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The Hybrid Origin of *Paulownia taiwaniana* Hu and Chang – Evidence from Isozyme Gene Markers

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Abstract

Based on an investigation of 6 enzyme systems coding for 13 gene loci, no variation between 202 *Paulownia taiwaniana* HU and CHANG trees was detected at any locus. The high level of heterozygosity (7 out of the 13 gene loci) is explained by the supposed hybrid origin of *P. taiwaniana*; the genetic uniformity is due to its exclusively vegetative propagation. The silvicultural significance of the findings (heterosis, susceptibility to diseases) as well as aspects of gene conservation are discussed. The potential of isozyme studies for a better understanding of the systematics of the genus *Paulownia* as well as for future breeding programmes is indicated.

Key words: *Paulownia* spp., isozymes, natural hybrid, heterosis, genotypic uniformity, gene conservation.

Introduction

The tree genus *Paulownia* (*Scrophulariaceae*) is widely distributed in China. Out of the 9 species described by the Chinese Academy of Forestry Staff (1986), three species are found on Taiwan: While Taiwan forms the eastern border of the wide range of natural distribution of *P. fortunei* HEMSL. and *P. kawakamii* ITO, *P. taiwaniana* HU and CHANG is endemic to Taiwan. The latter taxon was recently described for the first time (HU and CHANG, 1975). It is frequently assumed to be a natural hybrid between the former two species (LI, 1978, WANG and HONG, 1979), because many phenotypic features are reported to be intermediate between *P. kawakamii* and *P. fortunei*. The most prominent of these features are: Size and colour of flowers, mode of branching of inflorescences, size of fruits (capsules) (HU and CHANG, 1975); shape of trichomes (HU and LIN, 1975); and some features of the wood anatomy (WANG, 1985).

Both *P. kawakamii* and *P. fortunei* are very rare on Taiwan. In one year of intensive search by this author no more than 8 *P. fortunei* and 20 *P. kawakamii* trees could be found. It is reported that some of those trees are relics

of natural stands. The extreme rarity is the result of incidents — mainly intensive logging and typhoons — during the last decades. Natural stands of *P. taiwaniana* are not known. Cultivation of *Paulownias*, which are named *P. taiwaniana* since HU and CHANG's publication in 1975, started around the beginning of this century (LIN, 1979). *P. taiwaniana* plantations were established on a large scale during the 1970's, the total plantation area covering more than 19,000 ha in 1977 (LIN, 1979). In addition to these plantations for wood production, which were predominantly established in the eastern part of Taiwan (namely in Hualien county), *P. taiwaniana* is a frequently found roadside tree all over Taiwan. The trees have been seriously infected by mycoplasma like organisms (MLOs) causing witches-broom disease since the late 1970's. The disease caused a decline in the silvicultural importance of the genus on Taiwan, and no new plantations were established during the last ten years.

P. taiwaniana is propagated exclusively vegetatively by means of root cuttings. Plantations are thus clones or clone mixtures. However, due to the uncertain origin of the species, the degree of genetic differentiation within and between plantations is unknown. This study involving isozyme gene loci aimed at obtaining information on genetic differentiation patterns within and between the native *Paulownia* spp. on Taiwan and relating the findings to silvicultural features, breeding potential, and problems of gene conservation of the genus.

Materials and Methods

All trees belonging to the taxa *P. kawakamii* and *P. fortunei* according to their phenotypic appearance were included in the genetic inventory, as both species are extremely rare on Taiwan (see above). One *P. fortunei* tree near Liu-Kuei (Kaoshiung county) is reported to be the relic of a small natural stand; 7 more *P. fortunei* trees were obviously artificially propagated. Out of the 20

Table 1. — Locations of sampled *Paulownia taiwaniana* trees.

County	Number of trees sampled
Hualien	78
Nantou	41
Taipei	31
Taitung	30
Yunlin	9
Taichung	8
Taipei City	6
Total	203

identified *P. kawakamii* trees, 8 trees constituted a small, supposedly natural stand near Li-Shan, Taichung county. The remaining trees were presumably vegetatively propagated roadside trees in Taichung, Hualien, and Taipei county.

A total of 203 *P. taiwaniana* trees were included in the survey (Table 1). Material was collected from all major cultivation areas of the species. Trees of 11 different plantations for wood production and 26 different collection sites near roads, in parks or villages were included. One (in the case of isolated roadside trees) to 33 individuals per site were sampled. Additionally, 25 *P. taiwaniana* trees of the only seedling plantation of *Paulownia* on Taiwan (near Tai-Ma-Li, Taitung county) were included in the inventory. These trees were the only surviving seedlings of a provenance and progeny test, which was established some 20 years ago and included several thousand seedlings from many different locations.

Young leaves were collected from all sample trees, frozen in liquid nitrogen, and stored under refrigeration until electrophoresis was performed. The procedure of starch gel electrophoresis, genetic analysis, and geno-

typing is described elsewhere (FINKELDEY, 1992): investigated enzyme systems and underlying gene loci are given in table 2.

Results

While considerable genetic variation between species was found, there was almost no within species variation at any of the investigated gene loci. *P. kawakamii* and *P. fortunei* trees proved to be homozygous at all 13 investigated gene loci. *P. taiwaniana* trees were found to be heterozygous (A_1A_2) at those 7 gene loci at which *P. kawakamii* and *P. fortunei* were fixed on different alleles (A_1A_1 and A_2A_2). At the remaining 6 (presumed) gene loci, *P. kawakamii* and *P. fortunei* were fixed on identical alleles, and *P. taiwaniana* also showed this phenotype (Table 2).

Only one *P. taiwaniana*, a roadside tree near Li-Shan, differed in its multilocus genotype, as it was found to be homozygous at the locus SKDH-A (A_1A_1) but proved to be heterozygous at all other variable gene loci (A_1A_2). Furthermore, considerable genetic variation, but no new allele was detected when 25 trees of the only seedling plantation of *P. taiwaniana* near Tai-Ma-Li were analysed.

Discussion

Gene fixation in *P. kawakamii* and *P. fortunei*

Genetic structures of *P. kawakamii* and *P. fortunei* on Taiwan are characterized by high levels of gene fixation. No genetic variation within these species was detected at any of the loci investigated. The homozygosity of all individuals at 13 gene loci coding for 6 enzyme systems which are known to show substantial genetic variation in many other plant species is interpreted as a clear indication of a fixation of extensive parts of their genome. As the extreme rarity of both species is a very recent event on Taiwan, the current bottlenecks in population sizes

Table 2. — Investigated enzyme systems, their abbreviations, E. C. Numbers, controlling gene loci and genotypes of the native *Paulownia* spp. on Taiwan.

Enzyme System	Abbrev.	E.C. No.	Gene loci	Genotype		
				<i>P. fortunei</i>	<i>P. kawakamii</i>	<i>P. taiwaniana</i>
Shikimate-Dehydrogenase	SKDH	1.1.1.25	SKDH-A	A_1A_1	A_2A_2	A_1A_2
Isocitrate-Dehydrogenase	IDH	1.1.1.42	IDH-A ¹	A_1A_1	A_1A_1	A_1A_1
			IDH-B	B_2B_2	B_1B_1	B_1B_2
Phosphoglucose-Isomerase	PGI	5.3.1.9	PGI-B	B_2B_2	B_1B_1	B_1B_2
Leucine-Aminopeptidase	LAP	3.4.11.1	LAP-A ¹	A_1A_1	A_1A_1	A_1A_1
			LAP-B ¹	B_1B_1	B_1B_1	B_1B_1
Glutamate-Oxaloacetate-Transaminase	GOT	2.6.1.1	GOT-A	A_2A_2	A_1A_1	A_1A_2
			GOT-B ¹	B_1B_1	B_1B_1	B_1B_1
Malate-Dehydrogenase	MDH	1.1.1.37	MDH-A ¹	A_1A_1	A_1A_1	A_1A_1
			MDH-B	B_2B_2	B_1B_1	B_1B_2
			MDH-C ²	C_1C_1	C_2C_2	C_1C_2
			MDH-D ²	D_1D_1	D_0D_0	D_0D_1
			MDH-F ¹	F_1F_1	F_1F_1	F_1F_1

¹) Assessment of gene loci and genotypes is disputable as no variation was observed. It was inferred from other plant species, if ontogenetically and environmentally stable invariable banding patterns were observed in all three *Paulownia* spp. on Taiwan (FINKELDEY, 1992).

²) Genotype assessment was confirmed for those individuals of the species whose progenies were investigated in the course of genetic analysis. However, as genotyping was complicated by a "null"-allele (for MDH-D) and by intergenic heterodimers between zones MDH-B and MDH-D, which interfere with the observation of zone MDH-C, the given genotypes could not be determined for all trees (FINKELDEY, 1992).

are unlikely causes of the genetic impoverishment. More investigations on the mating system of *Paulownias* and on genetic structures of those species on the Chinese mainland are required in order to find plausible explanations for the results. One possible explanation for the genetic impoverishment is a long-lasting and very severe bottleneck during the colonization of Taiwan, a hypothesis which has been suggested to account for the genetic uniformity of an endemic Californian conifer, *Pinus torreyana* (LEDIG and CONKLE, 1983).

P. taiwaniana — Evidence for its hybrid origin

Isozyme studies are frequently stated to be of great significance for hybrid identification (MIRTON, 1983; RICHARDSON et al., 1986). However, complications arise if it turns out that putative source species share alleles (i.e. alleles which code for bands of identical mobility on the gel) at single gene loci, even if these alleles occur in different frequencies in the two species (JOLY and ADAMS, 1983). For this reason, the identification of single gene markers, which are completely differentiated between the source species (i.e. the source species have no allele in common) is crucial for hybrid identification. Thus, the fixation on different alleles in *P. kawakamii* and *P. fortunei* (i.e. the complete differentiation between the species) at 7 gene loci proves to be extremely helpful for the identification of their putative hybrid.

At all 7 polymorphic gene loci, the observed genotypes of *P. taiwaniana* are in perfect accordance with the expected types based on the hypothesis of the hybrid origin of the species. This inference is even supported by those six (presumed) gene loci which did not show variation between *P. kawakamii* and *P. fortunei*, as *P. taiwaniana* was found to be fixed on the same alleles as its supposed ancestors at these loci, which code for highly variable enzyme systems in many plant species.

These conclusions are based on the assumption that genetic structures of those "source trees" whose mating gave rise to the taxon *P. taiwaniana* did not differ from those of the few relic trees of *P. kawakamii* and *P. fortunei* which were investigated in the present study at any of the loci examined. The failure to falsify this assumption may be viewed as an indication that the genetic impoverishment of *P. kawakamii* and *P. fortunei* is no recent event.

However, experiments did not allow to distinguish whether the formation of the taxon *P. taiwaniana* was due to a single mating event between one *P. fortunei* and one *P. kawakamii* tree and subsequent exclusively vegetative propagation of one offspring, or whether *P. taiwaniana* arose from a number of interspecific matings between trees of the source species, perhaps even at different locations and/or times. This consideration is of some interest, as in the latter case some unrecognized genetic variation within the source species might have been passed to the hybrid, while the former case applies to the formation of one single clone without any genetic variation.

Investigations of *P. taiwaniana* progenies allowed genetic analysis (FINKELDEY, 1992). All polymorphic gene loci showed regular segregation, no significant deviations from the assumption that nuclear genes of a diploid species code for the enzymes being observed. While segregation ratios in *P. taiwaniana* progenies confirmed the diploid state of the species, no statement is proposed as to which of the source species (*P. kawakamii* or *P. fortunei*) contri-

buted the maternal and which the paternal portion to the formation of *P. taiwaniana* or whether even both possible pathways were followed, as only nuclear genes were observed.

Heterosis in *P. taiwaniana*

The genetic construction of *Paulownia* spp. as outlined here resembles genetic structures which result from the hybridization of pure lines. This breeding method, which has been frequently applied in agriculture and horticulture, is characterized by the creation of largely homozygous lines via inbreeding (typically selfing) for several generations and subsequent crossing between these lines (ALLARD, 1960). F₁ hybrids between inbred lines are heterozygous at extensive parts of their genome but genotypically uniform (KONAREV, 1976). Maize (*Zea mays* L.) hybrids produced in this way showed considerably increased yield (SPRAGUE, 1983). However, the technique has never been applied to forest tree species due to their pronounced inbreeding depression and long generation cycles (HATTEMER und BERGMANN, 1987). Hybrids between forest tree species, whether resulting from natural events or created by man, mostly are established without prior formation of inbred lines. Hence, the F₁ hybrid population usually is genotypically variable. The value of hybridization in forestry is mostly attributed to combining of traits (NAMKOONG et al., 1988), which differs fundamentally from the heterosis effect due to hybridization of pure lines.

The peculiar genetic structure of *P. taiwaniana* (compared to other forest tree species) make them interesting objects to study heterosis. Unfortunately, there is no proof of a superior performance of *P. taiwaniana*, as no systematic species trials have been established. The exclusively vegetative propagation of *P. taiwaniana* all over Taiwan and the experience of Taiwanese foresters are the only indications of its superiority, e.g. in terms of rate of vegetative growth.

Genotypic uniformity of *P. taiwaniana* and its consequences

Although *P. taiwaniana* trees were found to be highly heterozygous ($H = \text{proportion of heterozygous gene loci} = \frac{7}{13} = 0.54$ for all trees), genotypic variation within species was virtually absent at all of the gene loci examined. The number of observed gene loci might be regarded as insufficient to verify the hypothesis that the taxon *P. taiwaniana* is one single clone. However, the hypothesis could not be falsified and results clearly indicate an extremely low level of within species variation. Low genetic variation, which might be due to clonal propagation or any other reason (e.g. serious bottlenecks in population history) comprises a high risk situation for the future survival of populations per se (HEYBROEK, 1984; BERGMANN et al., 1990). Thus, the susceptibility of *P. taiwaniana* to pathogens, in particular to the MLO caused witches-broom disease, is explained by the large scale planting of the species during the 1970's, which enabled the pathogen to become adapted to a homogeneous substrate and thus to spread quickly.

The evolutionary potential of the genus *Paulownia* on Taiwan

As *P. fortunei* and *P. kawakamii* are assumed to be genetically fixed over extensive parts of their genome, their potential for future adaptation processes is poor at best. Obviously, this does not hold true for their hybrid *P. taiwaniana*: Considerable amounts of genetic variation were found in its offspring at single gene loci (FINKELDEY,

1992). However, the adaptive potential, measured by the genetic multiplicity, i.e. the number of alleles at a locus irrespective of their frequencies (FINKELDEY and GREGORIUS, in press), is low, too: No more than two alleles can be found at any of the gene loci at which its presumed ancestors were fixed (as the vast majority of all loci probably are, as mentioned above).

Furthermore, individual heterozygosity is expected to decrease in subsequent generations and a breakdown of coadapted gene complexes (TEMPLETON, 1986), which might have been originated from the evolution of the genetically impoverished *P. kawakamii* and *P. fortunei*, is expected to occur in *P. taiwaniana* seedlings. Therefore, viability and/or fertility are expected to decrease in *P. taiwaniana* progenies, as is observed in consecutive generations of hybrid maize, for example (ALLARD, 1960). This expectation is corroborated by the following observations:

Natural regeneration of *P. taiwaniana* is extremely poor. Only one out of 203 trees investigated (a roadside tree near Li-Shan; see "results" section) showed a multilocus genotype, which testified to its presumed origin as a natural *P. taiwaniana* progeny.

As explained above, an unsuccessful progeny and provenance test at Tai-Ma-Li (Taitung county) was characterized by extremely high mortality of *P. taiwaniana* seedlings during all stages of their growth. Out of several thousand seedlings originally germinating, only 25 trees still survive today, most plantlets already having died in the nursery, but survival at the planting site was poor also (Hu, pers. communication).

Out of the 25 seedlings which still survive at that site, only two trees fructified sparsely in 1988, the remaining 23 trees not having borne any capsules at all, even though most of the trees had flowered in the spring of that year. Out of 33 vegetatively propagated *P. taiwaniana* trees growing adjacent to those seedlings, only 5 trees, all heavily infected by witches-broom disease, did not fructify, and 6 trees fructified sparsely. The remaining 22 trees fructified abundantly in that year (pers. obs.). This might be viewed as an indication of a much reduced fertility of *P. taiwaniana* seedlings. However, vegetatively propagated *P. taiwaniana* trees fructify abundantly each year all over Taiwan.

WANG and HONG (1979) compared the germination percentage of the three native *Paulownia* spp. on Taiwan under different environmental conditions simulated in the laboratory. Under (nearly) all conditions they found highly significant differences in germination percentage, the germination percentages of *P. taiwaniana* being much lower than those of *P. fortunei* and *P. kawakamii*. The values under "optimal" conditions are: 48.3% for *P. taiwaniana*, 73.8% for *P. fortunei*, and 80.3% for *P. kawakamii*. These findings can be explained by the breakdown of coadapted gene complexes in *P. taiwaniana* seedlings.

Consequences for gene conservation

As any *P. taiwaniana* tree showed all identified genetic variants of the genus on Taiwan at the investigated gene loci, gene conservation seems to be of minor concern. Yet, it should be emphasized that there might be some amount of unrecognized variation within species. Furthermore, the conservation of the few remaining *P. kawakamii* and *P. fortunei* genotypes, preferably by evacuation to easily accessible planting sites (e.g. in botanical gardens) deserves consideration. These genotypes are at a high risk of extinction; although their genetic information at single

gene loci might have been transferred to their hybrid *P. taiwaniana* and therefore may be regarded as sure to survive, the continuance of their genome as a whole is at risk. These few relic trees are highly interesting and probably unique botanical objects, which might be substantially differentiated from the provenances found on the Chinese mainland. This view is supported by their unique phenotypic appearance, which is very different from the phenotypes reported from the Chinese mainland, and by isozyme patterns of a few *P. fortunei* trees, which originated from the Chinese mainland and were found to differ from those observed in "Taiwanese" *P. fortunei* at 4 out of the 6 enzyme systems examined (pers. obs.). It is presumed that "Taiwanese" *P. kawakamii* and *P. fortunei* genotypes will be of high value in future breeding programmes, which might involve systematic intra- and interspecific hybridizations of many species (Chinese Academy of Forestry Staff, 1986), as a hybrid between one of these largely homozygous trees and any other *Paulownia* genotype might show some degree of heterosis.

Future progress in *Paulownia* breeding will rely heavily on a better understanding of the mating system within the genus as well as a better knowledge of its systematics. There is still considerable discussion on taxonomic problems within the genus, and hybridization between species might be a common phenomenon all over its distribution range (Chinese Academy of Forestry Staff, 1986). It is suggested, that isozyme analysis in connection with a rangewide survey of the genus might be a useful tool to obtain a better understanding of these problems.

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Analysis of Genetic Variation in a *Pinus strobus* x *P. griffithii* F₁ Hybrid Population

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Summary

28 *P. strobus* x *P. griffithii* full-sib and 2 half-sib (parents) families were arranged (during artificial inoculation with *Cronartium ribicola*) in a randomized complete block design. Each family was represented by a 14-seedling plot in each of three blocks. At age 6, the seedlings were transplanted in the field by using the same experimental design as in the inoculation tent. 13 traits were measured when the seedlings were 9 years old. The main results were, as follows: (1) Significant differences were found among hybrids for 11 out of 13 tested traits; (2) Differences among male and female trees were significant for the most traits, including blister rust resistance, diameter, basal area, volume and stem straightness; (3) Blister rust resistance, diameter, basal area and volume growth of the hybrids were 105%, 33%, 58% and 63%, respectively, higher than *P. strobus* and 33%, 25%, 114% and 400%, respectively, higher than *P. griffithii*; (4) The ratios GCA: SCA variance were 2:1 for basal area, 3:1 for number of stems, 1:1 for stem straightness and 1:0 for all the other traits; (5) Both positive and negative GCA effects which differed significantly from zero were found; (6) The narrow-sense heritabilities ranged from 0.383 for stem straightness to 0.853 for diameter; (7) If the best 2, 8, 14, and 20 out of 28 tested families were selected, a genetic gain of 14.1%, 9.0%, 6.1%, and 3.6%, respectively, in blister rust resistance and 25.2%, 16.1%, 10.9%, and 6.4%, respectively, in volume growth rate could be achieved.

Key words: *Pinus strobus*, *P. griffithii*, hybrid, *Cronartium ribicola*, resistance, general combining ability, genetic correlation, additive variance, heritability, genetic gain.

Introduction

Hybridization and backcrossing in advanced generations can be used as mean of combining desirable traits from two species into a new strain which can then be used to advantage in a tree breeding programme. Interspecific hybridization between eastern white pine (*Pinus strobus* L.) and blue pine (*P. griffithii* Mc.CLELL) was performed by some workers, mainly for improving blister rust (*Cronartium ribicola* FISCH. ex RABENH.) resistance (PATTON,

1964; HEIMBURGER, 1964; BLADA, 1987) and growth traits (ZSUFFA, 1979a; KRIEBEL, 1982; LEANDRU, 1982). To date, the main results obtained from *P. strobus* x *P. griffithii* hybridization have been:

— Hybrid progenies contained a higher percentage of resistant seedlings than intraspecific *P. strobus* crosses (HEIMBURGER, 1962; PATTON, 1964; ZSUFFA, 1979b; BLADA, 1987);

— One year old hybrid progenies showed considerable variability in height, crown size and needle length (PATTON, 1964);

— Juvenile F₁ hybrids outgrew in height the *P. strobus* controls (ZSUFFA, 1979a; LEANDRU, 1982; BLADA, 1987);

— Differences were found among *P. griffithii* male parents in their ability to transmit resistance to the hybrids with *P. strobus* (PATTON, 1964; BLADA, 1987);

— The best families were from 22% to 44% superior in volume to the best *P. strobus* families in three 17 to 22 years old progeny tests (KRIEBEL, 1982);

— According to KRIEBEL (1982), some workers suggest that non-additive variance was most important in interspecific hybridization of white pines whereas in a *P. strobus* x *P. griffithii* F₁ population the additive genetic variance was predominant (BLADA, 1987);

— Blister rust resistance and height growth in 5-year-old hybrids were shown to be under polygenic control and heritable; narrow-sense heritabilities, at family level, were 0.64 and 0.65 for blister rust and height growth, respectively; the expected gains were 11% in resistance and 3% in height growth if the best 8 families were selected (BLADA, 1987).

This paper reports the results of factorial analyses of some traits in a 9 year old *P. strobus* x *P. griffithii* F₁ hybrid population.

Materials and Methods

Initial materials and mating design

The mating design and genetic model followed those of KOMSTOCK and ROBINSON'S (1952) Experiment II adapted to this case. Both populations and parents were taken at