DO LEAF FUNCTIONAL TRAITS DIFFER BETWEEN 20–35-YEAR-OLD TRANSPLANTED AND WILD SOURCE POPULATIONS? A CASE STUDY INVOLVING FIVE ENDANGERED TREE SPECIES

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Conservation of threatened species through translocation has become an effective way to combat species extinction worldwide. Plant functional traits are good predictors of plant performance and can reflect the adaptation strategies of plants to the environment. However, it is still unclear whether transplanted populations have comparable levels of leaf functional traits to their wild source populations. To assess the effectiveness of conservation-based translocation of long-living endangered tree species, we investigated the long-term (20–35 years) population dynamics of five co-existing endangered tree species (*Davidia involucrata*, *Dipteronia sinensis*, *Pterostyrax psilophyllus*, *Tapiscia sinensis*, and *Tetracentron sinense*) in transplanted populations, and compared the leaf functional traits between the transplanted and their wild source populations. We found that the survival rates of the five species in the transplanted populations ranged from 42.86% to 73.81%, and most of these species could blossom and yield fruit. All species had significant differences in some leaf functional traits between transplanted and wild populations. The intraspecific traits variation of some species in the transplanted populations was decreased compared with that in the wild populations on the whole. We conclude that after a long period of translocation, these species in transplanted populations were able to grow normally and most species become more efficient in resource acquisition or utilisation and more resources were available for growth. However, the intraspecific traits variation of some species in transplanted populations may lead to competitive exclusion, affect species coexistence, and thus affect their performance.

Key words: conservation-based translocation, intraspecific trait variation, long-living tree species, long-term monitoring, population dynamics

Introduction

The rate of extinction caused by human activities is approximately 1000 times the rate of environmental background extinction, and the rate of extinction will continue to rise in the future (Dirzo & Raven, 2003; Pimm et al., 2014). At present, approximately 20% of plants are at risk of extinction, and since plants are crucial to the maintenance of ecological processes and the survival of life (Newton, 2008), the conservation of plants becomes extremely urgent. Conservation of threatened species by transplanting them to new, safe locations has become an effective way to address the worldwide extinction of endangered plant species (Havens et al., 2006; Mounce et al., 2017), and now, it may be a major approach for ensuring their long-term survival (Oldfield, 2009).

However, when plants were transplanted to a new habitat, they may exhibit maladaptation due to the change in selection pressure, such as climate, soil, and competition (e.g. Ensslin et al., 2015; Cho et al., 2019). Therefore, long-term monitoring of the transplanted population is needed. One criterion for the success of translocation is the formation of a self-sustaining and self-renewing population (Griffith et al., 1989; Reiter et al., 2016). So, we need to monitor the population dynamics and life history of transplanted populations, such as survival and reproduction, to evaluate the effectiveness of translocation (Ren et al., 2016; Izuddin et al., 2018). Current studies about the population monitoring are mainly focusing on herbs or shrubs with relatively short growth cycles (Wendelberger et al., 2008; Gomes et al., 2018), but monitoring the long-term population dynamics of trees species under transplanted conservation are still scarce.

Plant functional traits are a series of physiological and ecological indicators closely related to their survival, growth and reproduction (Ackerly, 2004; Violle et al., 2007), and they are useful predictors of plant performance (Westoby et al., 2002; Poorter & Bongers, 2006). For instance, species with high traits value of specific leaf area (SLA) and leaf nitrogen content (LNC), tend to have higher individual growth and fecundity (Adler et al., 2014). When transplanted to a new habitat, plants may cope with the changes through the plasticity of leaf functional traits (Agrawal, 2001; Zhu et al., 2020). Therefore, comparison of leaf functional traits between transplanted and wild collections may useful to reflect the plant performance and adaptation strategies on the translocation site.

Intraspecific trait variation is a major component of biodiversity (Mimura et al., 2017). Populations with higher trait variation are more stable and better able to adapt to rapid changes in the environment (Albert et al., 2011). A study on intraspecific trait variation of invasive species showed that the higher variation of intraspecific traits was related to the stronger resource utilisation ability (Heberling et al., 2016). Therefore, it is useful to determine whether transplanted populations harbour similar levels of intraspecific trait variation to their wild source populations. However, current studies about the comparison of phenotypic traits between transplanted and wild populations have mainly focused on herbs with relatively short growth cycles (Cho et al., 2019; Rauschkolb et al., 2019; Ensslin & Godefroid, 2020), studies on long-living tree species are still scarce (Li et al., 2012).

Since the 1980s, the Jiugongshan National Nature Reserve has undertaken the conservation-based translocation of endangered plants within and around central China (Wang et al., 1988; Ye et al., 2000). More than 30 endangered species have been transplanted here for conservation. In this study, we investigated the population dynamics of five dominant endangered tree species (*Davidia involucrata* Baill., *Dipteronia sinensis* Oliv., *Pterostyrax psilophyllus* Diels ex Perkins, *Tapiscia sinensis* Oliv., and *Tetracentron sinense* Oliv.) approximately 20–35 years after their establishment on the translocation site, and compared leaf functional traits between transplanted and wild populations, to assess the conservation effectiveness of long-living endangered tree species. Specifically, we put forth the following questions: 1) What are the survival and reproductive statuses of the five endangered tree species after 20–35 years of translocation? 2) Do leaf functional traits differ between transplanted and wild source populations of the five endangered tree species after a long-term translocation?

Material and Methods

Study sites

This study was carried out at the Houhe National Nature Reserve (Wild site; 30.071833° N, 110.542753° E) and the Jiugongshan National Nature Reserve (Translocation site; 29.364911° N, 114.568081° E) (Fig. 1). The two regions have similar climates, with a subtropical monsoon climate. The mean annual temperature and precipitation of these two sites are 11.5 °C and 1776 mm, and 10 °C and 1512 mm, respectively (Table 1).

The Houhe National Nature Reserve is located in Wufeng Tujia Autonomous County, in the southwest of Hubei Province, China. There exists a special type of plant community, in which a variety of ancient, relict, and endangered plants naturally grow together. These endangered species have survived from a long-term natural selection, in addition to the unique environmental conditions; the overall advantage of the special community composition may also be an important reason. Inspired by this, Ye et al. (2000) proposed the idea of simulating plant communities to protect endangered plants at translocation sites, and put it into practice in Jiugongshan National Nature Reserve.

The Jiugongshan National Nature Reserve is located in Tongshan County, in the southeast of Hubei Province, China. The conservation-based translocation of endangered species has been carried out here since 1986. Seedlings of endangered species were first transplanted in 1986 and again in 1997. A total of 35 species of endangered plants are preserved there, covering an area of 3000 m^2. The species distribution pattern was referenced to the community at the wild site, and the plant arrangement and density in transplantation sites was designed according to the actual distribution status in the wild site. The five endangered tree species often appeared in the same community as dominant species or co-dominant species, according to the number of individuals of each species in the wild community, we designed the transplant number of each species ranged from 20 to 70. The total density of trees in the wild community was 0.22 trees/m^2, so the plant row spacing was designed 2–4 m in transplanted site (Ye et al., 2000).

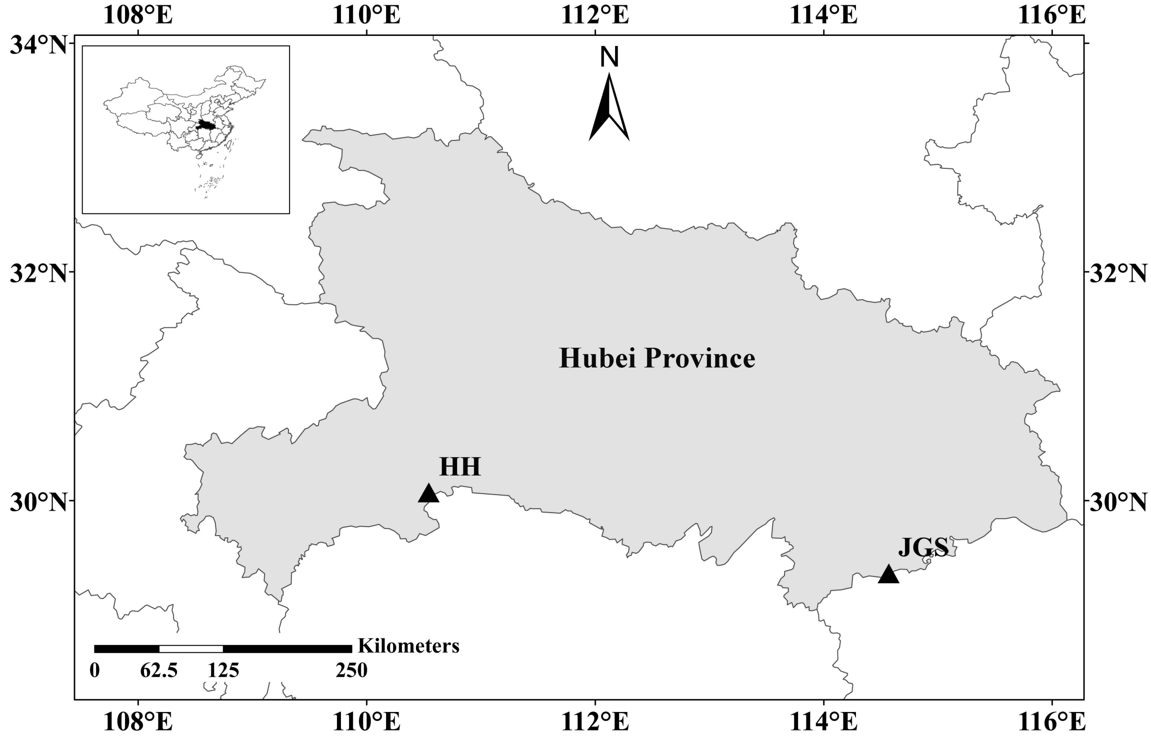

Fig. 1. Location of the two study sites, namely Houhe National Nature Reserve (HH), Jiugongshan National Nature Reserve (JGS), China.

Table 1. Climate and soil condition of the two study sites

Site	Population	MAT (°C)*	MAP (mm)*	Soil C (mg/g)	Soil N (mg/g)	Soil P (mg/g)	Soil C:N
Houhe	Wild	10.0	1512	97.34 ± 52.04a	7.55 ± 3.16a	0.70 ± 0.19a	9.26 ± 1.78a
Jiugongshan	Transplanted	11.5	1776	69.41 ± 7.48a	6.46 ± 0.63a	0.59 ± 0.06a	10.71 ± 0.19a

Note: * – Climate data were obtained from the global climate database (WorldClim, http://www.worldclim.org/). The same lowercase letter (a) indicates that there was no significant difference in soil element content between the two study sites.

Study species

We selected five endangered species in the community as the study subjects, namely *Davidia involucrata*, *Dipteronia sinensis*, *Pterostyrax psilophyllus*, *Tapiscia sinensis*, and *Tetracentron sinense* (Table 2). All these five species are deciduous trees or small trees that are endemic to China or East Asia. Among them, *Davidia involucrata*, *T. sinensis*, and *T. sinense* are tertiary relict species. The five species are mainly distributed in moist evergreen deciduous broad-leaved mixed forests or evergreen broad-leaved forests in the subtropical mountains. The main threats to these species are human disturbance or poor natural regeneration, or both. At present, *D. involucrata* and *T. sinense* are classified as national key protected wild plants in China. *Pterostyrax psilophyllus* and *D. sinensis* are listed as vulnerable and rare species, respectively, according to the China Plant Red Data Book (Fu & Jin, 1992).

Population survey and data collection

We collated the population dynamics data during the period of translocation conservation from the original records of retired colleagues and our field investigations. Data between 1987 and 2001 were obtained from previous records, except that the data for the year 2000 were missing. Data in 2017 were obtained by field investigation, while the data from 2002 to 2016 were missing or incomplete. Finally, we obtained fifteen survey datasets for *Davidia involucrata*, *Pterostyrax psilophyllus*, *Tapiscia sinensis* and *Tetracentron sinense* with a span of 31 years and five survey datasets for *Dipteronia sinensis* with a span of 21 years. From June 2017 to August 2018, we investigated the number of survivors and the flowering, fruiting, and regeneration statuses of the five endangered tree species in transplanted populations. The survival rate is the ratio of the current survival number to the original cultivated number of each species. The current survival number was recorded during the field investigation in 2017 and the original cultivated number were obtained from previous records.

Sample collection and trait measurements

In August 2018, leaf and soil samples were collected in both the transplanted and wild populations. Five individuals of each species were randomly selected from both transplanted and wild populations (Table 2). Thirty healthy, intact and fully matured leaves were collected from the sun-exposed branches of each individual. The positions (i.e. aspect and height) of the sampled leaves are similar for transplanted and wild populations. In order to avoid the decrease of leaf fresh mass during the daytime by the vigorous transpiration, all leaf samples were collected in the morning. Finally, we collected a total of 1500 leaf samples from 50 individuals from the transplanted and wild populations. Leaf fresh masses were measured in the field, and then leaf samples were stored separately and immediately brought back to the laboratory. Soil sample collections were performed using a five-point sampling method, and the surface soil (0–30 cm) was collected after the removal of litter. As the five species grow together in both the transplanted and wild populations, three soil samples were randomly taken from each site and returned to the laboratory.

Leaf samples were scanned separately using a colour image scanner (CanoScan LiDE 110), and the images were used to measure the leaf length, width and leaf area. Then they were placed in an oven, dried at 60 °C to a constant weight, and used for the measurement of the leaf dry mass. Soil samples were air-dried to a constant weight. All samples were ground and sieved through a 100-mesh sieve to determine the element content of nitrogen and phosphorus.

The fresh and dry masses of leaf samples were determined with an electronic balance that was accurate to 0.001 g. The leaf area was measured by using «Digimizer» (https://www.digimizer.com/). The SLA was calculated as the one-sided leaf area per leaf dry mass, expressed as $m^2 \times kg^{-1}$. The leaf dry matter content (LDMC) was calculated as the ratio of the leaf dry mass to the leaf fresh mass, expressed as $mg \times g^{-1}$. LNC, soil C and soil N were measured with an elemental analyser (Vario EL cube), and leaf phosphorus content (LPC) and soil P were measured via the molybdenum-antimony anti-spectrophotometric method (UV-755B).

Data analysis

An independent-samples *t*-test was used to compare the mean values of leaf functional traits between transplanted and wild populations. All data were LN- or SQRT-transformed to satisfy the normality and homogeneity of residuals. Data analysis and mapping were performed using SPSS 21.0 (IBM, Armonk, NY, USA) and Origin 8.5 (OriginLab, Northampton, USA).

Results

Soil factors

There was no significant difference in soil C, N and P contents between the wild and translocation site ($p > 0.05$). The range of soil C and N contents of the wild site is higher than on the transplanted site, but there was no significant difference in Soil C:N ratio between wild and transplanted site ($p > 0.05$) (Table 1).

Population dynamics and reproductive status

From 1987 to 2017, the overall population dynamics of the five endangered species at the translocation site fluctuated in the early stages of transplantation, then decreased and gradually became stable in the later stage (Fig. 2). However, the population of *Tetracentron sinense* declined only after the second planting, while it increased during the first five years after the first planting, caused by continuous artificial replant.

The final survival rates of the five species on the translocation site ranged from 42.86% to 73.81%. All surviving individuals could grow normally. Apart from *Tetracentron sinense*, blooming and fruiting have been observed in all the other four species. In addition, *Pterostyrax psilophyllus* seedlings were observed near its large trees (Table 2).

Table 2. Characteristics, survival rate (transplanted population), and sample size of the five endangered species

Species	Family	Endangered category	Endemic	Reproductive status	Survival rate (%)	Sample size	
						Wild	Transplanted
Davidia involucrata	Nyssaceae	Rare	China	Flower and fruit	42.86	5	5
Dipteronia sinensis	Aceraceae	Rare	China	Flower and fruit	73.81	5	5
Pterostyrax psilophyllus	Styracaceae	Vulnerable	East Asia	Flower, fruit and seedling	56.25	5	5
Tapiscia sinensis	Staphyleaceae	Rare	China	Flower and fruit	67.67	5	5
Tetracentron sinense	Tetracentraceae	Rare	East Asia	Vegetative growth	55.56	5	5

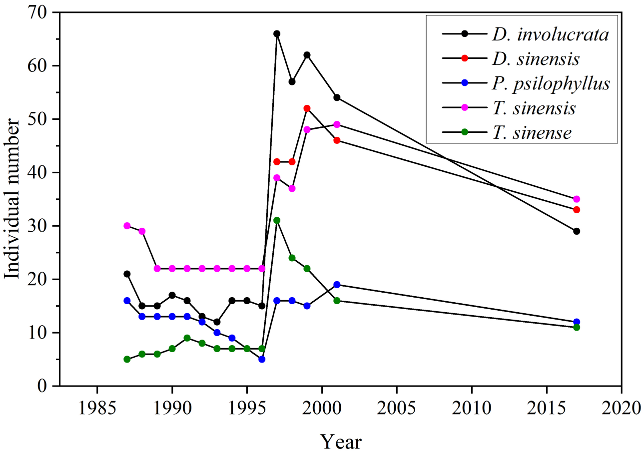

Fig. 2. Population dynamics of the five endangered tree species in transplanted populations from 1987 to 2017.

Leaf functional traits

We found that all species had significant differences in some leaf functional traits between transplanted and wild populations (Fig. 3). *Dipteronia sinensis* showed a significantly lower SLA ($p < 0.05$) but significantly higher LDMC ($p < 0.01$) in the transplanted population, while both *Pterostyrax psilophyllus* and *Tapiscia sinensis* had a significantly higher SLA ($p < 0.05$) in transplanted populations. *Davidia involucrata* and *Tetracentron sinense* had significantly higher LNC ($p < 0.05$) and LPC ($p < 0.01$ or $p < 0.05$) in transplanted populations than in the wild populations. Compared with the wild population, the LNC and/or LPC values of the five species were all changed significantly in the transplanted population ($p < 0.01$ or $p < 0.05$). However, there was no significant difference in leaf N:P ($p > 0.05$) between transplanted and wild populations except *T. sinensis* ($p < 0.01$). There was no significant difference in leaf area between the transplanted and wild populations ($p > 0.05$) either.

Intraspecific trait variation

We found the changes in intraspecific trait variation between wild and transplanted populations were different among species. The trait CV-values of the five tree species were ranged from 0.49% to 12.79% in the transplanted population and 0.98% to 13.95% in the wild populations. Intraspecific traits variation of *Davidia involucrata* and *Pterostyrax psilophyllus* in the transplanted populations was similar or decreased compared with that in the wild populations. Compared with wild populations, *Dipteronia sinensis* and *Tapiscia sinensis* showed higher CV-values only in LPC and leaf N:P, and *Tetracentron sinense* showed higher CV-values in leaf area, SLA and LDMC in the transplanted populations (Fig. 4).

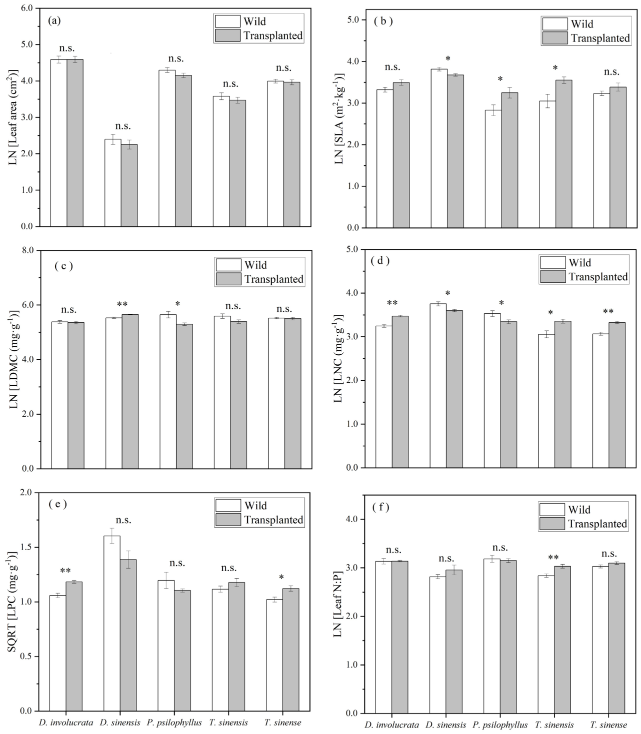

Fig. 3. Mean values (± SE) of leaf functional traits of the five endangered tree species in the transplanted and wild populations. Designations: SLA – specific leaf area; LDMC – leaf dry matter content; LNC – leaf nitrogen content; LPN – leaf phosphorus content; *p*-value designations: * – $p \leq 0.05$; ** – $p \leq 0.01$; n.s. – not significant.

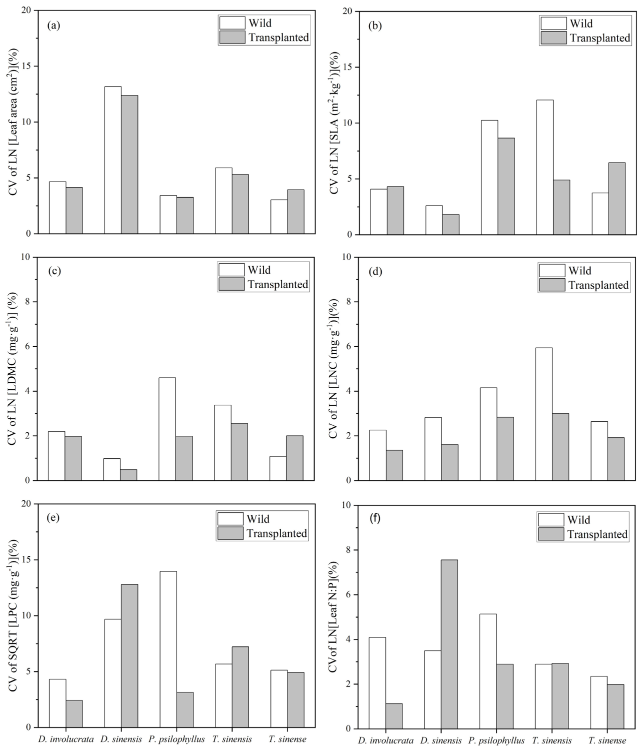

Fig. 4. Coefficients of variation of the functional traits of the five endangered tree species in the transplanted and wild populations. Designations: SLA – specific leaf area; LDMC – leaf dry matter content; LNC – leaf nitrogen content; LPN – leaf phosphorus content; CV – coefficient of variation.

Discussion

Population dynamics and reproductive statuses

A high survival rate is important for species to become established and persist in new environments (Wendelberger et al., 2008; Gomes et al., 2018). According to the standard of Román-Dañobeytia et al. (2012), the survival rate of *Davidia involucrata* (42.86%) can be classified as «moderate» (26–50%), and the other four species (56.25–73.81%) can be classified as «good» (51–75%). The relatively high survival rates observed in our study can be explained by the climate similarity theory (Mayr, 1906) because the two sites are both located in subtropical areas of China with similar climate and soil conditions (Table 1).

One criterion for the success of translocation is the formation of a self-sustaining and self-renewing population (Griffith et al., 1989; Reiter et al., 2016). In our study, after a long period of translocation, *Pterostyrax psilophyllus* could produce naturally regenerated seedlings, while *Davidia involucrata*, *Dipteronia sinensis* and *Tapiscia sinensis* were only able to blossom and yield fruit, basically meeting the «from seed to seed» criteria for successful conservation (He, 2002). *Tetracentron sinense* could grow normally, but no flowers or fruit was observed on this species. Two potential explanations for this disparity are proposed. First, the cultivation time (20–35 years) was not long enough for some species to become mature. For example, *D. involucrata* usually requires 30–40 years to blossom and produce fruit. Secondly, a high rate of self and low viability of seeds in transplanted populations with small population sizes (Fig. 2).

Changes in leaf functional traits

In our study, *Pterostyrax psilophyllus* and *Tapiscia sinensis* had a higher SLA in transplanted populations compared to the wild ones. *Davidia involucrata* and *Tetracentron sinense* had a higher LNC and LPC in transplanted compared to the wild population. However, the SLA, LNC, and LPC of *Dipteronia sinensis* were all lower or similar in transplanted compared to the wild population. The SLA is positively correlated with relative growth rates. The LNC tends to be closely correlated with photosynthetic rate, and the LNC and LPC are often correlated with each other (Pérez-Harguindeguy et al., 2013). Thus, the results indicated that the efficiency of resource acquisition or utilisation of all species expect *D. sinensis* in transplanted populations increased and more resources were available for growth (Aerts & Chapin, 2000; Vance et al., 2003; Adler et al., 2014). This may be due to the reduction of interspecific competition in the transplanted populations, because only endangered species were transplanted there, the number of species decreased in the translocation site (Plein et al., 2016).

However, *Dipteronia sinensis* presented the opposite trend with a lower SLA, LNC and a higher LDMC in the transplanted population. The LDMC can represent the proportion of resources invested in these structures, and plants with a higher LDMC are more resistant to physical damage (Cornelissen et al., 2003). That is, the investment in growth decreased while the investment in structure increased, which may be due to the increased intraspecific competition (Rolhauser et al., 2019). On the wild site, there are many species of Aceraceae in the endangered species community, but most of them are non-endangered species. Thus, when simulated the community in the translocation site, a large number of the endangered species *D. sinensis* was transplanted to the translocation site to serve as the main substitute of Aceraceae species (Ye et al., 2000). The large individual number of the same species, *D. sinensis*, may contribute to an intense interspecies competition on the translocation site. Therefore, we should pay attention to the number of species and individuals in the future translocation.

It was worth noting that although all species showed a significant difference in the LNC and/or LPC values between transplanted and wild populations, there was no significant difference in leaf N:P except for *Tapiscia sinensis*. According to the homeostasis hypothesis, the relatively active plant organs need to maintain a certain nutrient level to ensure the material production and energy utilisation efficiency (Zhang et al., 2018). Therefore, most of these species still maintained their original nitrogen and phosphorus homeostasis on the translocation site, which may be due to the similar community structure and microhabitat to that on the wild site.

Changes in intraspecific trait variation

Intraspecific trait variation can enhance plant resistance to environmental changes and conducive to species co-existence (Carlucci et al., 2015). The intraspecific variation in certain traits of *Dipteronia sinensis*, *Tapiscia sinensis* and *Tetracentron sinense* was different. *Dipteronia sinensis* and *T. sinensis* showed lower CV-values in leaf area, SLA, LDMC and LNC, but higher ones in LPC and leaf N:P, while *T. sinense* showed lower CV-values in LNC, LPC and leaf N:P, but higher ones in leaf area, SLA and LDMC, in the transplanted population than in the wild population. That may be due to the different heterogeneity of light and soil condition of different species on the wild and the translocation site (Boucher et al., 2013).

However, the habitat filter causes the functional traits of plants to become more similar, which will lead to a reduction in the intraspecific variation of traits (Liu et al., 2018). In our study, the intraspecific traits variation of *Davidia involucrata* and *Pterostyrax psilophyllus* in the transplanted population was lower than or similar to that in the wild population; that is, leaf traits of these two species tended to be similar, which might be related to the similar microhabitats within species on the translocation site (Boucher et al., 2013; Karbstein et al., 2020). *Davidia involucrata* and *P. psilophyllus* are both tall, fast-growing trees located at the top layer of the community, so the microhabitats of different individuals, such as light conditions, were similar in the translocation site. Similar leaf traits may lead to competitive exclusion and affect species co-existence, which is detrimental to their performance (Adler et al., 2013; Li et al., 2018). Sides et al. (2014) suggested that the larger the local distribution area of a species, the higher its traits variation will be. Therefore, we propose to expand the planting area appropriately in future translocation.

Phenotypic plasticity and genetic adaptation play very important roles in shaping leaf functional traits (Bresson et al., 2011; Vitasse et al., 2014; de Villemereuil et al., 2016). In our study, species in the transplanted population had covered the genetic diversity present in their original population (Xiao et al., 2021). In addition, individuals in transplanted populations were directly transplanted from wild populations, so the leaf traits were probably similar between the two populations immediately after the transplantation. Therefore, changes in leaf traits in this study were mainly caused by phenotypic plasticity.

Conclusions

After a long period of translocation, these five endangered tree species in transplanted populations were able to grow normally and four of the five species (*Davidia involucrata*, *Pterostyrax psilophyllus*, *Tapiscia sinensis* and *Tetracentron sinense*) become more efficient in resource acquisition or utilisation and more resources were available for growth. However, the intraspecific trait variation of some species (*D. involucrata* and *P. psilophyllus*) in the translocation site was decreased as a whole, which may lead to a competitive exclusion and affect species co-existence, and affect their performance.

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ОТЛИЧАЮТСЯ ЛИ ФУНКЦИОНАЛЬНЫЕ ПРИЗНАКИ ЛИСТА МЕЖДУ 20–35-ЛЕТНИМИ ТРАНСЛОЦИРОВАННЫМИ И ПРИРОДНЫМИ ПОПУЛЯЦИЯМИ? ТЕМАТИЧЕСКОЕ ИССЛЕДОВАНИЕ ПЯТИ ВИДОВ ДЕРЕВЬЕВ, НАХОДЯЩИХСЯ ПОД УГРОЗОЙ ИСЧЕЗНОВЕНИЯ

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Сохранение видов, находящихся под угрозой исчезновения, посредством транслокации стало эффективным способом противодействия исчезновению видов во всем мире. Функциональные признаки растений являются хорошими предикторами продуктивности растений и могут отражать стратегии адаптации растений к окружающей среде. Однако до сих пор неясно, имеют ли трансплантированные популяции сопоставимые уровни функциональных признаков листа с таковыми в популяциях в дикой природе. Чтобы оценить эффективность природоохранной транслокации деревьев-долгожителей, находящихся под угрозой исчезновения, мы исследовали многолетнюю (20–35 лет) популяционную динамику пяти сосуществующих исчезающих видов деревьев (*Davidia involucrata*, *Dipteronia sinensis*, *Pterostyrax psilophyllus*, *Tapiscia sinensis* и *Tetracentron sinense*) в транслоцированных популяциях и сравнили функциональные признаки листьев между транслоцированными и исходными (природными) популяциями. Мы обнаружили, что выживаемость пяти видов в транслоцированных популяциях колебалась от 42.86% до 73.81%, и большинство этих видов могли цвести и плодоносить. Все виды имели статистически значимые различия в некоторых функциональных признаках листьев между транслоцированными и природными популяциями. В целом, внутривидовая изменчивость некоторых видов в транслоцированных популяциях была снижена по сравнению с таковой в природных популяциях. Мы пришли к выводу, что после длительного периода транслокации эти виды в транслоцированных популяциях были способны нормально расти, и большинство видов характеризовались более эффективным приобретением или использованием ресурсов, и для их роста стало доступно больше ресурсов. Однако внутривидовая изменчивость некоторых видов в транслоцированных популяциях может привести к конкурентному исключению, повлиять на сосуществование видов и, таким образом, повлиять на их продуктивность.

Ключевые слова: внутривидовая изменчивость признака, деревья-долгожители, динамика популяции, долговременный мониторинг, природоохранная транслокация