

Tree Mortality and Collecting Botanical Vouchers in Tropical Forests¹

O. L. Phillips

School of Geography, University of Leeds, Leeds LS2 9JT, U.K. and Missouri Botanical Garden, Box 299, St. Louis, Missouri 63166, U.S.A.

P. Nuñez V.², and M. E. Timaná³

Missouri Botanical Garden, Box 299, St. Louis, Missouri 63166, U.S.A.

ABSTRACT

There is growing concern about the potential impact of researchers on tropical forest ecology, but few data. The aim of this paper is to examine the effects of collecting botanical specimens from tropical forest trees on their subsequent survivorship, using mortality data from plots in Amazonian Peru that were established in 1989 and re inventoried in 1994. In total, 2017 trees were originally tagged and collections were made from 948 trees. Making voucher collections always involved using unsterilized telescopic plant collecting poles to cut representative small branches, and sometimes also involved using iron-spiked tree-climbing gear to gain access to the canopy. Annual mortality in the four plots averaged 1.99 percent. Among the whole population of dicotyledonous trees, there was no detectable difference between the mortality rate of collected trees (1.96%) and noncollected trees (2.29%). We conclude that in spite of the physical damage caused to collected trees, collecting voucher specimens from tropical moist forest trees may not affect their survivorship, at least in the short-term. Further studies are needed to fully evaluate the potential impacts of research activities on permanent forest plots in the tropics.

RESUMEN

En este estudio se examina la tasa de mortalidad anual en árboles colectados y no colectados en cuatro parcelas permanentes de una hectárea cada una en la Amazonía Peruana. Las parcelas fueron establecidas en 1989 y reevaluadas en 1994. En total, 2017 árboles fueron inicialmente marcados con placas de aluminio y especímenes de herbario fueron preparados para 948 árboles. La preparación de los especímenes implicó en todos los casos el uso de tijeras telescópicas para cortar pequeñas ramas representativas, y en algunos casos se tuvo que usar subidores metálicos con espigas de acero para tener acceso al dosel. La mortalidad anual en las cuatro parcelas fue de 1.99 por cien en promedio. Entre la población de árboles dicotiledones no hubo mayor diferencia entre la tasa de mortalidad de árboles colectados (1.96%) y no colectados (2.29%). Concluimos que a pesar del aparente daño en la corteza en algunos árboles, la colección de especímenes en bosques húmedos tropicales probablemente no afecta la sobrevivencia de especies arbóreas, al menos en el corto plazo. Se sugieren estudios adicionales para evaluar más completamente los efectos potenciales de las actividades científicas en parcelas permanentes en los trópicos.

Key words: Amazonia; collecting; permanent plots; Peru; tree mortality; tropical forests; voucher specimens.

THE INSTALLATION AND REINVENTORY OF PERMANENT TREE PLOTS are important prerequisites for the investigation of tropical forest diversity and ecological processes. Permanent plots have become increasingly popular research tools (Dallmeier & Comiskey, in press). At least 70 floristically inventoried permanent tree plots of one ha or greater had been

established in western Amazonia by early 1994 (Clinebell *et al.* 1995), and a subsequent tally made in late 1995 revealed at least 90 permanent plots (Rose 1996). Tropical forest inventory plots have been variously used to examine regional and pan-tropical patterns of forest structure (Ashton & Hall 1992), tree diversity (Gentry 1988a,b), tree turnover (Phillips & Gentry 1994, Phillips 1996), possible linkages between productivity and diversity (Phillips *et al.* 1994), and hypotheses of community structure (Terborgh *et al.* 1996). Larger plots, up to 50 ha in area and sampling a quarter of a million individual trees, are providing insights into the mechanisms by which the diversity of tropical

¹ Received 17 November 1995; revision accepted 12 December 1996.

² Current address: Biodiversidad Amazónica, Umachata 136, Cusco, Peru.

³ Current address: Department of Botany, University of Texas at Austin, P.O. Box 7640, Austin, TX 78713-7640, U.S.A.

forest plants and animals is maintained (Condit *et al.* 1992, Condit 1995). Additionally, by generating site-specific long-term observations, permanent plots provide an invaluable baseline against which natural and anthropogenic changes can be detected (Risser *et al.* 1993). Such baseline studies have assumed a new importance with the current need to understand and predict the effects of global and regional change on the remaining tropical forests. With so much depending on them, it is critical that permanent plots generate reliable information on the systems they purport to represent. One potential source of bias that might compromise the validity of the long-term plot results could be the research activity itself, if it has an impact on the forest ecology.

Permanent plots are established for various reasons. For example, systematists or floristically-oriented ecologists may be more interested in gaining information on the full spectrum of plant diversity and composition, while foresters may seek to understand the growth of commercial timber species. Investigators concentrating on making inventories might not be particularly concerned about the possible impacts of their research on the forest, and this could have implications for interpreting long-term ecological data derived from the same plots. Even in studies where long-term research objectives are considered a high priority from the outset, there is still a danger that the research activity itself could damage components of the forest. Examples of research activity that could have a substantial impact on the system being studied are: (1) trees and lianas are often climbed and/or parts are cut from them to prepare botanical specimens; (2) trees are often labelled with aluminum nails and tags, the nail penetrating at least through the phloem and usually into the xylem; (3) initial surveying, mapping, collecting, and measuring, and later reinventory, of permanent plots causes repeated localized trampling of seedlings and ground layer vegetation, and some soil compaction; and (4) these and other research activities might displace pollinators, seed-dispersors (or their predators), potentially affecting the relative future recruitment success of different plant species. Sheil (1995) has made a detailed consideration of these various methodological issues in relation to plots in Africa. The ecological research community has recently become more sensitive to these potential impacts (*e.g.*, Burrows *et al.* 1994, Ginsberg *et al.* 1995, Ingram & Lowman 1995, Moffett & Lowman 1995) and given the scientific significance of permanent plots, tests of possible "researcher effects" on population dynamics are

highly desirable. Yet to our knowledge no such tests have been attempted so far for plant populations at any site in the tropics.

The purpose of this paper is to look at possible impacts of botanical collection on tropical trees in particular, and to highlight the need for investigation into the wider issue of research impacts on tropical forests in general. The impetus for this study came from the finding that tropical forest plots have experienced increased tree turnover (Phillips & Gentry 1994), and several independent suggestions (*e.g.*, B. Nelson, pers. comm.; D. Sheil, pers. comm.) that the initial or cumulative impact of research activity on tree survivorship in permanent plots could be an artifactual explanation for this finding (Phillips 1995). These suggestions caused us to examine our inventory data, to see if we could detect such an effect in forests where we had reliable records of exactly which individual trees were collected in inventory plots. There is some reason to suspect a tree "collection effect" on mortality, since a collected tree is often subject to multiple wounds to the cambium of its main stem and smaller branches. Complete inventories of most groups of plants or animals are notoriously difficult to make in tropical forests, and canopy trees and lianas are particularly hard to collect, often requiring the use of physically damaging techniques to access plant parts up to 30 m above the forest floor. We hypothesize that the damage involved in collecting botanical samples could increase the probability of mortality of a collected tree by making it more vulnerable to pathogenic infections.

Botanists use several approaches to gain access to the canopy. One favored method when dozens of canopy climbs are needed is to use a pair of heavy spiked climbing irons (Mori & Prance 1987). Skilled users can rapidly climb tree trunks to a sufficient height to make collections, but the spikes cause noticeable damage to the tree bark, penetrating 5–10 mm deep, and scraping off shallow segments up to 50 mm long from the outer bark. A typical 15 m climb results in over 400 small wounds to the tree bole [seven spikes per iron, 50 cm per step = 30 steps up, 30 steps down, two steps at the top to gain a comfortable position: total = $(7 \times 30) + (7 \times 30) + (7 \times 2) = 434$ wounds; these totals would obviously vary according to the particular brand and type of spiked climbing equipment used]. Qualitative observations at numerous forest localities in Peru suggest that most tree species (with the main exception of arborescent palms) have a macroscopic physiog-

nomic wound response to tree tagging or collection marks, while some taxa (such as *Inga*, *Eschweilera*, Myristicaceae) can sometimes bear marks from these small wounds for up to 10 yr or more (P. Nuñez, pers. obs.; R. Vásquez, pers. comm.; R. Ortiz, pers. comm.). Such is the visible damage that climbing irons cause that some canopy biologists have suggested that they should not be used at all by responsible biologists (Moffett & Lowman 1995). Additional damage to the tree, albeit less visible to a ground-based observer, results from using extendable aluminum clipping poles to collect ample material to make herbarium duplicates from each tree. Collections are made from one or more accessible canopy branches up to 40 mm in diameter, and additional branches are frequently cut to gain better access to the preferred branches. Neither the climbing irons nor the clipper-poles are ever sterilized, so each wound not only gives airborne pathogens opportunities for infection, but theoretically could also facilitate transmittal of infection from one tree to another, and infection by pathogen propagules in the soil and the leaf litter.

STUDY SITE

In the course of projects begun by the late A. H. Gentry, we have established and recensused 13 permanent forest plots at four Peruvian sites. However, we only have reliable records of exactly which individual trees were collected and which were not at four inventory plots in the Cuzco Amazónico Reserve. This dataset allows us to investigate the potential impact of an initial period of tree collecting activity on subsequent tree survivorship over 4–5 yr. The reserve covers 10,000 ha centred at 12°35'S, 69°09'W, in Madre de Dios, Southeast Peru, at about 200 m altitude on the north bank of the Madre de Dios river (Duellman & Koechlin 1991) (Fig. 1). Annual rainfall is between 2000 and 2400 mm (estimated from data available from the town of Puerto Maldonado and the nearby Tambopata Reserved Zone, Phillips 1993), with a moderate dry season that includes three consecutive months averaging less than 100 mm. Although the macroscale topography is almost flat, the reserve is covered by a mosaic of contrasting types of lowland tropical moist forest. Well-drained, species-rich high forest grows on the slightly higher alluvial terraces of the recent, Holocene floodplain of the Madre de Dios river (Räsänen *et al.* 1992); poorly-drained swamps cover the old backwashes and channels of the same recent floodplain. Most swamps are dominated by a few tree species (es-

pecially *Mauritia flexuosa* and *Ficus* sp.) and/or by dense stands of rhizomatous monocotyledonous herbs. By the standards of neotropical forests, the alluvial soils of the area have high concentrations of available nutrients (Clinebell *et al.* 1995). The reserve is subject to hunting pressure and occasional selective logging, and may eventually become isolated from other forested regions as farmers clear land along its edges.

METHODS

In May 1989 A. H. Gentry and all three authors established permanent forest plots at Cuzco Amazónico, tagging and measuring all trees and lianas ≥ 10 cm diameter in four transects of 20 by 500 m. Vouchers were collected with clipper poles and climbing irons between 1989 and 1991. The plots mostly represent the well-drained, species-rich forest, but patches within the plots are ecotonal with the species-poor swamp forest. At no point before, during, or after any collections were made was the climbing and collecting equipment sterilized. The plots were recensused in August 1994 by O. P. and P. N., at which time all tree, strangler and liana deaths and all new recruits into the 10 cm diameter class were noted. The mean time that elapsed between plot censuses was 5.25 yr, and the time elapsed between the median collection date and the recensus date averaged 4.27 yr. Of the 2017 trees that were tagged in 1989, voucher collections were subsequently made from 948 trees, 221 of which were collected twice and 17 of which were collected three times. Some trees were also climbed, in order to get closer to collectable leaves, flowers, or fruits on the same tree. Occasionally a tree was climbed to gain access to the canopy of a very large or inaccessible adjacent tree or liana, but in such cases collections were also made from the climbed tree, itself, so as to gain maximum benefit from the effort expended climbing the tree. We did not record which individual trees were climbed, but we estimate that they comprise about 20 percent of all collected trees.

With very few exceptions, each species was collected at least once. However, most species in large, taxonomically difficult tree families (*e.g.*, Fabaceae, Lauraceae, Moraceae, Sapotaceae) were collected multiple times because it was not usually possible to confirm their specific identification from the ground without having a voucher collection in hand. Some individual trees were also collected more than once, in order to gain fertile material from trees that may have been sterile when initially

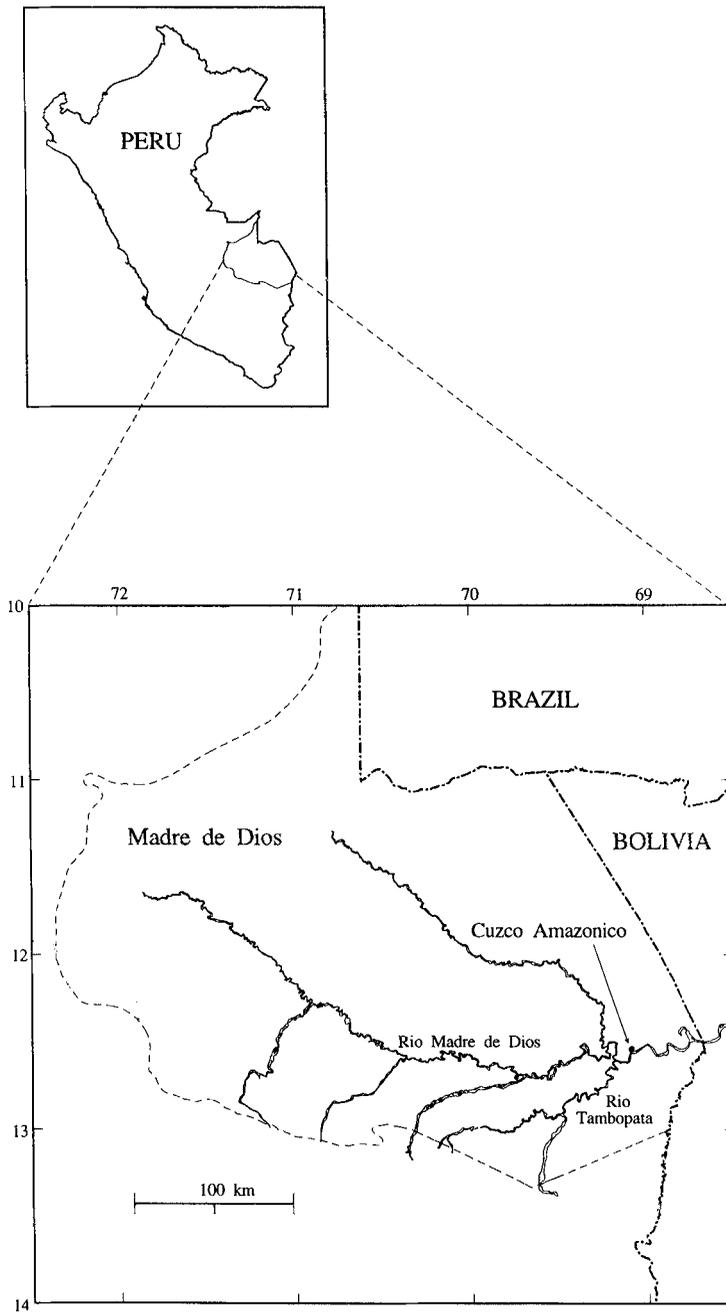


FIGURE 1. Map of Peru and Madre de Dios, showing the location of Cuzco Amazónico (map courtesy of Sam Rose).

collected. Collection effort was therefore spread among most taxa, but in most cases was also distributed in approximate proportion to a taxon's density in each plot.

However, the initial population of collected

trees was slightly different from the population of noncollected trees in two respects that could potentially bias the comparison in their mortality rates. First, the most structurally significant component of the forest, large palms, were very rarely

TABLE 1. Size distribution of collected and non-collected trees.

Size-Class	Collected	Not collected	Total
Numbers in brackets represent percentage of totals.			
(A) All species			
10–19.9 cm d.b.h.	620 (31%)	674 (33%)	1294 (64%)
20–29.9 cm d.b.h.	161 (8%)	232 (12%)	393 (19%)
≥30 cm d.b.h.	167 (8%)	163 (8%)	330 (16%)
Total	948 (47%)	1069 (53%)	2017
(B) Dicotyledonous species			
10–19.9 cm d.b.h.	618 (37%)	477 (29%)	1095 (66%)
20–29.9 cm d.b.h.	161 (10%)	112 (7%)	273 (16%)
≥30 cm d.b.h.	167 (10%)	121 (7%)	288 (17%)
Total	946 (57%)	710 (43%)	1656

collected. Arborescent palms are easy to identify to “morphospecies” (Gentry 1982) from the ground and are very time-consuming to collect, and so we consciously avoided collecting them (only two arborescent palm individuals were collected in the plots). Since palms comprise 18 percent of all free-standing stems ≥ 10 cm diameter in the Cuzco Amazónico plots, any intrinsic differences in mortality rates between populations of palms and dicotyledonous trees should be controlled for when comparisons are made between the mortality rates of the collected and noncollected trees. The second difference between collected and noncollected trees is related to size. We applied a simple *a priori* size-class classification, scoring all trees as being either “small”, *i.e.*, between 10 and 20 cm diameter at breast height (DBH), “medium”, *i.e.*, between 20 and 30 cm DBH, or “large”, *i.e.*, ≥ 30 cm DBH. As Table 1a shows, there was a slight tendency to overcollect large trees and undercollect medium sized trees relative to the number of trees in each size-class. However, a chi-squared test shows that the apparent association between tree size-class and collection effort was not statistically significant ($X^2 = 7.89$, $df = 5$, $P > 0.1$). Once palms are taken out of the analysis, then any difference in collection effort allocated to each size-class of tree disappears (Table 1b.). Thus, among dicotyledonous trees the size-class distributions of collected and noncollected trees were indistinguishable ($X^2 = 0.68$, $df = 5$, $P \geq 0.95$). In sum, the starting populations of the collected and noncollected dicotyledonous trees are similar in terms of taxonomy and size, giving us confidence that any difference in their mortality rates would be principally an effect of collection activity.

To test for a collection effect on survivorship, we compared mortality rates of collected trees and

noncollected trees using a paired *t*-test. This was done separately first for all trees and then for the dicot tree subset in order to control for the potentially complicating factor of under-collection of palms. A comparison of climbed vs. nonclimbed trees could not be made, as we did not have records of which trees were climbed. Annual mortality rates were calculated according to standard procedure (Swaine & Lieberman 1987), by the formula $[\ln((N_o - N_d) / (N_o) / t) \times (-100\%)]$, where N_o is the population originally censused, N_d is the number of trees dying by the time of the second census, and t is the time elapsed (yr) between censuses. Confidence intervals for mortality rates were computed using the normal approximation to the binomial variance (Condit *et al.* 1995), to assess the statistical significance of any differences in mortality rates.

RESULTS

Averaged across all four plots, the annualized tree mortality rate was 1.99 percent (lowest plot mortality rate 1.17%, greatest plot mortality rate 2.92%). If the data from all four plots are pooled and the mean period length of 4.27 yr is used to calculate mortality for all trees, the average mortality rate is 2.01 percent (95% confidence intervals for the rate: 1.71%, 2.32%). These values indicate that the forests at Cuzco Amazónico are certainly dynamic, but not exceptionally so when compared to the high tree mortality rates that seem to characterize many Amazonian forests (Phillips *et al.* 1994).

MORTALITY OF COLLECTED VS. NOT COLLECTED TREES.—Across all plots, mortality rates for collected trees ($2.07 \pm 0.32\%$) could not be distinguished

TABLE 2. Total numbers of trees inventoried, collected, and dead.

Plot	Area (ha)	Time ^a	Total trees	Trees collected	Trees not collected	Total trees dead	Total trees collected dead	Total trees not collected dead	Annual mortality (%), all trees	Annual mortality (%), collected	Annual mortality (%), non-collected
(A) All species											
1	1.0	4.14	482	364	118	38	27	11	1.984	1.862	2.364
2	1.0	4.14	499	211	288	28	10	18	1.395	1.173	1.559
3	1.0	4.14	469	239	230	42	22	20	2.266	2.333	2.197
4	1.0	4.65	567	134	433	58	17	41	2.320	2.918	2.139
Sum	4.0		2017	948	1069	166	76	90	2.011 ^b	1.957 ^b	2.060 ^b
Mean		4.27	504	237	267	41.5	19.0	22.5	1.991 ^c	2.071 ^c	2.065 ^c
Std. error of mean		0.11	18	57	57	5.40	3.14	5.60	0.183	0.320	0.152
(B) Dicotyledonous species											
1	1.0	4.14	405	363	42	34	27	7	2.118	1.867	4.404
2	1.0	4.14	367	210	157	17	10	7	1.146	1.179	1.102
3	1.0	4.14	402	239	163	37	22	15	2.333	2.333	2.332
4	1.0	4.65	482	134	348	54	17	37	2.555	2.918	2.417
Sum	4.0		1656	946	710	142	76	66	2.100 ^b	1.961 ^b	2.285 ^b
Mean		4.27	414	237	177.5	35.5	19.0	16.5	2.038 ^c	2.074 ^c	2.564 ^c
Std. error of mean			21	41	54.8	6.56	3.14	6.14	0.269	0.319	0.591

^a From median collection date to reinventory.

^b Data pooled from all plots.

^c Results averaged from each plot.

from those of not collected trees ($2.07 \pm 0.15\%$) (data from Table 2a). Once palms are excluded from the sample we are left with 1656 dicotyledonous trees, of which 946 were collected by poles or by poles and climbing irons. For this slightly smaller group, collecting also has no apparent detrimental effect on survivorship. Across all plots, the mortality rate of collected dicots is slightly lower than the mortality rate of not collected dicots (respectively, 2.07 ± 0.32 vs. $2.56 \pm 0.59\%$; $t = 0.71$, $P = 0.53$) (data from Table 2b). Note that the power of this paired t -test is low, however, at only 0.17.

We also pooled the data from all four plots to calculate one mortality rate for the whole collected and noncollected populations; this too suggested that there is no apparent difference between the two groups (Fig. 2). However, since the sample sizes of each initial population and the number of trees that died are rather small, there is a wide spread between lower and upper confidence intervals illustrating the degree of uncertainty attached to each mortality rate estimate.

Two further calculations shed light on the comparisons between mortality rates in the non-collected and collected populations. First, the

minimum difference in mortality rates that could be distinguished—given the sample size—was estimated according to the criterion suggested by Condit (1995, pers. comm.) and Hall (pers. comm.) that the upper 95 percent confidence interval of the lower rate be no greater than the lower 95 percent confidence interval of the higher rate. (This is probably rather conservative, since two rates with nonoverlapping 95 percent confidence intervals tend to differ under t -tests at $P \sim 0.01$.) If the mortality of noncollected dicots (2.29%) is fixed at the observed rate, in order for collected dicots to have a different mortality rate either at least 129 collected dicots would need to have died at an annual rate of 3.43 percent (significantly greater, $t = 2.56$, $P \sim 0.01$), or no more than 53 would need to have died at an annual rate of 1.35 percent (significantly less, $t = 2.5$, $P \sim 0.01$). Second, the initial sample size required to distinguish between the observed mortality rates of collected and not collected dicots was computed by the criterion of nonoverlapping 95 percent confidence intervals. This value is 7650 (at which point, the observed mortality rate of collected dicots would be marginally less than that of noncollected dicots)—a good indication of the

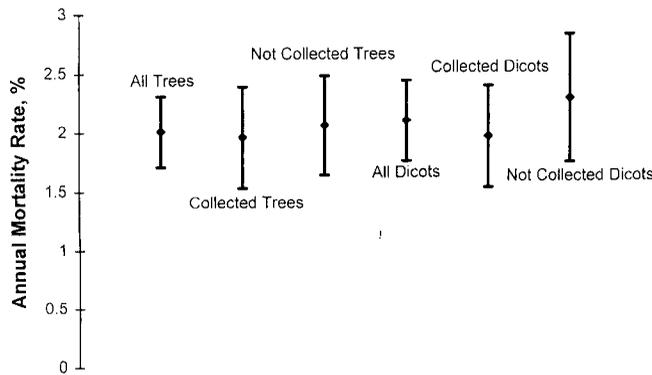


FIGURE 2. Annual mortality rates of trees, irrespective of plots. The mean and the upper and lower 95 percent confidence intervals are given for measured mortality rates of each tree population at Cuzco Amazónico (all trees, collected trees, not collected trees, all dicots, collected dicots, not collected dicots).

similarity of the two rates. So, it is reasonable to conclude that while the limited sample sizes constrain the strength of the test of the null hypothesis, the similarity in the measured mortality rates indicates that it is very unlikely that collecting can have had a substantial effect of enhancing tree mortality rates.

DISCUSSION

Botanical collection activity did not appreciably increase the risk of tree death, at least for the duration of the study. This is an encouraging first result, but it should be interpreted with caution. Because of the limitations in the dataset, we cannot rule out the possibility of a weak effect of collecting on mortality. Moreover, this is the only report of which we are aware that has investigated the possible impact of *any* research activity on large trees. Clearly, this single result should certainly not be taken to imply that permanent plot research cannot have a substantial impact on the lowland tropical forests.

There are several ways by which researchers could still be having an unintentional impact on the plant populations they study within permanent plots. For example, populations of seedlings and regenerating saplings underneath collected trees are likely to be both reduced and perhaps compositionally altered by the activities of eager botanists (although arguably the trampling effects of botanists may come close to simulating the actions of large mammals that until very recently may have been quite abundant in many tropical forests!). Other possibilities are that adult tree mortality induced by intense collection might not become ap-

parent until after five yr of observation, or that collection could cause a long-term decline in tree vigor relative to noncollected trees. Future censuses of these plots should help to clarify any of these possible longer-term impacts of collecting (as well as improving the power of the test of the null hypothesis of no difference between collected and not collected trees). However, collecting voucher specimens is only one form of research activity performed in permanent plots, even though its physical impact is particularly obvious. At Cuzco Amazónico, for example, every tree was also tagged with an aluminum nail and tag, and vertebrates were intensively censused and collected from the plots in 1989–90. We have no controls for these activities. Our results, therefore, only apply to the relative impact on tree survivorship of these activities *plus* tree collection activities, versus these activities alone. In spite of these caveats, our results do indicate that intensive collection activity does not have a substantial effect on the survivorship of adult trees, at least for the standard, permanent plot methodology in tropical forests in which all trees ≥ 10 cm DBH are inventoried. We hope that our analysis will serve to encourage more permanent plot researchers to explore whether and how their research might be impacting the system they are studying.

ACKNOWLEDGMENTS

The Cuzco Amazónico plots were established with support from the National Geographic Society (BIOTROP program grant to W. E. Duellman (University of Kansas) and to A. H. Gentry (Missouri Botanical Garden)) and further collections were enabled by a MacArthur Foun-

dation award to the Missouri Botanical Garden. Reinventory was supported by a Michaux Award to Oliver Phillips from the American Philosophical Society. We thank Nestor Jaramillo for his valuable help in the field, Rodolfo Vásquez for advice, Sam Rose for producing the map, and Pamela Hall, Karel Jacobs, Jim Miller, and Peggy

Stern for valuable comments and advice on the manuscript. Pamela Hall drew our attention to the method for computing binomial confidence intervals for mortality. Suggestions from Bruce Nelson, Douglas Sheil and Val Kapos first stimulated us to examine our permanent plot data for a collection effect.

LITERATURE CITED

- ASHTON, P. S., AND P. HALL. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *J. Ecol.* 80: 459–481.
- BURROWS, R., H. HOFER, AND M. L. EAST. 1994. Demography, extinction, and intervention in a small population: the case of the Serengeti wild dogs. *Proc. Royal Soc.* 256: 281–292.
- CLINEBELL, R., O. L. PHILLIPS, A. H. GENTRY, N. STARK, AND H. ZUURING. 1995. Prediction of neotropical woody plant diversity from climatic and soil data. *Biodiv. Cons.* 4: 56–90.
- CONDIT, R. 1995. Research in large, long-term tropical forest plots. *Trends Ecol. Evol.* 10: 18–22.
- , S. P. HUBBELL, AND R. B. FOSTER. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *Am. Nat.* 140: 261–286.
- , ———, AND ———. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Mon.* 65: 419–439.
- DALLMEIER, F., AND J. COMISKEY (EDS.). In press. *Measuring and monitoring biological diversity*, Smithsonian Institution Press, Washington, DC.
- DUJELLMAN, W. E., AND J. E. KOECHLIN. 1991. The Reserva Cuzco Amazónico, Peru: biological investigations, conservation, and ecotourism. *Univ. Kansas Mus. Nat. Hist. Occ. Papers* 142: 1–38.
- GENTRY, A. H. 1982. Patterns of Neotropical plant species diversity. *Evol. Biol.* 15: 1–84.
- . 1988a. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* 75: 1–34.
- . 1988b. Tree species richness of upper Amazonian forests. *Proc. Nat. Acad. Sci., U.S.A.* 85: 156–159.
- GINSBERG, J. R., K. A. ALEXANDER, S. CREEL, P. W. KAY, J. W. MCNUFF, AND M. G. L. MILLS. 1995. Handling and survivorship of African wild dogs (*Lycan pictus*) in five ecosystems. *Cons. Biol.* 9: 665–674.
- INGRAM, S. W., AND M. D. LOWMAN. 1995. The collection and preservation of plant material from the tropical forest canopy. In M. D. Lowman, and N. M. Nadkarni (Eds.), *Forest canopies*, pp. 587–603. Academic Press, San Diego, California.
- MOFFETT, M. W., AND M. D. LOWMAN. 1995. Canopy access techniques. In M. D. Lowman, and N. M. Nadkarni (Eds.), *Forest canopies*, pp. 3–26. Academic Press, San Diego, California.
- MORI, S. A., AND G. T. PRANCE. 1987. A guide to collecting Lecythidaceae. *Ann. Mo. Bot. Gard.* 74: 321–330.
- PHILLIPS, O. L. 1993. The potential for harvesting fruits in tropical rainforests: new data from Amazonian Peru. *Biodiv. Cons.* 2: 18–38.
- . 1995. Evaluating turnover in tropical forests. *Science* 268: 864–865.
- . 1996. Long-term environmental change in tropical forests: increasing tree turnover. *Env. Cons.* 23: 235–248.
- , AND A. H. GENTRY. 1994. Increasing turnover through time in tropical forests. *Science* 263: 954–958.
- , P. HALL, A. H. GENTRY, R. VÁSQUEZ, AND S. A. SAWYER. 1994. Dynamics and species richness of tropical rain forests. *Proc. Nat. Acad. Sci., U.S.A.* 91: 2805–2809.
- RASANEN, M., R. NELLER, J. SALO, AND H. JUNGNER. 1992. Recent and ancient fluvial deposition systems in the Amazonian foreland basin, Peru. *Geol. Mag.* 129: 293–306.
- RISSE, P. G., J. LUBCHENCO, N. L. CHRISTENSEN, P. J. DILLON, L. DIEGO GOMEZ, D. J. JACOB, P. L. JOHNSON, P. MATSON, N. A. MORAN, AND T. ROSSWALL. 1993. Ten-year reviews of the national science foundation long-term ecological research (LTER) program. National Science Foundation, Arlington, Virginia.
- ROSE, S. 1996. Classification and mapping of Amazonian tree biodiversity. Ph.D. Thesis, School of Geography, University of Leeds, U.K.
- SHEIL, D. 1995. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. *For. Ecol. Man.* 77: 11–34.
- SWAINE, M. D., AND D. LIEBERMAN. 1987. Note on the calculation of mortality rates. *J. Trop. Ecol.* 3: ii–iii.
- TERBORGH, J., R. B. FOSTER, AND P. NÚÑEZ V. 1996. Tropical tree communities: a test of the nonequilibrium hypothesis. *Ecol.* 77: 561–567.
-