

Notes and Comments

Demographic Genetic Analyses of the American Beech (*Fagus grandifolia* Ehrh.). Genetic Variations of Seed Populations in Maryland

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Genetic variability in seed populations play an initial role in establishing the demographic substructure for succeeding generations. Gene flows of plant populations are mediated by both pollen and seed dispersal. Limited pollen and seed dispersals may lead to pollen pool heterogeneity, genetically distinct seed shadows among maternal plants (Linhart et al., 1981), and eventually to the development of genetic structure within populations (Hamrick and Nason, 1996). Spatial genetic substructuring within populations has been reported for many woody species (Epperson, 1989; Epperson and Allard, 1989; Knowles, 1991; Xie and Knowles, 1991; Perry and Knowles, 1991; Young and Merriam, 1994; Geburek and Tripp-Knowles, 1994; Alvarez-Buylla and Garay, 1994; Alvarez-Buylla et al., 1996; Epperson and Alvarez-Buylla, 1994; Boshier et al., 1995; Shapcott, 1995; Leonardi et al., 1996).

In the genus *Fagus*, genetic spatial substructurings have also been reported for European beech (Merzeau et al., 1994; Leonardi and Menozzi, 1996). The Japanese beech populations (Kitamura et al., 1997a,b; Kawano and Kitamura, 1997) have also been shown to have extremely localized genetic patterns at the local population scales.

In this short communication, we report on genetic substructuring of the North American beech (*Fagus grandifolia* Ehrh.) in a population in Maryland, on the Inner Coastal Plain. The American beech is widespread throughout eastern North America and occurs in a wide range of habitats. The American beech shows mast flowering and fruiting about every three to four years (Fowells, 1965). The goal of the study was to determine the genetic variability in seed populations pro-

duced by mother trees in an area where individuals had been mapped and genetically identified (Kitamura and Kawano, 1996). We sought to determine the degree of variability in the pollen pool among mother trees, estimate outcrossing rates, and evaluate the importance of genetic heterogeneity of the seed population in influencing the spatial and temporal genetic substructurings in the study area.

Materials and Methods

Fifteen mother trees were chosen within a study plot (20 × 100 m) that had been established at the Smithsonian Environmental Research Center, Edgewater, Maryland. Diameters of mother trees ranged from 33.4 to 104.7 cm (Table 1). In 1994, we observed all of the trees in this population whose diameter at breast height was larger than 30 cm, and which flowered and bore fruits. Seeds from each mother tree were collected using seed traps in October 1994. The seeds were stratified at 5°C for three months and germinated in a greenhouse. After the first two true leaves developed, leaves were removed and stored at –80°C until the enzymes were extracted.

Enzyme extractions (Shiraishi, 1988) and polyacrylamide vertical slab gel electrophoreses (Davis, 1964; Orstein, 1964) were carried out. Nine polymorphic loci from eight enzyme systems were scored: *6Pgdh2*, *6Pgdh3*, *Adh1*, *Amy1*, *Fum*, *Got1*, *Lap*, *Pgi*, and *Pgm*.

Genetic variability measures such as genotype, allelic frequencies, and heterozygosity (*He*) (Nei and Roychoudhury, 1974) of progenies were compared among mother trees. Relationships between genetic diversity of progenies and the number of heterozygous loci for mother trees were examined by Kendall's coefficient of rank correlation (τ) (Sokal and Rohlf, 1995).

Table 1. Diameter, numbers of analyzed seed progenies, and genotypes of 15 mother trees.

Mother tree	D ¹⁾ (cm)	N ²⁾	<i>6Pgdh2</i>	<i>6Pgdh3</i>	<i>Adh1</i>	<i>Amy1</i>	<i>Fum</i>	<i>Got1</i>	<i>Lap</i>	<i>Pgi</i>	<i>Pgm</i>
mt147 ³⁾	38.8	7	<i>aa</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt154	49.3	31	<i>aa</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt464 ³⁾	34.7	8	<i>aa</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt465	34.7	16	<i>ab</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bc</i>
mt489	71.6	34	<i>bb</i>	<i>bc</i>	<i>ab</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt497	54.1	40	<i>aa</i>	<i>bb</i>	<i>ab</i>	<i>ab</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt541 ³⁾	36.6	3	<i>bb</i>	<i>cc</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt542 ³⁾	33.4	8	<i>aa</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt545	36.6	41	<i>bb</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>cc</i>	<i>bb</i>	<i>bb</i>
mt710	77.0	128	<i>aa</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>bc</i>	<i>bb</i>	<i>cc</i>	<i>bb</i>	<i>bb</i>
mt811	47.4	59	<i>ab</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt838	54.1	144	<i>ab</i>	<i>bc</i>	<i>ab</i>	<i>bb</i>	<i>ab</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bc</i>
mt864	84.7	29	<i>ab</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>bb</i>	<i>ac</i>	<i>bb</i>	<i>bb</i>
mt913 ³⁾	35.3	8	<i>aa</i>	<i>bc</i>	<i>bb</i>	<i>ab</i>	<i>bb</i>	<i>bb</i>	<i>ce</i>	<i>bb</i>	<i>bb</i>
mt943	104.7	82	<i>aa</i>	<i>bc</i>	<i>bb</i>	<i>bb</i>	<i>ab</i>	<i>bb</i>	<i>cc</i>	<i>bb</i>	<i>bb</i>
Total		638									

¹⁾ Diameter at breast height, ²⁾ the number of seed progenies analyzed,

³⁾ mother tree with less than ten progenies was excluded from estimation of outcrossing rates.

For estimation of single-locus (t_s) and multilocus (t_m) outcrossing rates, we used ten mother trees with more than ten seed progenies (Table 1), and applied the mixed mating model of Ritland and Jain (1981). We used the computer program MLTR supplied by K. Ritland (Ritland, 1990). Standard errors of outcrossing rates were calculated based on 100 bootstraps. Pollen pool allele frequencies were obtained by the Estimation-Maximization method, and heterogeneity among mother trees was tested by chi-square test of independence (Sokal and Rohlf, 1995).

Results

A total of 638 progenies were analyzed, with the numbers of progeny per mother tree ranging from three to 144 (Table 1). Allele frequencies of seed population for each mother tree and totals for all seed populations are shown in Table 2. Two loci, *Got1* and *Pgi*, did not show allelic polymorphism (Table 1), however, immigrant alleles were observed in low frequencies, one mother tree for *Got1* and two for *Pgi* (Table 2).

Genotypic components for seed progenies differed among mother trees. For example, Fig. 1a shows genotype frequencies of seed population for each mother tree in the *Fum* locus. Mother trees located at the right side of the study plot (mt147, 154, 838, 864, 913 and 943) had a greater frequency of genotypes with *Fum-a* allele compared to those in the left side of the plot. An-

other trend was observed for *6Pgdh3* (Fig. 1b) and *Pgm* (Fig. 1c), in which specific genotypes appeared only in limited maternal trees (mt489 and 838).

The relationship between the number of heterozygote loci of the maternal tree and the heterozygosity of its seed population was highly significant based on Kendall's coefficient of rank correlation ($\tau=0.62$; $p<.0006$). The result suggests that the greater the number of heterozygote loci in the mother tree, the higher is the genetic diversity of its seed progeny. Levels of genetic differentiation in seed populations among mother trees were measured by $G_{ST}=0.05$.

The estimated outcrossing rates (t_s and t_m) are shown in Table 3. Single-locus estimation of outcrossing rate (t_s) ranged from 0.912 for tree mt545 to 0.973 for tree mt838. The average t_s over all mother trees was 0.955. Multilocus estimates (t_m) ranged from 0.930 for tree mt545 to 1.000 for tree mt465, mt497 and mt838. The average t_m for all mother trees was 1.000, which indicates a high degree of outcrossing.

Estimated pollen allele frequencies for ten mother trees are shown in Table 4. Differences in pollen allele frequencies among mother trees were significant ($p<0.05$) in *Amy1*, and highly significant ($p<0.01$) in *6Pgdh2*, *6Pgdh3*, *Adh1*, *Fum*, and *Lap*.

Discussion

Genetic substructuring could be influenced by among

Table 2. Allele frequencies and heterozygosities (*He*) of seed population for each mother tree.

Locus	Allele	mt147	mt154	mt464	mt465	mt489	mt497	mt541	mt542	mt545	mt710	mt811	mt838	mt864	mt913	mt943	Total
<i>6Pgdh2</i>	<i>a</i>	.86	.83	.86	.59	.33	.79	.00	.75	.34	.76	.65	.66	.69	.79	.88	.69
	<i>b</i>	.14	.17	.14	.41	.67	.21	1.00	.25	.66	.24	.35	.34	.31	.21	.12	.31
	<i>He</i>	.24	.29	.24	.48	.44	.33	.00	.38	.45	.37	.45	.45	.43	.34	.21	.43
<i>6Pgdh3</i>	<i>a</i>	.00	.00	.00	.00	.03	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
	<i>b</i>	.93	.69	.63	.59	.52	.88	.50	.42	.54	.61	.55	.49	.59	.50	.55	.58
	<i>c</i>	.07	.31	.38	.41	.45	.12	.50	.58	.46	.39	.45	.51	.41	.50	.45	.42
<i>Adh1</i>	<i>He</i>	.13	.43	.47	.48	.53	.21	.50	.49	.50	.47	.50	.50	.48	.50	.49	.49
	<i>a</i>	.00	.06	.50	.50	.13	.20	.00	.00	.02	.04	.09	.02	.06	.00	.02	.07
	<i>b</i>	1.00	.94	.50	.50	.87	.80	1.00	1.00	.98	.96	.91	.98	.94	1.00	.98	.93
<i>Amy1</i>	<i>He</i>	.00	.12	.50	.50	.23	.32	.00	.00	.05	.07	.17	.04	.11	.00	.04	.13
	<i>a</i>	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.94	.70	.93	.96	1.00	1.00	.99	.92
	<i>b</i>	.00	.00	.00	.00	.00	.00	.00	.00	.06	.30	.07	.04	.00	.00	.01	.08
<i>Fum</i>	<i>He</i>	.00	.00	.00	.00	.00	.00	.00	.00	.11	.42	.13	.07	.00	.00	.02	.15
	<i>a</i>	.25	.13	.19	.07	.07	.03	.25	.00	.10	.10	.05	.27	.31	.33	.27	.17
	<i>b</i>	.75	.83	.75	.82	.89	.93	.75	1.00	.81	.59	.86	.68	.69	.67	.68	.72
<i>Got1</i>	<i>c</i>	.00	.04	.06	.11	.04	.04	.00	.00	.09	.31	.09	.06	.00	.00	.05	.11
	<i>He</i>	.38	.30	.40	.31	.20	.13	.38	.00	.32	.55	.25	.47	.43	.44	.47	.44
	<i>a</i>	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.06	.00	.00
<i>Lap</i>	<i>b</i>	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.94	1.00	1.00
	<i>He</i>	.00	.00	.00	.00	.00	.00	.00	.00	.00	.01	.00	.00	.00	.12	.00	.00
	<i>a</i>	.00	.05	.06	.03	.01	.01	.00	.06	.07	.02	.03	.01	.14	.00	.01	.03
<i>Pgi</i>	<i>c</i>	.50	.61	.25	.25	.47	.29	.67	.50	.72	.72	.62	.58	.52	.69	.65	.59
	<i>d</i>	.00	.00	.00	.00	.12	.08	.00	.06	.00	.01	.00	.00	.02	.00	.00	.01
	<i>e</i>	.50	.34	.69	.72	.40	.63	.33	.38	.21	.26	.36	.41	.33	.31	.34	.37
<i>Pgm</i>	<i>He</i>	.50	.51	.46	.42	.61	.52	.44	.60	.43	.42	.49	.50	.61	.43	.46	.51
	<i>b</i>	1.00	.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	.99	1.00
	<i>c</i>	.00	.02	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.01	.00
<i>Pgm</i>	<i>He</i>	.00	.03	.00	.00	.00	.00	.00	.00	.00	.00	.00	.01	.00	.00	.01	.00
	<i>a</i>	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.02	.00	.00	.00	.00
	<i>b</i>	1.00	.98	1.00	.97	.91	.99	1.00	.94	1.00	.97	.96	.76	.95	1.00	.97	.92
<i>Average</i>	<i>c</i>	.00	.02	.00	.03	.09	.01	.00	.06	.00	.03	.04	.23	.05	.00	.03	.08
	<i>He</i>	.00	.03	.00	.06	.16	.02	.00	.12	.00	.06	.07	.38	.10	.00	.06	.15
	<i>He</i>	.14	.19	.23	.25	.24	.17	.15	.18	.21	.26	.23	.27	.24	.20	.20	.25

features including the degree of cross-pollination, embryo survival, seed dispersion, seedling establishment, and environmental heterogeneity. Genetic substructuring could also be influenced by the genetic heterogeneity of pollen and maternal trees.

The present study revealed the existence of a high degree of genetic heterogeneity in the pollen pool among maternal plants (Table 4). Seeds produced by maternal plants also had a high level of genetic heterogeneity (Fig. 1, Table 2). The genetic relationship found between mother trees and seed progeny indicated that the genetic diversity of the seed population is primarily influenced by the maternal genotype. Similar results for the genetic heterogeneity in the pollen pool (Merzeau et al., 1989; Rossi et al., 1996) and seed populations (Gregorius et al., 1986) have been reported for European beech populations.

Plant species exhibit a great variety of breeding systems, and many studies have documented that trees are predominantly outcrossing (summarized in Brown, 1989; Muona, 1989; Perry and Knowles, 1990; Morgante et al., 1991; Lewandowski et al., 1991; Coates and Sokolowski, 1992; Cottrell and White, 1995; Kjaer and Suangtho, 1995). The American

beech population studied in Maryland demonstrated a high degree of outcrossing ($t_m = 1$) which is typical of anemophilous pollinated flower. High outcrossing rates (0.94–0.98) were also reported in the European beech (Rossi et al., 1996).

Evidence of limited gene flow would greatly affect the effective population size, and suggest the prediction for long-distance pollen flow in long-lived woody species with anemophilous flowers (summarized in Hamrick and Godt, 1989, 1997). The evidence of rare genotypes within the seed population examined indicate pollen flow from remote mature trees (Table 2, Fig. 1).

The observed level of genetic differentiation ($G_{ST} = 0.05$) provides evidence for heterogeneity in seed populations among mother trees. American beech has a typical barochory type of seed dispersal, resulting leptokurtic seed shadows (Kitamura and Kawano, 1996). The subsequent phenomena, such as limited seed dispersal and post-dispersal environmental heterogeneity of an establishment site, would produce much higher genetic differentiation on a fine spatial scale.

In conclusion, main findings of this study are; 1) a long distance pollination bring new genes, at a less fre-

Table 3. Estimation of single- and multilocus outcrossing rates for ten mother trees.

Locus	mt154	mt465	mt489	mt497	mt545	mt710	mt811	mt838	mt864	mt943	Whole
<i>Lap</i>	.96 (.01)	.97 (.01)	.94 (.03)	.97 (.00)	.92 (.02)	.93 (.01)	.97 (.00)	.90 (.01)	.96 (.03)	.95 (.01)	.972 (.007)
<i>6Pgdh2</i>	.91 (.01)	.90 (.02)	.91 (.02)	.92 (.01)	.92 (.02)	.93 (.01)	.91 (.01)	.91 (.01)	.98 (.00)	.89 (.01)	.968 (.009)
<i>6Pgdh3</i>	.92 (.02)	.84 (.09)	.91 (.02)	.85 (.02)	.88 (.01)	.90 (.01)	.88 (.00)	.90 (.00)	.87 (.03)	.89 (.01)	.912 (.024)
<i>Fum</i>	.91 (.02)	.91 (.04)	.90 (.02)	.89 (.02)	.91 (.01)	.91 (.02)	.90 (.01)	.94 (.02)	.92 (.02)	.93 (.02)	.967 (.006)
<i>Pgm</i>	.86 (.03)	1.00 (.00)	.89 (.01)	.87 (.02)	.84 (.00)	.89 (.00)	.88 (.00)	1.00 (.00)	.87 (.02)	.89 (.01)	.967 (.010)
<i>Pgi</i>	.90 (.02)	.83 (.00)	.87 (.00)	.87 (.00)	.88 (.00)	.89 (.00)	.88 (.00)	.90 (.00)	.86 (.00)	.90 (.01)	.900 (.000)
<i>Adh1</i>	.91 (.01)	.82 (.00)	1.00 (.00)	1.00 (.00)	.90 (.01)	.90 (.00)	.91 (.01)	1.00 (.00)	.91 (.01)	.90 (.00)	.991 (.002)
<i>Amy1</i>	.86 (.00)	.81 (.00)	.86 (.00)	.86 (.00)	.90 (.00)	.90 (.02)	.91 (.01)	.90 (.00)	.85 (.00)	.89 (.01)	.885 (.020)
<i>Got1</i>	.87 (.00)	.83 (.00)	.87 (.00)	.88 (.00)	.88 (.00)	.90 (.00)	.88 (.00)	.89 (.00)	.86 (.00)	.89 (.00)	.900 (.001)
$t_s^{1)}$.928 (.007)	.943 (.005)	.952 (.004)	.949 (.003)	.912 (.025)	.937 (.003)	.917 (.007)	.973 (.000)	.937 (.021)	.932 (.005)	.955 (.006)
$t_m^{2)}$.999 (.023)	1.000 (.000)	.999 (.016)	1.000 (.000)	.930 (.055)	.998 (.012)	.955 (.062)	1.000 (.000)	.968 (.055)	.995 (.014)	1.000 (.000)

¹⁾ Average across single-locus estimations of outcrossing rate, ²⁾ multilocus estimation of outcrossing rate. Standard errors are given in parentheses.

Table 4. Allele frequencies of pollen pool for ten of the mother trees shown in Table 1.

Locus		mt154	mt465	mt489	mt497	mt545	mt710	mt811	mt838	mt864	mt943
<i>6Pgdh2</i> **	N	26	16	30	38	35	118	53	132	27	79
	a	.65 (.09)	.64 (.16)	.67 (.09)	.58 (.07)	.74 (.09)	.51 (.05)	.79 (.08)	.78 (.05)	.96 (.00)	.76 (.05)
	b	.35 (.09)	.36 (.16)	.33 (.09)	.42 (.07)	.26 (.09)	.49 (.05)	.21 (.08)	.22 (.05)	.04 (.00)	.24 (.05)
	c										
<i>6Pgdh3</i> **	N	27	16	30	38	38	121	55	133	27	79
	a	.04 (.00)	.06 (.00)	.07 (.04)	.03 (.00)	.03 (.00)	.01 (.00)	.02 (.00)	.01 (.01)	.04 (.00)	.01 (.00)
	b	.36 (.10)	.67 (.15)	.56 (.16)	.74 (.06)	.51 (.11)	.72 (.06)	.58 (.11)	.47 (.06)	.64 (.13)	.60 (.07)
	c	.61 (.10)	.27 (.15)	.37 (.17)	.23 (.06)	.46 (.11)	.27 (.06)	.40 (.11)	.52 (.06)	.33 (.13)	.39 (.07)
<i>Adh1</i> **	N	31	15	34	40	41	128	55	140	26	82
	a	.13 (.06)	.06 (.00)	.03 (.00)	.02 (.00)	.05 (.04)	.07 (.02)	.19 (.05)	.01 (.00)	.12 (.06)	.04 (.02)
	b	.87 (.06)	.94 (.00)	.97 (.00)	.98 (.00)	.95 (.04)	.93 (.02)	.81 (.05)	.99 (.00)	.88 (.06)	.96 (.02)
	c										
<i>Amy1</i> *	N	30	16	34	40	41	128	59	144	29	82
	a	.97 (.00)	.94 (.00)	.97 (.00)	.98 (.00)	.87 (.05)	.87 (.04)	.86 (.05)	.92 (.02)	.97 (.00)	.98 (.01)
	b	.03 (.00)	.06 (.00)	.03 (.00)	.02 (.00)	.13 (.05)	.13 (.04)	.14 (.05)	.08 (.02)	.03 (.00)	.02 (.01)
	c										
<i>Fum</i> **	N	23	14	28	36	35	116	50	131	24	77
	a	.26 (.08)	.14 (.08)	.14 (.06)	.06 (.04)	.22 (.07)	.21 (.04)	.11 (.04)	.06 (.03)	.62 (.10)	.08 (.04)
	b	.65 (.09)	.64 (.12)	.78 (.07)	.86 (.05)	.60 (.08)	.68 (.05)	.70 (.07)	.83 (.04)	.33 (.10)	.82 (.05)
	c	.09 (.05)	.21 (.11)	.07 (.04)	.08 (.04)	.18 (.07)	.12 (.04)	.19 (.06)	.11 (.03)	.04 (.01)	.11 (.03)
<i>Got1</i> n.s.	N	31	16	34	40	41	128	59	144	29	82
	a	.03 (.00)	.06 (.00)	.03 (.00)	.02 (.00)	.03 (.00)	.01 (.00)	.02 (.00)	.01 (.00)	.03 (.00)	.01 (.00)
	b	.97 (.00)	.94 (.00)	.97 (.00)	.98 (.00)	.97 (.00)	.99 (.00)	.98 (.00)	.99 (.00)	.97 (.00)	.99 (.00)
	c										
<i>Lap</i> **	N	31	16	34	40	41	128	59	144	29	82
	a	.09 (.06)	.06 (.04)	.03 (.02)	.02 (.02)	.15 (.06)	.03 (.01)	.05 (.03)	.02 (.01)	.05 (.04)	.02 (.02)
	b										
	c	.84 (.06)	.06 (.00)	.59 (.10)	.02 (.00)	.39 (.08)	.43 (.05)	.91 (.03)	.67 (.06)	.23 (.09)	.29 (.06)
<i>Pgi</i> n.s.	N	31	16	34	40	41	128	57	144	28	82
	a	.97 (.02)	.94 (.00)	.97 (.00)	.98 (.00)	.97 (.00)	.99 (.00)	.98 (.00)	.99 (.01)	.96 (.00)	.99 (.01)
	b										
	c	.03 (.02)	.06 (.00)	.03 (.00)	.02 (.00)	.03 (.00)	.01 (.00)	.02 (.00)	.01 (.01)	.04 (.00)	.01 (.01)
<i>Pgm</i> n.s.	N	30	16	34	40	36	128	55	144	28	82
	a	.03 (.00)	.06 (.00)	.03 (.00)	.02 (.00)	.03 (.00)	.01 (.00)	.02 (.00)	.03 (.01)	.04 (.00)	.01 (.00)
	b	.94 (.03)	.89 (.00)	.80 (.06)	.95 (.02)	.94 (.00)	.93 (.02)	.91 (.04)	.96 (.01)	.86 (.06)	.93 (.03)
	c	.03 (.03)	.06 (.00)	.17 (.06)	.02 (.02)	.03 (.00)	.06 (.02)	.08 (.04)	.01 (.00)	.11 (.06)	.06 (.03)

Results of chi-square test of independence among mother trees are given as follows.

n.s., Not significant; *, significant ($p < 0.05$); **, highly significant ($p < 0.01$).

N: Number of seed progenies analyzed.

Standard errors are given in parentheses.

quency into the local population, 2) the genetic variability of maternal trees mostly influence the genetic diversity of the seed, 3) genetic heterogeneities of pollen pools and seed populations exist among mother trees, and 4) limited seed dispersal may lead to genetic substructurings.

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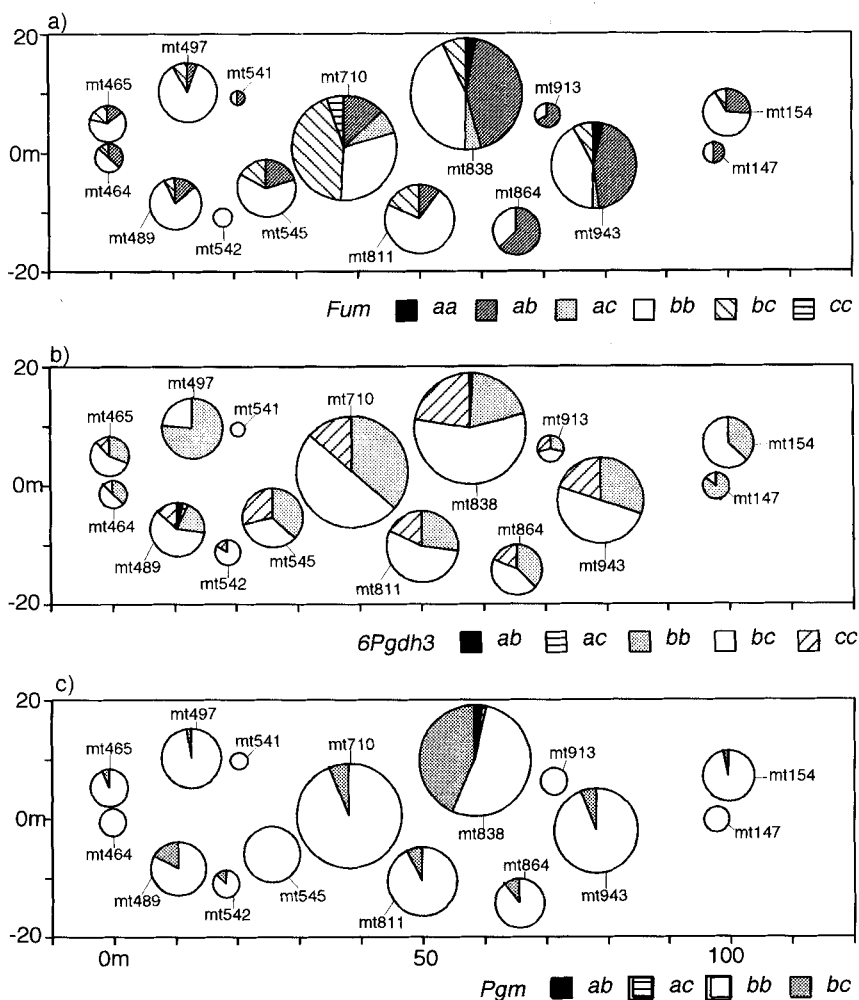


Fig. 1. Genotypic frequencies of seed populations for 15 mother trees. Location of the pie diagram is identical to that of mother tree. Diameter of each pie diagram is relative to the number of progenies analyzed. a) *Fum*, b) *6Pgdh3*, c) *Pgm*.

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