

The seeds of invasive plant *Triadica sebifera* never changed when they return to provenance for five years

Yu-Lin Li

Yunnan University

Yun-Tao Xiong

Yunnan University

Chao-Nan Wang

Fudan University

Jie-Ren Jing

Fudan University

Zhi-Li Pan

Yunnan University

Yan Wang

Yunnan University

Yi Wang (✉ yiwang@ynu.edu.cn)

Yunnan University

Research Article

Keywords: Chinese tallow tree (*Triadica sebifera*), co-evolution, seed properties, reintroduction

Posted Date: January 12th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-2463731/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Plant Ecology on June 29th, 2023. See the published version at <https://doi.org/10.1007/s11258-023-01335-z>.

Abstract

Successful germination and establishment of invasive plants is a key early step in the invasive process which influences the invasive potential. Previous studies have focused on differences in traits between native and invasive plants, but few studies have explored the evolutionary changes in seeds when invasive plants were reintroduced into their homeland.

We planted seeds (F1) of 13 *Triadica sebifera* populations that invaded the United States into their native habitat (31°45'N, 114°39'E, Dawu, China) in 2014. After F1 seeds matured (2019), we collected their seeds (F2) and the seeds of 30 native populations. We tested the differences in physical and chemical properties, seed hormones, and germination traits between the seeds of reintroduced and native *Triadica sebifera* populations.

Although we did not find significant differences in physical and chemical properties and germination traits between the seeds of reintroduced and native *Triadica sebifera* populations, generally the various contents in reintroduced *Triadica sebifera* populations were higher than native *Triadica sebifera* populations. Besides, we found that the seeds of reintroduced populations had significantly higher levels of abscisic acid (ABA) and three gibberellins (GAs) but significantly lower l-aminocyclopropane-l-carboxylic acid (ACC) and the ratios of total GA (TGA) to ABA than the seeds of native populations. Dewaxed seed masses and TGA were positively correlated with germination traits, while ACC and ABA were negatively correlated with germination traits.

These results suggested that the seeds of invasive plant *Triadica sebifera* never changed when they from the United States return to its provenance for five years, which could enrich our poor cognition about seed properties changes after experiencing different environments and were beneficial to control invasive plants.

Introduction

The invasive process of alien plants is generally divided into four stages: introduction, colonization, adaptation, and spread (Blackburn et al., 2011). Successful germination and establishment of invasive plants is a key early step in the invasive process that influences invasive potential (Ferrerias and Galetto, 2010; Gioria and Pyšek, 2017). Differences in resource allocation within seeds may cause plant growth differences in their invasive and native ranges (Widmer et al., 2007). Therefore, studying plant seed material changes about the allocation and performance after experiencing different environments will help to explain invasive mechanisms (Zhang, 2019). For example, comparing the seed biomass of co-occurring native and invasive species from different families, Daws et al. (2007) found that increasing seed biomass is conducive to plant invasion. The variations in seed size (mass or volume) among species, and even among individuals within the same populations may be affected by genetic factors, maternal investments, and environmental conditions (Bhatt et al., 1989; Suárez et al., 2017). Seeds typically contain stored soluble proteins, lipids, and carbohydrates. The content levels of these materials

can significantly affect germination (Adawy et al., 2003; Suda and Giorgin, 2000) and seedling survival rate (Elamrani et al., 1992; Mtambalika et al., 2014). Similarly, hormones can regulate seed dormancy and germination (William and Gerhard, 2006). For instance, the abscisic acid (ABA) can induce dormancy in many species but the gibberellins (GAs) and ethylene often break dormancy (Nonogaki, 2014).

Non-native invasive plants and organisms introduced for biological control are ideal systems for studying whether and how organisms quickly adapt to changing environments (Sun and George, 2019). Plants can respond to changing environments through adaptive evolution (Colautti and Barrett, 2013; Agrawal et al., 2015), phenotypic plasticity (Castillo et al., 2014; Liu et al., 2016) and differential resource allocation (Alexander et al., 2009; Xiao et al., 2018). There's a big environmental gap between native and invasive areas, so invasive plants have various strategies in different areas (Huberty et al., 2014; Sakata et al., 2017). The evolution of the increased competitive ability (EICA) hypothesis predicts that reduced herbivory from native specialist herbivores allows invasive plants to shift their resource allocations from defense to growth or reproduction contributing to enhanced competitiveness (Blossey and Nötzold, 1995). However, these adaptations may make plants from non-native ranges more susceptible to herbivores and pathogens in their native ranges (Blossey and Nötzold, 1995). Thus, reintroducing them to the native ranges may result in the poor overall performance of the invasive plant.

However, the consequences of such evolutionary responses in native ranges of invasive species are poorly understood (Pal, et al., 2020). This begs the question of what changes in seed properties when the invasive plant returns to its native area. We hypothesize that the physical and chemical properties, related hormones, and the germination traits of seeds of reintroduced populations would be significantly different from those of native populations. To test this hypothesis, we take the Chinese tallow as experimental subject. The Chinese tallow (*Triadica sebifera*, hereafter '*T. sebifera*') is native to China and it was introduced to the United States in 1772 because of its great economic value (Bruce et al., 1997). In the United States, *T. sebifera* had no herbivory pressure from specialist insects and faced almost no herbivory from generalists. So it spread rapidly in southern coastal areas (Nijjer et al., 2002) and currently is listed as one of the most invasive plants in the United States. Here we compared the seeds of native populations in China to those which are collected from reintroduced populations re-exposed to herbivory for 5 years to elucidate the changes in seed traits.

Materials And Methods

Seed collection

The Chinese tallow (*Triadica sebifera*, Euphorbiaceae) is a perennial tree grown for its oil and ornamental value in China, and there are more than 200 herbivorous insects depending on it (Zhang et al., 2015). In 2014, we collected seeds from 13 *T. sebifera* populations (Supplementary Table 1, Fig. 1b) across seven states in the United States and planted them in a natural environment in China (Yangjiafan Village, Sigu Town, Dawu County, Hubei province, 31°45'N, 114°39'E), which had subtropical monsoon climate,

uniform rainfall all year around, and annual average temperature between 14.9°C-15.7°C. We selected 10 trees per population and grew them freely under natural levels of herbivory at the site before collecting.

Between October 2019 and January 2020, we collected seeds from 30 native populations (Supplementary Table 1, Fig. 1a) across 10 provinces in China. Spanning most of the species' ranges, these populations often occurred in farmlands, roadsides and wastelands and they were at least 10 m apart from each other. During the same period, mature seeds were collected from the 13 populations reintroduced into China.

Seed Physical And Chemical Properties Test

T. sebifera seeds have a waxy coating, and seed masses were determined both with and without wax. Dewaxing simulates seeds condition that be fed and then be excreted to the outside of the body. Masses were obtained by 50 randomly selected seeds from all reintroduced and native populations. Seeds were soaked in laundry detergent to dissolve the wax on the surface, then air-dried for about 3 hours at room temperature prior to weighing. The dried seeds were deeply buried in fine sands and then placed in a refrigerator at 4°C for low temperature stratification for subsequent germination experiments.

We assayed compounds in seeds related to germination, including soluble protein, crude fat and hormones. We randomly selected one native population in each province (ten populations in total) and ten reintroduced populations of dewaxed seeds. After mixing, they were randomly divided into three parts as three replicates (2 origins * 10 populations * 3 index * 3 replicates = 180 samples), and then frozen them with liquid nitrogen. The frozen dewaxed seeds were pulverized using a mixer mill (MM400, Retsch, Laichi, Germany) with zirconia beads for 1.5 min at 30 Hz and stored at -80°C until needed. We used the Bradford method (Bradford, 1976) to determine soluble protein content and used the Soxhlet extraction method (Anderson, 2004) to detect crude fat.

According to seed hormones, we assayed 15 hormones from four hormone classes, including two abscisic acids, one ethylene precursor, ten kinds of gibberellins and two kinds of strigol (Supplementary Table 2). Using ultra-high performance liquid chromatography (UPLC, ExionLC™ AD) and Tandem Mass spectrometry (Tandem Mass L /MS /MS) (QTRAP® 6500+) to determine seed hormone types and content. Linear equations and correlation coefficients of the standard curves of the tested substances in this experiment are shown in Supplementary Table 4. Phytohormone contents were detected by MetWare (<http://www.metware.cn/>) based on the AB Sciex QTRAP 6500 LC-MS/MS platform.

Seed Germination Test

In August 2020, after 60 days of low temperature stratification, seeds were sown in a greenhouse (24°50'N, 102°52'E, Kunming, China) with 50–80% relative humidity, 13/11 h light/dark cycle, 30°C days, and 18°C nights. We sowed one seed per cell in 72-cell seedling trays for each of 36 populations (72 seeds * 36 populations = 2592 seeds). Each seedling tray was randomly placed on a greenhouse bed, and

the position of each seedling tray was randomly adjusted weekly. To water the seeds twice a day and record the germinational parameters every day which include the days to first germination, days to the first true leaf, days to 50% germination per population, the germinative force (calculated as n/N , this n is the total number of germinated seeds on the day when the number of newly germinated seeds reach its peak, with N being 72) and final germination rate. In addition, we conducted a separate germination experiment in a laboratory climate box (MGC-350BP, Shanghai TENSUC; relative humidity 50%-60%, 12/12h light/dark cycle, 28°C days, and 25°C nights).

Statistical analysis

We used one-way analysis of variance (ANOVA) when data were normally distributed and homoscedastic, and Wilcoxon rank sum tests to analyze differences between reintroduced and native populations in physical (with-wax and dewaxed seed masses) and chemical properties (soluble protein and crude fat), seed hormones levels (ABA, ACC, GA1, GA15, GA19, GA24, GA53, 5DS, GA:ABA), and germination parameters (days to first germination, days to the first true leaf, days to 50% germination, germinative force, and final germination rate). We also calculated the fold change (representing the ratio of the two groups) for each hormone, and selected those with fold change ≥ 2 and ≤ 0.5 as the final differential metabolites. We carried out Pearson correlation analyses between seed physical and chemical properties and germination traits of all *T. sebifera* populations.

All data were analyzed with R version 3.6.2 (R Core Team, 2020).

Results

Seed physical and chemical properties

There were no significant differences in physical and chemical properties mass of the with-wax ($F_{1, 39} = 2.873$, $P = 0.098$) and dewaxed seeds ($F_{1, 37} = 0.045$, $P = 0.833$) between reintroduced and native populations (Supplementary Table 3). Similarly, nor were their significant differences in crude fat content ($F_{1, 18} = 0.189$, $P = 0.669$) or soluble protein content ($F_{1, 18} = 0.13$, $P = 0.722$) (Supplementary Table 3).

Among the 15 hormones analyzed, seven were not detected in any population samples (Supplementary Table 2). Seeds from reintroduced populations had significantly higher levels of ABA ($P < 0.001$), GA53 ($P < 0.001$), GA24 ($P < 0.001$), and GA19 ($P < 0.01$), while native populations had higher levels of ACC ($P < 0.05$), GA1 ($P < 0.01$) (Fig. 2a), and TGA : ABA (Fig. 2b). Levels of GA15 and 5DS were no significant differences. Reintroduced populations had ≥ 2 -fold more GA19, GA24, and GA53 contents than native populations.

Seed Germination Traits

There were no significant differences between reintroduced and native populations in final germination rate ($F_{1, 28} = 0.003$, $P = 0.958$), days to first germination ($F_{1, 28} = 0.045$, $P = 0.834$), days to 50% germination ($W = 40.5$, $P = 0.4752$), days to first true leaves ($F_{1, 32} = 0.168$, $P = 0.684$), or germinative force ($W = 77$, $P = 0.7508$) (Supplementary Table 3). The germination results in the climate box were consistent with the greenhouse germination experiment. There was no significant difference between the germination rate of the reintroduced and native populations ($W = 67.5$, $P = 0.9137$) (Supplementary Table 3).

Seed Mass And Germination Correlation Analysis

There were significant positive correlations between seed mass and germination in germination rate ($R = 0.6$, $P = 0.00065$) (Fig. 3a) and germinative force ($R = 0.41$, $P = 0.028$) (Fig. 3b). In addition, there was significant negative correlation between seed mass and days to 50% germination ($R = -0.47$, $P = 0.0094$) (Fig. 3c). But there was no significant correlation between seed mass and days to first germination ($R = -0.34$, $P = 0.072$) (Fig. 3d).

The Principal Component Analysis

The first PC axis explained 24.91% of the variation and the second PC axis explained 18.07%, resulting in 42.98% of the total variation explained in the dataset by the first two principal components (Supplementary Table 4). The first axis was influenced predominantly by germination traits (days to first true leaves, days to 50% germination, germination rate, and germinative force), whereas the second axis was influenced primarily by ACC, crude fat, and 5DS (Fig. 4). The dewaxed mass and total gibberellins of seeds were positively correlated with germination rate and germinative force, and negatively correlated with the days to first germination, days to 50% germination, and days to first true leaves. The correlation between abscisic acid and germination traits was opposite to dewaxed mass and total gibberellins, and abscisic acid was negatively correlated with total gibberellins. TGA : ABA and 5-Deoxystrigol were negatively correlated with the days to first germination, days to 50% germination, and days to first true leaves. ACC were negatively correlated with germination rate and germination force. Crude fat was negatively correlated with soluble protein.

Discussion

In this experiment, we found that there were significant correlations between seed mass and germination. The more mass, the better germination. This accorded with our common sense that more mass could offer more energy and nutrition to support for the seed germination process. In addition, the results showed that the levels of abscisic acid (ABA) and three gibberellins (GAs) of Chinese tallow seeds were significantly higher in reintroduced populations than native populations, while the levels of 1-aminocyclopropanecarboxylic acid (ACC) and GA (TGA) : ABA were significantly lower than those of native populations. The ABA typically inhibits seed germination (Nonogaki, 2014) and the TGA : ABA ratio also

affects seed dormancy (William and Gerhard, 2006), but generally there were no significant differences in germination between reintroduced and native populations in this experiment. Similarly, there were no significant differences in physical and chemical properties of seeds between reintroduced and native populations. Consequently, we found that no significant differences in seeds of reintroduced *T. sebifera* populations when they from US returns to their provenance for five years than native *T. sebifera* populations. Our results were contrary to our original hypothesis.

The naturalized populations for five years were that reintroduced populations. In terms of the seed levels, after a period of time, their physical, chemical characteristics and germination characteristics will not be significantly different from the native populations, because they diverted part of their growth or reproductive resources to defense resource, reducing the germination advantages enhanced by invasion. According to the evolution of increased competitive ability (EICA) hypothesis suggests that *T. sebifera* populations invaded the United States were able to allocate large amounts of resources to growth or reproduction because they faced less feeding pressure (Blossey and Nötzold, 1995). When the invasive *T. sebifera* populations were reintroduced to China, they will again be predated by a large number of specialist and general insects, and they will take some time for the defensive resource allocation to recover to a defense level similar to that of the native populations. This explains that the seed germination performance has no longer advantage.

Many studies have shown that the seeds of invasive populations germinate faster than native populations, or that they can germinate under broader conditions (Leiblein et al., 2014; Udo et al., 2017; Hirsch et al., 2012). In contrast, native populations of *T. sebifera* germinate at higher rates than invasive populations, in both native and invasive common gardens (Zhang, et al., 2020). Our research is consistent with Zhang and provides evidence on resource allocation strategies and reproductive changes of invasive plants that have experienced ecological release for multiple generations following successful invasion of another environment, which may help us understand invasion mechanisms and plan management of *T. sebifera* and other invasive plants that reproduce by seeds.

Conclusion

In this experiment, we found that the more mass, the better germination. In addition, the results showed that the levels of abscisic acid (ABA) and three gibberellins (GAs) of Chinese tallow seeds were significantly higher in reintroduced populations than native populations. But there were no significant differences in physical and chemical properties of seeds and germination performance between reintroduced and native populations. Hence, these results suggested that no significant differences in seeds of reintroduced *Triadica sebifera* populations when they from the United States return to provenance for five years, which could enrich our poor cognition about seed properties changes after experiencing different environments and were beneficial to control invasive plants.

Declarations

Supplementary Data

Table S1: Seed collection information for the 43 *Triadica sebifera* populations used in this study. Populations selected for tests of crude fat, soluble protein, and phytohormones are in bold.

Table S2: Seed hormones tested in this experiment and the number of samples detected by each indicator (N).

Table S3: One-way ANOVO and Wilcoxon rank sum test results.

Table S4: Principal component analysis results.

Author contributions YLL, YTX, and YW planned and designed the research. YLL, YTX and ZLP collected the data and analyzed the data. YLL, CNW and JRJ interpreted the results and wrote the manuscript. All authors contributed critically to the drafts.

Funding The study was supported by National Natural Science Foundation of China (32101414, U2102218) and the National Key Research and Development Program of China (2022YFC2601100).

Declarations The authors declare that there is no conflict of interest.

References

1. Adawy TE, Rhma EE, Bedawey AA, et al. (2003) Nutritional potential and functional properties of germinated mung bean, pea and lentil seeds. *Plant Foods for Human Nutrition* 5:8-13.
2. Agrawal AA, Hastings AP, Bradburd GS, et al. (2015) Evolution of plant growth and defense in a continental introduction. *American Naturalist* 186:E1-E15.
3. Alexander JM, Edwards PJ, Poll M, et al. (2009) Establishment of parallel altitudinal clines in traits of native and introduced forbs. *Ecology* 90:612-622.
4. Anderson S (2004) Soxtec: its principles and applications. In Luthria DL (ed). *Oil Extraction and Analysis—Critical Issue and Comparative Studies*. Champaign, IL: AOCS Press 11–24.
5. Bhatt AK, Bhalla TC, Agrawal HO, et al. (1989) Effect of seed size on protein and lipid contents, germination and imbibition in true potato seeds. *Potato Research* 32:477-481.
6. Blackburn TM, Pyšek P, Bacher S, et al. (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26(7):333-339.
7. Blossey B and Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. *Journal of Ecology* 83(5): 887-889.
8. Bradford M (1976) A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principles of protein dye binding. *Analytical Biochemistry* 72:248-254.
9. Bruce KA, Cameron GN, Harcombe PA, et al. (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum*(L.) Roxb. *Natural Areas*

Journal 17:255–260.

10. Castillo JM, Grewell BJ, Pickart A, et al. (2014) Phenotypic plasticity of invasive *Spartina densiflora* (Poaceae) along a broad latitudinal gradient on the Pacific Coast of North America. *American Journal of Botany* 101:448-458.
11. Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* 342:364-366.
12. Daws MI, Hall J, Flynn S, et al. (2007) Do invasive species have bigger seeds? Evidence from intra and inter specific comparisons. *South African Journal of Botany* 73:138-143.
13. Elamrani A, Raymondand P, Saglio P. (1992) Nature and utilization of seed reserves during germination and heterotrophic growth of young sugar beet seedlings. *Seed Science Research* 2:1-8.
14. Ferreras AE and Galetto L (2010) From seed production to seedling establishment: important steps in an invasive process. *Acta Oecol* 36:211–8.
15. Gioria M and Pyšek P (2017) Early bird catches the worm: germination as a critical step in plant invasion. *Biological Invasions* 19: 1-26.
16. Hirsch H, Wypior C, Wehrden HV, et al. (2012) Germination performance of native and non-native *Ulmus pumila* populations. *Neobiota* 15:53-68.
17. Huberty M, Tielboerger K, Harvey JA, et al. (2014) Chemical defenses (glucosinolates) of native and invasive populations of the range expanding invasive plant *Rorippa austriaca*. *Journal of Chemical Ecology* 40:363-370.
18. Leiblein WMC, Kaviani R and Tackenberg O. (2014) Germination and seedling frost tolerance differ between the native and invasive range in common ragweed. *Oecologia* 174:739-750.
19. Liu W, Maung DK, Strong D R, et al. (2016) Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. *Journal of Ecology* 104:173-181.
20. Liu, C., et al. (2020). "Most invasive species largely conserve their climatic niche." *Proc Natl Acad Sci U S A* 117(38): 23643-23651.
21. Mtambalika K, Munthali C, Gondwe D, et al. (2014) Effect of seed size of *Azelia quanzensis* on germination and seedling growth . *International Journal of Forestry Research* 2014:1-5.
22. Nijjer S, Lankau RA, Rogers WE et al. (2002) Effects of temperature and light on Chinese tallow (*Sapium sebiferum*) and Texas sugarberry(*Celtis laevigata*). *The Journal of Science* 54:63-68.
23. Nonogaki H (2014) Seed dormancy and germination-emerging mechanisms and new hypotheses. *Frontiers in Plant Science* 5:233.
24. Pal RW, Maron JL, Nagy DU, et al. (2020) What happens in Europe stays in Europe: apparent evolution by an invader does not help at home. *Ecology* 101(8):e03072.
25. Sakata Y, Craig TP, Itami JK, et al. (2017) Parallel environmental factors drive variation in insect density and plant resistance in the native and invaded ranges. *Ecology* 98:2873-2884.
26. Suárez VE, Sampedro L and Zas R (2017) Is the benefit of larger seed provisioning on seedling performance greater under abiotic stress? *Environmental & Experimental Botany* 134:45-53.

27. Suda CNK and Giorgini JF (2000) Seed reserve composition and mobilization during germination and initial seedling development of *Euphorbia heterophylla*. *Brazilian Journal of Plant Physiology* 12:226-245.
28. Sun Y and George K (2019) Rapid evolution of invasive traits facilitates the invasion of common ragweed, *Ambrosia artemisiifolia*. *Journal of Ecology* 107:2673-2687.
29. Udo N, Tarayre M and Atlan A (2017) Evolution of germination strategy in the invasive species *Ulex europaeus*. *Journal of Plant Ecology* 10:375-385.
30. Widmer T, Guermache F, Dolgovskaia M, et al. (2007) Enhanced Growth and Seed Properties in Introduced vs. Native Populations of Yellow Starthistle (*Centaurea solstitialis*). *Weed Science* 55(5):465-473.
31. William EFS and Gerhard LM (2006) Seed dormancy and the control of germination. *New Phytologist* 171(3):501-523.
32. Xiao L, Herve´ MR, Carrillo J, et al. (2018) Latitudinal trends in growth, reproduction and defense of an invasive plant. *Biological Invasions* 21(1):189-201.
33. Zhang JL, Siemann E, Tian BL, et al. (2020) Differences in seed properties and germination between native and introduced populations of *Triadica sebifera*. *Journal of Plant Ecology* 13:70-77.
34. Zhang JL, Wang Y, Ding JQ (2015) List of Chinese tallow tree pests. *Chinese Forest Diseases and Insects* 34(05):25-35.
35. Zhang JL (2019) The effect of reproduction mode and environmental stress on the reproduction input of invasive plants. University of Chinese Academy of Sciences (Wuhan Botanical Garden, Chinese Academy of Science).

Figures

Figure 1: *Triadica sebifera* seed collection locations in the native (a, filled circle) and invasive (b, green area) ranges.

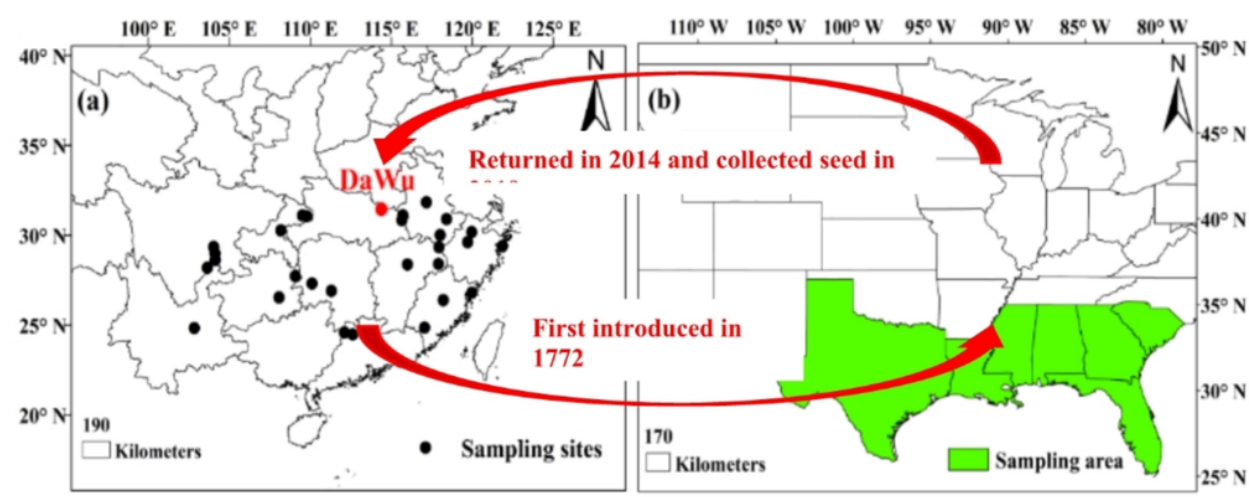


Figure 1

Triadica sebifera seed collection locations in the native (a, filled circle) and invasive (b, green area) ranges.

Figure 2: (a) Phytohormone and (b) TGA : ABA of *Triadica sebifera* seeds collected from reintroduced (US, white) and native (China, black) ranges. Populations selected for phytohormone testing are given in Supplementary Table 1. Means $\pm$ 1 SE are shown. Differences between the reintroduced and native ranges were determined by one-way ANOVO or Wilcoxon rank sum test (P<0.05, “*”; P<0.01, “**”; P<0.001, “***”).

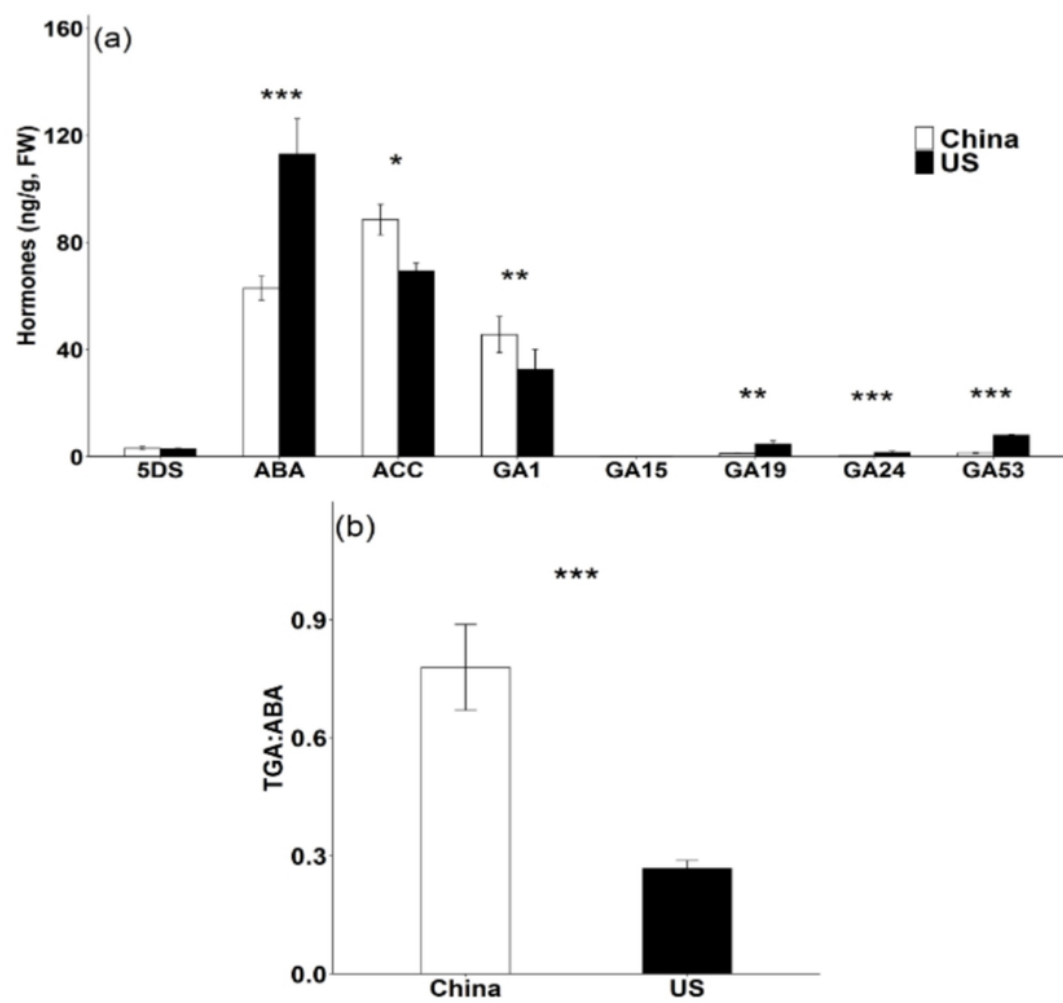


Figure 2

See image above for figure legend

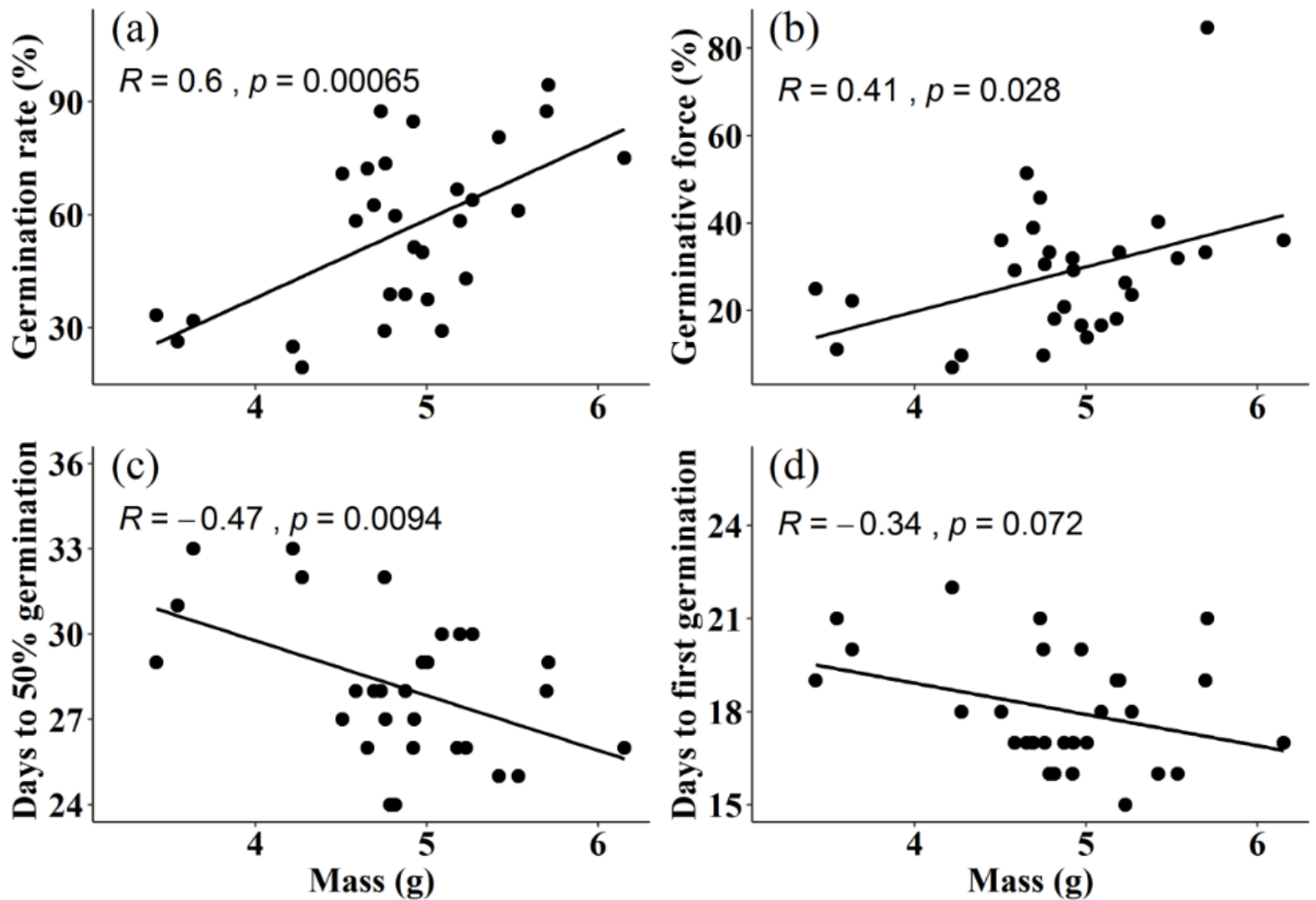


Figure 3

Relationships between germination traits and dewaxed mass for all *Triadica sebiferapopulations*: (a) germination rate, (b) germinative force, (c) days to 50% germination, (d) days to first germination; The R and P value are from Pearson correlation analysis, solid lines represent linear correlations.

PCA - scaling 2

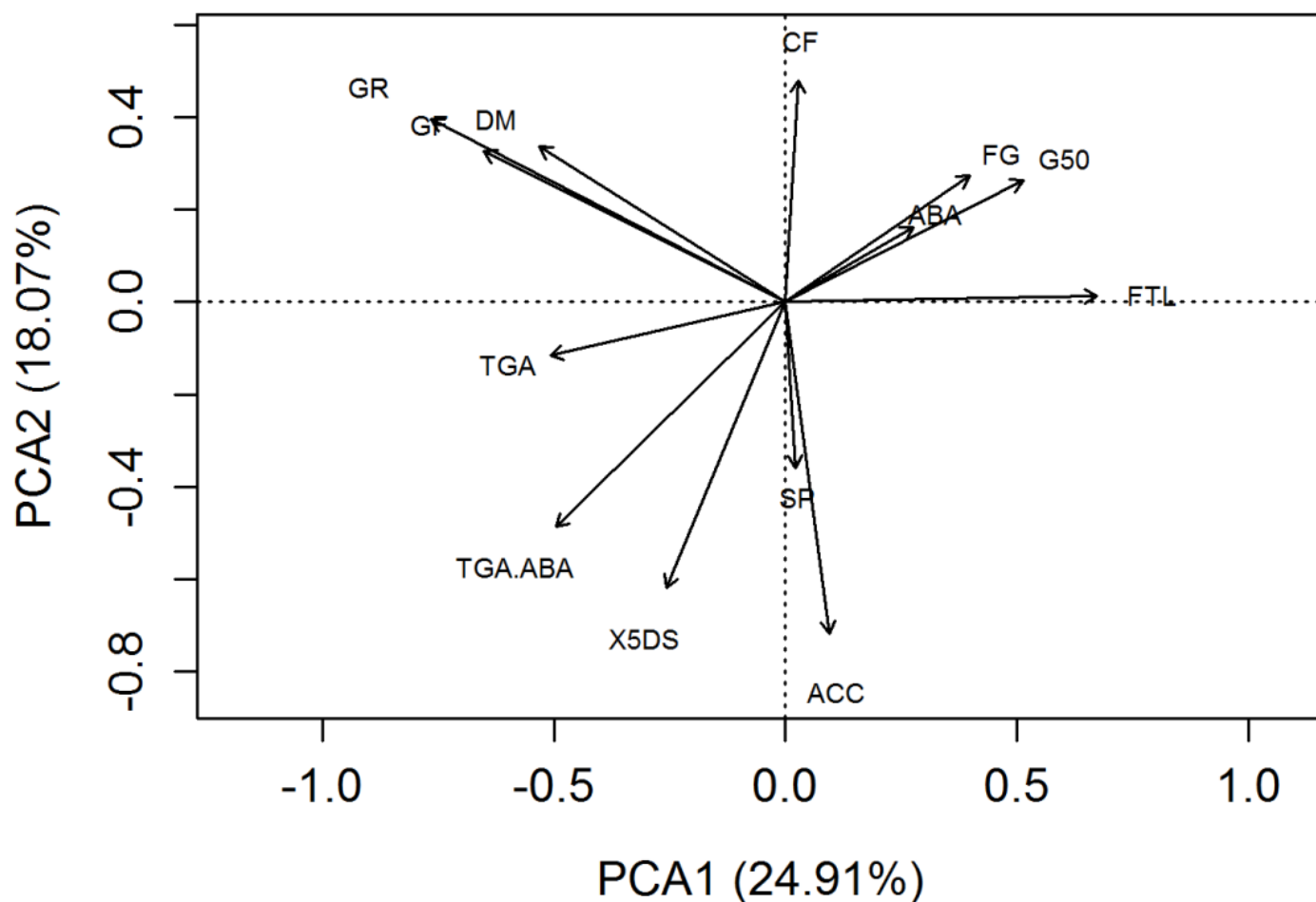


Figure 4

First two principal components and the loadings of seed physical properties, chemical properties, and germination traits. Dewaxed mass (DM), crude fat (CF) soluble protein (SP), total gibberellins (TGA), abscisic acid (ABA), TGA : ABA, l-aminocyclopropane-l-carboxylic acid (ACC), 5-Deoxystriol (X5DS), germination rate (GR), days to 50% germination (G50), days to first germination (FG), days to first true leaves (FTL), and germinative force (GF).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryData.docx](#)