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Genetic bottlenecks in agroforestry systems: results of tree nursery surveys in East Africa

Ard G. Lengkeek[1,2,*], Hannah Jaenicke[1,3] and Ian K. Dawson[1]
[1]*World Agroforestry Centre (ICRAF), PO Box 30677, Nairobi, Kenya;* [2]*Wageningen University and Research Centre, Biosystematics Group, Gen. Foulkesweg 37, 6703 BL, Wageningen, The Netherlands;* [3]*Forestry Research Programme. Park House, Bradbourne lane, Aylesford ME20 6SN United Kingdom;* **Author for correspondence (e-mail: Ard.Lengkeek@zonnet.nl; tel.: +31 317 483170; fax: +31 317 484917)*

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Abstract

Seedlings sourced through tree nurseries are expected to form an important component of future tree cover on farms. As such, the genetic composition of nursery seedlings is expected to impact on the productivity and sustainability of agroforestry ecosystems. By surveying current practices of nursery managers in five areas from Kenya, Tanzania and Uganda, we quantified parameters associated with the collection, production and distribution of tree germplasm in East Africa. Considerable variation for seed-propagated nursery species was observed in the number of maternal parents (mother trees) sampled to establish nursery lots, the quantity of seedlings raised in nursery lots and the projected number of clients for nursery lots. Current seed collection practice was the most obvious limiting bottleneck in delivering high levels of genetic diversity to farmers. In the 143 cases analysed, seed to establish nursery lots was collected from a mean of only 6.4 maternal parents. In 22% of cases, nursery lots were established from a single maternal parent. On average, each maternal parent produced sufficient progeny to provide all the seedlings received by an individual nursery client. Consequently, the potential impact on farm and landscape genetic diversity of possible non-randomisation of progeny within nurseries is serious. In two instances, pair-wise analysis of transformed data suggested significant differences between geographic areas in the projected number of clients for nursery lots. We discuss improved nursery practices likely to promote genetic diversity, in particular increased maternal parent sampling and germplasm exchange.

Introduction

In areas where natural forest cover is contracting, farmers are increasingly dependent on agroforestry ecosystems to provide useful products and services (Simons et al. 2000). The productivity and sustainability of these systems depend on the vitality of their individual species, an essential component of which is determined by genetic processes (SGRP, 2000). The long-term viability of on-farm tree stands depends upon a wide genetic base providing the capacity to adapt to environmental fluctuations or changing farmer requirements. Moreover, many tree species are out-breeding and therefore require a wide genetic base to withstand potential inbreeding depression during generations of farmer propagation (Simons et al. 1994; Boshier 2000). Among other factors, inbreeding depression may result in losses in vigour, productivity, survival and seed set (Charlesworth and Charlesworth 1987; Griffin 1990; Turnbull 1996). Intraspecific genetic resource management (GRM) therefore plays a critical role in determining the ecological stability of agroforestry systems.

A number of authors have indicated that farmers and nursery managers frequently collect tree germplasm from a narrow range of maternal parents (mother trees) during propagation (Kindt 1997; Weber 1997; Holding and Omondi 1998). In a preliminary survey of on-farm tree nurseries around Meru in Central Kenya, Lengkeek et al. (2003) suggested that genetic issues are of particular concern during nursery lot establishment. Germplasm used to establish nursery lots was collected on average from 5.9 maternal parents, with a range of 1 − 20 trees sampled. Of particular concern, over one third of nursery lots examined were established from single maternal parents. Furthermore, after initial farm introductions, most germplasm for subsequent generations of planting was harvested from trees on the same farm or, less frequently, from neighbouring farms. Data therefore indicated that intraspecific tree diversity in on-farm stands may be initially limited by current nursery practices and further reduced in subsequent generations.

To more widely assess genetic concerns raised by Lengkeek et al. (2003) this study examined tree nurseries in five areas from Kenya, Tanzania and Uganda. Our objective was to determine if common issues applied across the region, allowing general recommendations for improved tree nursery GRM to be made.

Materials and methods

Nursery surveys were undertaken in five areas of East Africa where changes in tree cover are currently occurring (FAO, 2001). Survey areas were selected based on the presence of logistical support, on-going agroforestry research and geographic spread. Areas chosen were (i) Meru District, Kenya, where on-farm nurseries were sampled across the District (the same nurseries assessed by Lengkeek et al., 2003), (ii) Nairobi, Kenya, where urban and peri-urban nurseries were sampled in and around Nairobi and Kiambu, (iii) Kabale District, Uganda, where nurseries were sampled across the District, including the buffer zone of Bwindi Impenetrable Forest, (iv) Mabira, Mukono District, Uganda, including on-farm nurseries in the buffer zone to the Mabira Forest Reserve; and (v) Arusha, Tanzania, where both peri-urban and rural nurseries around Arusha were assessed.

For each area except Arusha, survey involved visits to individual nurseries and interviews with nursery managers. Selection of nurseries within areas was generally undertaken in collaboration with government departments of forestry and agriculture, as well as with early survey interviewees. Emphasis was placed on private nursery operators rather than government-operated nurseries. Depending on area, the date of nursery visits ranged between December 1998 and April 2001. Visits in each area were timed to coincide with rainy seasons, such that nursery stocks were expected to be at a maximum level. At Arusha, data were not collected by nursery visits but rather from nursery managers during a training course on tree nursery management held in Arusha in July 2000.

Interviews with nursery managers were normally conducted in the local language and focused on the two seed-propagated tree species in each nursery that were considered by the manager to be of highest importance. Occasionally, more species were included, particularly if the number of known nurseries available for survey in an area was limited. In each case, the interviewee was asked to provide data on (i) the number of maternal parents sampled to establish a given nursery population (or lot) (N_m), (ii) the quantity of seedlings in that nursery lot (N_s); and (iii) the projected number of clients (based on experience over previous years) for the nursery lot (N_c). Nursery managers who raised trees only for their own use were counted as single clients. On some occasions, nursery managers were unable to estimate N_c. In other cases, N_m was unknown because seed had been obtained from non-governmental projects or seed dealers, or managers could not recall from how many trees they had sampled seed. Included in our analysis were only those cases where N_m was available.

In order to provide some verification of responses, N_s values were checked directly by the interviewer in a number of cases from each area (except Arusha). Observations generally confirmed the estimates of nursery managers. In some cases, where values for N_m, N_s and N_c appeared unrealistic or inconsistent (for example, if $N_c > N_s$), data were excluded from our analysis.

Results

Data for the region

Data on 143 cases from 71 nurseries were analysed, representing a total of 43 species (Table 1). Fifteen species (35%) were indigenous to the region (according to regional Flora), although indigenous species represented only 27 cases (19%). The five species most frequently represented in analysis were all ex-

Table 1. Data collected in a survey of seed-propagated tree species in tree nurseries from five areas in East Africa.

	Survey area (country)					All areas
	Kabale (Uganda)	Mabira (Uganda)	Nairobi (Kenya)	Meru (Kenya)	Arusha (Tanzania)	
Nurseries [client data*]	7 [6]	9 [7]	21 [16]	12 [8]	22 [22]	71 [59]
Cases [client data]	15 [8]	26 [16]	31 [25]	17 [10]	54 [54]	143 [113]
All species	11	14	16	7	16	43
Indigenous species	3	6	6	1	3	15
Cases indigenous species	4	10	6	2	5	27
Cases five most common species	2	3	11	10	40	66
Cases of unique species occurrence	3	6	6	2	5	22
Single tree collections all species	7	4	8	7	5	31
Single tree collections indigenous species	2	1	2	0	1	6
Maternal parents per nursery lot, N_m: mean (SD)	3.7 ± 1.8 (3.6)	5.1 ± 2.3 (6.0)	5.8 ± 3.1 (8.9)	5.7 ± 3.1 (6.5)	8.2 ± 3.8 (14.1)	6.4 ± 1.7 (10.3)
Log_{10} maternal parents per nursery lot, $log_{10} N_m$: mean (SD)	0.38 ± 0.21 (0.41)	0.51 ± 0.15 (0.39)	0.54 ± 0.15 (0.42)	0.49 ± 0.24 (0.50)	0.69 ± 0.11 (0.40)	0.57 ± 0.07 (0.43)
Seedlings per nursery lot, N_s: mean (SD)	871 ± 712 (1408)	2060 ± 1408 (3661)	787 ± 432 (1228)	1339 ± 1011 (2127)	1543 ± 676 (2535)	1378 ± 401 (2446)
Log_{10} seedlings per nursery lot, $log_{10} N_s$: mean (SD)	2.27 ± 0.46 (0.91)	2.84 ± 0.25 (0.66)	2.38 ± 0.25 (0.72)	2.53 ± 0.36 (0.77)	2.83 ± 0.16 (0.61)	2.64 ± 0.12 (0.72)
Clients per nursery lot, N_c: mean (SD)	12 ± 14 (20)	41 ± 27 (55)	17 ± 9 (22)	81 ± 92 (149)	22 ± 5 (20)	28 ± 10 (53)
Log_{10} clients per nursery lot, $log_{10} N_c$: mean (SD)	0.71 ± 0.42 (0.61)	1.12 ± 0.38 (0.77)	1.01 ± 0.18 (0.46)	1.55 ± 0.32 (0.52)	1.15 ± 0.12 (0.45)	1.12 ± 0.10 (0.54)

The number of nurseries and cases analysed from each area are shown, as well as the total number of species and indigenous species. Pooled data for the five species most commonly detected based on overall case occurrence, *Grevillea robusta*, *Calliandra calothyrsus*, *Dovyalis caffra*, *Senna siamea* and *Cupressus lusitanica*, all of which are exotic, are shown. 95% confidence intervals and standard deviation (SD) values for the three main variables assessed in the survey (N_m, N_s and N_c), and their log_{10} transformations, are given. For further information, see Results and Discussion. * Client information was available for a subset of analysed nurseries and cases (values shown in square parentheses, [ ]). Mean values relating to clients are therefore calculated from this subset of data.

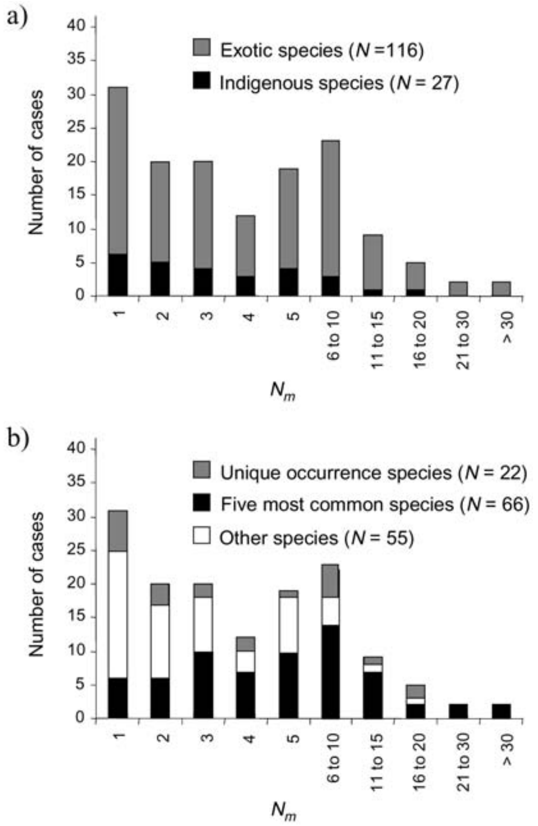

Figure 1. The numbers of cases with particular N_m values in a survey of seed-propagated tree species in tree nurseries from five areas in East Africa (data from 143 cases in total). N_m in the number of maternal parents collected for the establishment of a nursery lot. (a) split by indigenous and exotic status, (b) split by frequency of species occurrence. For further information, see Results.

otic: *Grevillea robusta*, *Calliandra calothyrsus*, *Dovyalis caffra*, *Senna siamea* and *Cupressus lusitanica* (34, 10, 8, 7 and 7 cases, respectively, total $N = 66$; individual values not shown in Table 1). Twenty-two species (51%) occurred once only in analysis.

The mean number of maternal parents collected for nursery lot establishment (mean N_m) was 6.4 ($N = 143$). In 31 cases (22%), nursery lots were established from a single maternal parent, of which 6 cases represented indigenous species. Considering exotic and indigenous species separately, mean N_m values were 6.8 ($N = 116$) and 4.5 ($N = 27$), respectively. For the five species most frequently represented in analysis, *G. robusta*, *C. calothyrsus*, *D. caffra*, *S. siamea* and *C. lusitanica*, mean N_m values were 8.6, 4.7, 21.6, 8.0 and 3.1, respectively (overall mean = 8.9, $N = 66$). Mean N_m for the 22 species that occurred once only in analysis was 5.9. Figure 1 illustrates the numbers of cases with particular N_m values. In only 18 cases (13%) was $N_m > 10$, while in only two cases was $N_m > 30$.

The mean number of seedlings raised in each nursery lot (mean N_s) was approximately 1,400 ($N = 143$), with a mean of 28 clients projected to receive seedlings from each lot (mean N_c, based on the 113 cases for which client data were available) (Table 1). A mean of approximately 370 seedlings was raised per maternal parent collected for nursery lot establishment (mean $[N_s/N_m]$; $N = 143$) and each client received on average 125 seedlings from a nursery lot (mean $[N_s/N_c]$; $N = 113$). Considering cases individually, in 106 cases ($N = 113$) the mean number of seedlings received by clients was $\geq N_m$. In 96 and 74 cases respectively, the mean number of seedlings received by clients was $\geq 2\ N_m$ and $\geq 5\ N_m$. Therefore, if progeny from separate maternal parents are randomised in the nursery, individual clients will generally receive seedlings from most of the initially collected maternal parents. However, if randomisation is not applied, clients may receive seedlings from considerably fewer mother trees, since mean N_s/N_c is relatively low compared to mean N_s/N_m (values of 125 and 370, respectively).

Variation among areas

The number of species represented in analysis varied from 7 at Meru to 16 at both Nairobi and Arusha, likely due in part to the greater overall number of cases analysed for the last two areas (see Table 1). Considering cases where nursery lots were established from single maternal parents, Kabale and Meru showed the highest proportion of cases (7/15 and 7/17, respectively), with Arusha the lowest proportion (5/54).

Mean N_m ranged by area from 3.7 at Kabale to 8.2 at Arusha, while mean N_s varied from < 800 at Nairobi to $> 2{,}000$ at Mabira (Table 1). Between areas, mean N_c varied most widely, with values ranging from 12 at Kabale to 81 at Meru. Within areas, N_m, N_s and N_c values varied very widely, including for particular species across nurseries. Data therefore showed heavily skewed distributions and large standard deviation values (Table 1). Undertaking $\log_{10}$ transformations resulted in more normal distributions, suggesting statistically significant differences between areas for $\log_{10} N_c$ values in two cases (Meru compared to both Kabale and Nairobi).

Discussion

In a preliminary survey of the Meru region of Kenya, Lengkeek et al. (2003) indicated that germplasm to establish nursery lots of important seed-propagated tree species came from an average of only 5.9 maternal parents. Results from the present study, which surveyed a wide area of East Africa, confirmed the low number of maternal parents sampled for nursery lot establishment, with a mean N_m of only 6.4. In only two cases were seed collected from the minimum number of 30 maternal parents recommended by Dawson and Were (1997) for adequately capturing genetic variation in trees. In 22% of cases nursery lot establishment from single trees was observed. Low mean N_m values were recorded for both exotic and indigenous categories of trees, and for both common and rare species. Values were low across all areas, with the highest mean N_m value, at Arusha, being only 8.2. Our data therefore indicate clearly that current seed collection practice may restrict on-farm tree genetic diversity in the East Africa region, thereby contributing a significant risk to the productivity and sustainability of agroforestry systems.

In the present study, the quantity of seedlings raised in a nursery lot (N_s) and the projected number of clients for a lot (N_c) were recorded in addition to N_m. A comparison of N_m, N_s and N_c values indicates the importance of randomising progeny from different maternal parents in the nursery. If such mixing is undertaken, clients will generally receive seedlings from most of the maternal parents used to establish nursery lots, thereby maximising the genetic diversity of material distributed. However, if such mixing is not applied (for example, if a nursery lot remains stratified based on a number of separate seed collections), clients may receive seedlings from considerably fewer maternal parents than originally collected. The wide range in N_m, N_s and N_c values observed in the current study within areas, including for particular species across nurseries, suggests further risks to genetic diversity through bottleneck effects. Risks are particularly high since managers, at least of on-farm nurseries, frequently return to their own or neighbouring farms for seed (Lengkeek et al., 2003). Countering this, however, is the longevity of tree species, which allows for overlapping generations and greater effective population sizes to be established.

A number of other factors determine the extent to which current nursery genetic management practices for seed-propagated species impact on farm and landscape tree genetic diversity. First, farm inventories of current tree cover (Lengkeek et al., 2004) and the preliminary nursery survey of Lengkeek et al. (2003) indicate the importance of other types of germplasm, including vegetative propagules, for on-farm tree establishment. Additional research that considers sampling issues for clonal material is therefore required.

Second, the impact of current practices will depend on the origin and history of a given species. Indigenous species may be less sensitive to genetic erosion because of remnant trees that input seed and pollen into subsequent generations of on-farm material. However, the availability of viable remnant trees at locations will likely decrease as the time since land clearance for agriculture increases. Loss of remnant trees may reduce outcrossing levels (Murawski et al. 1994), causing a greater proportion of overall genetic variation to partition among maternal parents (Hartl 1987). This will exacerbate diversity losses when seed is collected from a small number of mother trees. Exotic species depend substantially on the initial genetic base of introduced material, which may already have been narrow. This is particularly likely if introductions took place before the possible impacts of a narrow genetic base were widely appreciated. It appears likely that the most common species detected in the current survey, *G. robusta*, an exotic from Australia, was introduced to East Africa with a rather narrow genetic base (Harwood 1992).

Third, the impact of current practices will depend on issues of spatial scale. It was outside the scope of the current survey to assess the detailed geographic location of tree nurseries and their clients, but clearly this will have an important impact on patterns of tree genetic diversity. For example, if nursery seedlings are distributed over wide geographic areas, a more diverse landscape is expected than from restricted local distribution. In the current study, peri-urban nurseries surveyed from the Nairobi area likely have the widest client distribution, since Nairobi has a national function in tree seedling provision. Farm size will also impact on landscape diversity because of biological constraints to gene flow that homogenises genetic structure. Since farms are expected to be small within the current survey areas, opportunities exist for genetic exchange between them by pollen flow.

Based on the current study, a number of interventions to increase the provision of genetic diversity to farmers through tree nurseries can be postulated. Lengkeek et al. (2003) indicated that during seed collection by nursery managers the number of mother trees sampled depended at least partly on the quantity of seed required rather than the availability of seed-bearing trees. Thus, there appears scope to encourage the collection of a larger number of maternal parents during seed collection, by training of nursery managers. However, access to seed is apparently a limiting factor in much tree planting (Lengkeek and Carsan, 2003), due to low tree densities and aggregated distributions (Kindt et al., 2003; Lengkeek et al., 2004). In this situation, an appropriate intervention is the establishment of local nursery networks, through which germplasm can be exchanged and combined. Finally, our data indicate that encouraging nursery managers to randomise seedlings within nursery lots may have a significant impact on the genetic diversity received by nursery clients. Further research is required in order to more fully understand nursery genetic management issues in East Africa. In particular, alternative sources of tree germplasm should be quantified, the history of exotic introductions assessed, and the detailed spatial distribution of nurseries and their clients analysed.

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References

Boshier D.H. 2000. Mating systems.. In: Young A., Boshier D. and Boyle T. (eds), Forest Conservation Genetics: Principles and Practice, pp. 63-79. CSIRO Publishing, Melbourne, Australia and CABI Publishing, Wallingford, United Kingdom.

Charlesworth D. and Charlesworth B. 1987. Inbreeding depression and its evolutionary consequences. Annual Review of Ecology and Systematics 18: 237–268.

Dawson I.K. and Were J. 1997. Collecting germplasm from trees – some guidelines. Agroforestry Today 9(2): 6–9.

FAO 2001. Global Forest Resources Assessment 2000. FAO Forestry Paper No. 140. FAO, Rome, Italy.

Griffin A.R. 1990. Effect of inbreeding on growth of forest trees and implications for management of seed supplies for plantation programs.. In: Bawa K.S. and Hadley M. (eds), Reproduction Ecology of Tropical Forest Plants. Man and the Biosphere Series, Vol. 7, pp. 355-374. UNESCO, Paris, France and Parthenon Publishing, Carnforth, United Kingdom.

Hartl D.L. 1987. A Primer of Population Genetics. Sinauer Associates Inc., Sunderland, Massachusetts, USA.

Harwood C.E., Bell J.C. and Moran G.F. 1992. Isozyme studies on the breeding system and genetic variation in *Grevillea robusta*.. In: Harwood C.E. (ed.), *Grevillea robusta* in Agroforestry and Forestry, pp. 165-176. Proceedings of an international workshop, held in Nairobi, Kenya. International Centre for Research in Agroforestry, Nairobi, Kenya.

Holding C. and Omondi W. , (eds) 1998. Evolution of Provision of Tree Seed in Extension Programmes: Case Studies from Kenya and Uganda. SIDA Technical Report No. 19. Regional Land Management Unit, Swedish International Development Cooperation Agency, Nairobi, Kenya.

Kindt R. 1997. Local Perceptions on Tree Propagation and Domestication: Results from a Survey in Western Kenya. AFRENA Report No. 115. International Centre for Research in Agroforestry, Nairobi, Kenya.

Kindt R., Lengkeek A.G., Simons A.J., van Damme P., Boffa J.-M., Degrande A., Jourget J.- G., Mbosso C., van Oijen D.C.C. and Weber J.C. 2003. Tree species diversity on farms in Cameroonian, Kenyan and Ugandan landscapes.. In: Lengkeek A.G. (ed.), Diversity Makes a Difference: Farmers Managing Inter- and Intra-Specific Tree Species Diversity in Meru Kenya, pp. 39-54. PhD. Thesis. Wageningen University, Wageningen, The Netherlands.

Lengkeek A.G. and Carsan S. 2003. Diversity makes a difference: farmers' perception of tree species diversity in Meru district, Kenya.. In: Lengkeek A.G. (ed.), Diversity Makes a Difference: Farmers Managing Inter- and Intra-Specific Tree Species Diversity in Meru Kenya, pp. 17-37. PhD. Thesis. Wageningen University, Wageningen, The Netherlands.

Lengkeek A.G., Carsan S. and Jaenicke H. 2003. A wealth of knowledge: how farmers in Meru, central Kenya, manage their tree nurseries.. In: Lengkeek A.G. (ed.), Diversity Makes a Difference: Farmers Managing Inter- and Intra-Specific Tree Species Diversity in Meru Kenya, pp. 69-86. PhD. Thesis. Wageningen University, Wageningen, The Netherlands.

Lengkeek A.G., Kindt R., van der Maesen L.J.G., Simons A.J. and van Oijen D.C.C. 2004. Tree densities and germplasm source in agroforestry ecosystems in Meru, Mt Kenya. Genetic Resources and Crop Evolution (in press).

Murawski D.A., Gunatilleke I.A.U.N. and Bawa K.S. 1994. The effects of selective logging on inbreeding in *Shorea megistophylla* (Dipterocarpaceae) from Sri Lanka. Conservation Biology 8: 997–1002.

SGRP 2000. Genetic Resources Management in Ecosystems. Report of a workshop organized by the Center for International Forestry Research (CIFOR) for the CGIAR System-wide Genetic Resources Programme (SGRP), held in Bogor, Indonesia, June 2000. CIFOR, Bogor, Indonesia.

Simons A.J., MacQueen D.J. and Stewart J.L. 1994. Strategic concepts in the domestication of non-industrial trees.. In: Leakey R.R.B. and Newton A.C. (eds), Tropical Trees: the Potential for Domestication and the Rebuilding of Forest Resources, pp. 91-102. HMSO, London, United Kingdom.

Simons A.J., Jaenicke H., Tchoundjeu Z., Dawson I., Kindt R., Oginosako Z., Lengkeek A. and De Grande A. 2000. The future of trees is on farm: tree domestication in Africa.. In: Krishnapillay B., Soepadmo E., Lotfy Arshad N., Wong A., Appanah S., Wan Chik S., Manokaran N., Lay Tong H. and Kean Choon K. (eds), Forests and Society: the Role of Research. Proceedings of the XXIst IUFRO World Congress, held in Kuala Lumpur, Malaysia, August 2000, Sub-plenary Sessions Vol. 1, pp. 752-760. IUFRO Secretariat, Vienna, Austria and the Forest Research Institute Malaysia, Kuala Lumpur, Malaysia.

Turnbull J.W. 1996. Influence of collection activities on forest tree seed quality.. In: Yapa A.C. (ed.), Recent Advances in Tropical Tree Seed Technology and Planting Stock Production. Proceedings of an international symposium, held in Muak-Lek, Saraburi, Thailand, June 1995, pp. 29-35. ASEAN Forest Tree Seed Centre, Muak-Lek, Thailand.

Weber J.C., Labarta Chávarri R.L., Sotelo-Montes C., Brodie A.W., Cromwell E., Schreckenberg K. and Simons A.J. 1997. Farmers' use and management of tree germplasm: case studies from the Peruvian Amazon Basin.. In: Simons A.J., Kindt R. and Place F. (eds), Policy Aspects of Tree Germplasm Demand and Supply. Proceedings of an international workshop, held in Nairobi, Kenya, October 1997, pp. 57-63. International Centre for Research in Agroforestry, Nairobi, Kenya.