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# Notes and records

## Structuring of genetic diversity in *Albizia gummifera* C.A.Sm. among some East African and Madagascan populations

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### Introduction

The fast-growing, leguminous tree *Albizia gummifera* C.A.Sm. (Fabaceae, Mimosoideae) is a potentially useful species for ecological restoration of degraded forests. The species has multifunctional benefits such as timber, forage and medicine. However, it also has the potential to restore degraded soils as it forms mycorrhizal and rhizobial symbiotic associations (Hall, 2004), meaning ecological and economic benefits would be obtained simultaneously.

A key consideration in forest restoration is ensuring sustainability of the restored habitat, for which maximizing the suitability of planting material is important. In tree species, high levels of within-population genetic diversity and local adaptation are common phenomena. However, the strength and relative extent of local versus regional genetic structuring varies with species and depends on particular characteristics of life history (such as longevity, dispersal mechanisms and successional stage). Therefore if genetic hazards (e.g. maladaptation, inbreeding/outbreeding depression) are to be taken into account, species must be considered individually.

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Spatial genetic structure is the result of natural processes like migration, genetic drift, natural selection and historical events. Structure may reflect past population fragmentation and expansion, as well as patterns of gene exchange among populations (Hedrick, 2001) or may be influenced by more recent events. Due to its slow rate of intraspecific evolution, and its maternal inheritance in angiosperms, data derived from the chloroplast genome can provide information on both local patterns of seed dispersal and range wide evolutionary history, reflecting long-term gene flow.

As part of a wider assessment of genetic structure and adaptive variation in *A. gummifera*, an analysis of chloroplast DNA variation was undertaken to allow quantitative estimation of genetic distances between study populations and assessment of local genetic diversity of *A. gummifera* in East Africa (Uganda & Kenya) and Madagascar.

### Materials and methods

*Albizia gummifera* is a large (up to 20 m) deciduous tree, growing from 0 to 2,400 m altitude in humid/sub-humid forests from West Africa to Ethiopia and south to Mozambique and Madagascar (Maundu & Tengnäs, 2005). The study was undertaken at three sites: Uganda – Mabira Forest Reserve (0°22'N, 32°56'E); Kenya – Kedowa Forest (0°30'N, 35°20'E); Madagascar – Vohimana Forest Reserve (18°55'N, 48°30'E). In all populations, individuals were patchily distributed.

Thirty mature *A. gummifera* individuals separated by at least 100 m were sampled from each population. Leaves were collected and dried on silica gel. DNA was extracted using a DNeasy plant kit (Qiagen, Crawley, UK). Polymerase chain reaction (PCR) amplification of two chloroplast regions was undertaken: RPS/RPL and TFC/TGF (Hamilton, 1999). Reactions were carried out in 25 µL volume consisting of 5 µL of template DNA, 1.6 µL of dNTP (Promega, Southampton, UK), 0.4 µL of each primer (Thermo, Basingstoke, UK), 2 µL of buffer and 0.2 µL of Taq polymerase (New England Biolabs, Hitchin, UK) and run on an MBS 0.2G thermal cycler with the following programme: 3 min at 94°C, followed by 40 cycles of 94°C for 1 min,

**Table 1** Analysis of molecular variance (AMOVA) based on frequency of chloroplast haplotype per population

Source of variation	d.f.	SS	Percentage of total variation	P-value	$\Phi_{ST}$
Among populations	2	4.42	21	<0.01	0.209
Within populations	77	21.18	79	<0.01	–
Total	79	25.60	–	–	–

d.f. = degrees of freedom, SS = sum of squares,  $\Phi_{ST}$  = statistic summarising degree of population differentiation.

57°C for 1 min and 72°C for 10 min. Then, 5  $\mu$ L of each sample were digested at 37°C for 6 h with 0.1  $\mu$ L *Hinf*I (2  $\mu$ L buffer, 20  $\mu$ L total volume). The digest was visualised by

non-denaturing Polyacrylamide Gel Electrophoresis. Fragment sizes were scored by comparison to standards and mutations were identified by presence or absence of a fragment at each locus. The program GENALEX (Peakall & Smouse, 2005) was used to estimate Nei's unbiased haplotypic diversity ( $h_e$ ) and relative proportions of among- and within-population variation (analysis of molecular variance, AMOVA) and  $\Phi_{ST}$ .

## Results and discussion

Six mutations were detected, characterizing eight haplotypes, and total genetic diversity was  $h_{TOT} = 0.575$ . However, unbiased within-population diversity levels varied substantially, declining from Uganda ( $h_e = 0.777$ ), to Madagascar (0.763) and then Kenya (0.186). As for most

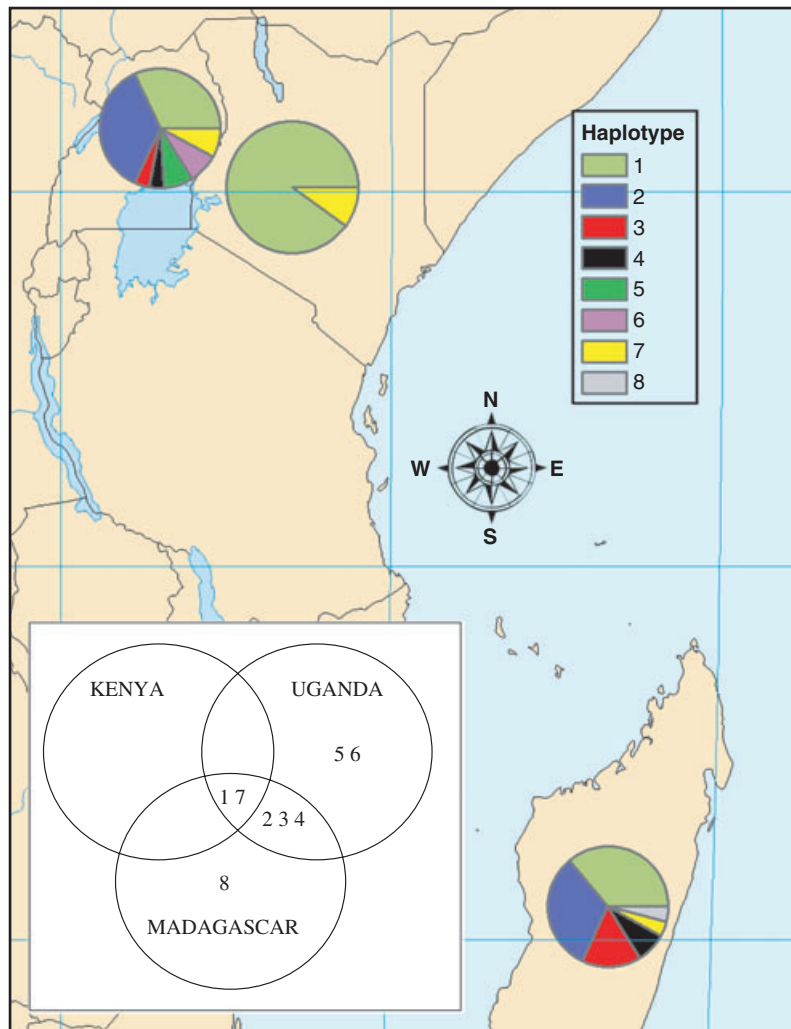


Fig 1 Map of Eastern Africa and Madagascar showing the number and distribution of haplotypes in the study populations (charts are proportional to population sample size, each colour represents a single haplotype). Inset: distribution of haplotypes among populations

tree species, and despite relatively limited seed-mediated dispersal of the chosen marker, the majority of genetic diversity was partitioned within populations (79%) with the remainder (21%) partitioned between populations ( $\Phi_{ST} = 0.209$ ,  $P > 0.01$ , Table 1). Private haplotypes (found only in that population) were present in Uganda (2) and Madagascar (1). Across all sites (Fig. 1), two haplotypes were common to all sites (haplotypes 1 and 7), whilst Madagascar and Uganda shared three.

Since chloroplast DNA commonly exhibits substantial geographic structuring among populations due to its maternal inheritance (hence limitation of gene flow to seed dispersal) and an inherently lower mutation rate in the chloroplast molecule (Wolfe, Li & Sharp, 1987), it has a slow rate of differentiation. Geographic structuring of chloroplast variation is therefore more likely to reflect long term processes. Certainly, the potential for contemporary gene flow between the study populations is highly restricted, given the distances involved as well as field observations which show widespread fruit abortion (hence low overall seed production) and seed orthodoxy. In the long term, the Mozambique Channel will clearly have formed a major geographic barrier, but the species restriction to humid and sub-humid habitat is also likely to have prevented ready dispersal among East African populations. Therefore shared haplotypes between populations most likely reflect shared ancestry, rather than long distance dispersal events.

In contrast, the observed variation in genetic diversity among sites may be influenced by more recent history. Habitat degradation erodes genetic variation due to population size reduction, increased genetic drift in smaller populations, elevated inbreeding and reduced gene flow, where population size falls below critical levels. In the Ugandan population, genetic diversity may have been retained as mature trees have persisted, representing the population prior to major forest degradation. In contrast, both the Madagascan and Kenyan sites have experienced more substantial recent degradation in terms of slash-and-burn and large scale forest clearance (Green & Sussman, 1990). Meta-population dynamics following the patchy and cyclical nature of slash and burn agriculture may

account for the retention of greater diversity in the Madagascan than in the Kenyan population.

These data, part of a larger study of local adaptation in *A. gummifera*, present a highly preliminary insight into population differentiation in the species, and the low population sample number prevents strong conclusions at this stage, but they suggest that both historical and contemporary forces have been important in shaping genetic structure.

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