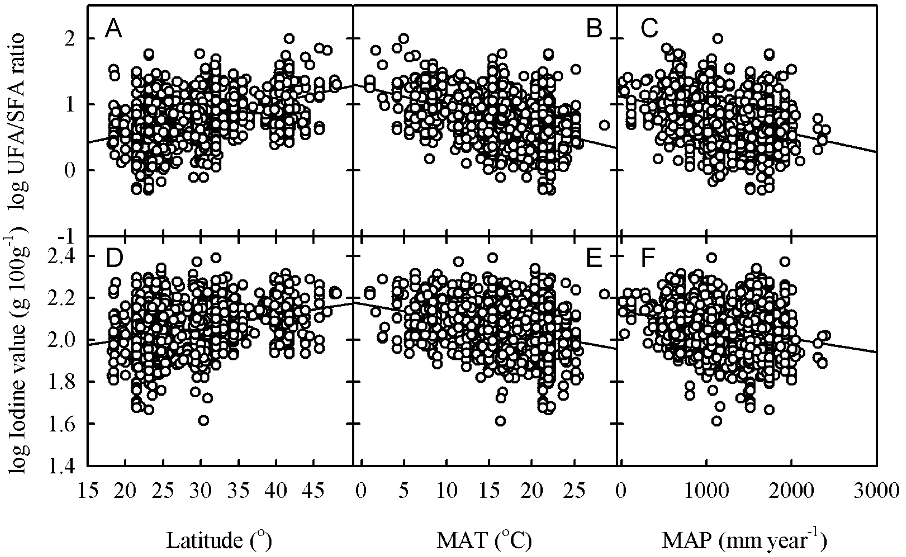

Fig. 6. Unsaturated fatty acid (UFA)/saturated fatty acid (SFA) ratio and iodine value in relation to latitude and climate variables: (A, D) latitude, (B, E) mean annual temperature (MAT), and (D, F) mean annual precipitation (MAP).

Table 2
Coefficients of partial correlation in the multiple linear regression of seed oil fatty acid composition with mean annual precipitation (MAP) and mean annual temperature (MAT).

	MAP	MAT	R^2	Number of observations
Total unsaturated fatty acid content (UFA)	−0.100**	−0.398***	0.218	1183
Oleic acid content	0.055	0.069*	0.020	1181
Linoleic acid content	−0.099**	−0.097**	0.048	1168
Total saturated fatty acid content (SFA)	0.087*	0.344***	0.227	1183
Palmitic acid content	0.088*	0.300***	0.186	1178
Stearic acid content	0.018	0.187***	0.063	1083
UFA/SFA ratio	−0.085**	−0.338***	0.219	1183
Iodine value	−0.073*	−0.215***	0.106	1183

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

has also been reported in experimental studies (e.g. Boschin et al., 2008). The three taxonomic ranks explained a very large proportion of the total variance in the relative abundance of individual fatty acids and degrees of unsaturation (Fig. 3). Seed oil fatty acid profiles are distinctive enough among species and genotypes that they are advocated as chemotaxonomic markers, for example in *Epilobium*, Onagraceae (Velasco and Goffman, 1999), Ranunculaceae (Aitzetmüller et al., 1999), *Orobanche*, Orobancheceae (Pujadas-Salvà, 2000), and *Quercus* (Galván et al., 2012; Özcan, 2007). In addition, some species possess very unusual fatty acid compositions that can be used in chemotaxonomy. For instance, our analysis showed that species from Myristicaceae tend to accumulate high contents (~57%) of myristic acid (tetradecanoic acid). These examples indicate that combining information from the relative abundance of common fatty acids and the presence of unusual fatty acids is useful in fatty acid profiles for taxonomic purposes (Özcan, 2013; Pujadas-Salvà, 2000). The overwhelming importance of genetics over environment in seed oil fatty acid composition indicated by this work and other studies (e.g. Boschin et al., 2008) suggests the adaptive significance of species-specific fatty acid compositions for successful regeneration from seeds. The parallel results for phylogenetic and non-phylogenetic correlations

Table 3
Coefficients of Pearson's and phylogenetically independent contrast (PIC) correlations of seed oil fatty acid composition with latitude and climate variables at the family level.

	Latitude		MAP		MAT	
	Pearson's	PIC	Pearson's	PIC	Pearson's	PIC
Total unsaturated fatty acid (UFA) content	0.656***	0.708***	−0.506***	−0.579***	−0.641***	−0.686***
Oleic acid content	−0.231***	−0.267*	0.196***	0.223*	0.196***	0.183
Linoleic acid content	0.159***	0.222*	−0.124***	−0.184	−0.131***	−0.158
Total saturated fatty acid (SFA) content	−0.488***	−0.713***	0.351***	0.574***	0.470***	0.685***
Palmitic acid content	−0.435***	−0.702***	0.324***	0.550***	0.423***	0.653***
Stearic acid content	−0.272***	−0.348***	0.169***	0.372***	0.250***	0.370***
UFA/SFA ratio	0.629***	0.657***	−0.457***	−0.531***	−0.597***	−0.629***
Iodine value	0.627***	0.588***	−0.449***	−0.452***	−0.562***	−0.554***

MAP, mean annual precipitation; MAT, mean annual temperature. $N = 88$.
* $P < 0.05$.
*** $P < 0.001$.

(Table 3) indicate strongly convergent evolutionary trends for the selection of fatty acids in seeds.

We hypothesized that the degree of seed oil fatty acid unsaturation increases in colder and/or drier climates based on the direction of adaptive acclimation responses (Nishida and Murata, 1996). We did find that the degree of fatty acid unsaturation of seed oils in China increased with latitude and decreased with mean annual temperature and mean annual precipitation (Fig. 6), with fatty acid unsaturation being affected more strongly by temperature than by precipitation (Table 2). A significant negative correlation between the content of unsaturated fatty acids and temperature has been found in comparisons of species, cultivars and genotypes of certain plant groups (e.g. Ayerza, 2011; Barbosa et al., 2014; Kim et al., 2011; Linder, 2000; Schulte et al., 2013; Werteker et al., 2010). Interestingly, the relative contents of oleic and linoleic acids were negatively correlated, and the content of linoleic acid (which has the greater degree of unsaturation of the two) was the main driver of the observed increase in unsaturated fatty acid content with latitude. Palta et al. (1993) found that an increase in linoleic acid occurs in the plasma membrane phospholipids of *Solanum* species with cold acclimation. Low temperature causes acclimation responses to increase the proportion of unsaturated fatty acids (e.g. Ayerza, 2011; Dornbos and Mullen, 1992; Nishida and Murata, 1996). Although we do not have data on fatty acid desaturases (FADs), other studies indicate that the genes encoding FADs are induced by low temperature (Nakamura and Nara, 2004; Wada et al., 1990), whereas drought has no or little effect on their expression (Berberich et al., 1998; Matteucci et al., 2011). In terms of differences among genotypes and species, it is likely that species with higher unsaturated fatty acids possess greater constitutive levels of expression of some specific FADs (e.g. Thambugala et al., 2013).

The results reported here have significant ecological implications: most importantly by providing new evidence suggesting fatty acid composition may constrain the distribution of plants at large geographical scales. Because the majority of lipids in seeds reside in lipid bodies as energy storage, the degree of unsaturation does not necessarily indicate membrane fluidity. At high latitudes, seeds with higher proportions of unsaturated fatty acids in their oils have a competitive advantage because they can germinate earlier and grow more rapidly at low temperatures even though they store less total energy than seeds with a higher proportion of saturated fatty acids (Baskin and Baskin, 1998; Linder, 2000). High levels of seed lipid saturation may interfere with the fatty acid metabolism of germinating seeds during the cold season. Consequently, fatty acid unsaturation of seed oils allows plants to distribute toward higher latitudes and altitudes (Ayerza, 2011). In contrast, at higher temperatures, seeds with a higher proportion of saturated fatty acids will be selectively favored because their oils will provide more energy, without a penalty in the rate of energy acquisition. The scatter of data points showing the percentage of total unsaturated fatty acids against latitude (Fig. 4) exhibited a threshold response suggestive of an increase in the minimum necessary unsaturated fatty acid content with increasing latitude. In contrast, a wide range of unsaturated fatty acid contents was observed in warmer climates (Fig. 4). Unlike unsaturated fatty acids, saturated fatty acids did not show an obvious threshold response (Fig. 5), but high degrees of fatty acid saturation were observed in species from warmer climates (Fig. 6). This indicates that higher saturated fatty acid contents may be selected for seed survival or maintenance of seed reserve integrity in warmer climates.

5. Conclusion

This study suggests that seed oil fatty acid composition exhibits geographical patterns in relation to climate, and that the interspecific variation in seed oil fatty acid unsaturation is explained more by temperature than by precipitation. These results strongly suggest that seed oil fatty acid composition plays an important role in the ecological adaptation of plants. The negative association of seed oil fatty acid unsaturation with mean annual temperature could help predict plant adaptations to climate warming and indicates the potential importance of the genetic manipulation of seed oil fatty acid composition as part of the climate adaptation strategy of economically useful plants.

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