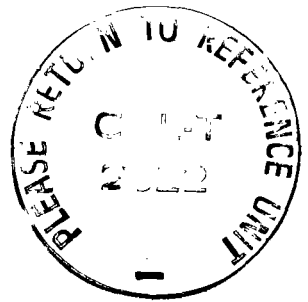# LONG-TERM MONITORING OF BIOLOGICAL DIVERSITY IN TROPICAL FOREST AREAS

METHODS FOR ESTABLISHMENT AND INVENTORY OF PERMANENT PLOTS

Edited by
Francisco Dallmeier

MAB DIGEST 11

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Methods for establishment and inventory of permanent plots

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PREFACE

About this series...

The MAB Digest Series was launched by UNESCO in 1989. Several types of publications are included: distillations of the substantive findings of MAB activities; overviews of recent, ongoing and planned activities within MAB in particular subject or problem areas; and proposals for new research activities. The target audience varies from one digest to another. Some are designed with planners and policy-makers as the main audience in mind. Others are aimed at collaborators in the MAB Programme. Still others have technical personnel and research workers as the target, irrespective of whether or not they are involved in MAB.

...and MAB Digest 11

This digest describes methods for establishing and maintaining permanent inventory plots in tropical forests, with emphasis on sites designated as biosphere reserves. Underlying aims are to facilitate the documented inventory of plant diversity and to provide long-term data on the growth, mortality, regeneration, and dynamics of forest trees. As such, the approach and methods set out in this digest are intended to support the development of an information base for research and education that will contribute to the conservation and management of biosphere reserves and other protected areas throughout the world and to the monitoring of long-term environmental change.

The digest contains two sections: a description of the methods for establishing long-term biodiversity inventory plots in tropical forests is complemented by a case study of Luquillo Biosphere Reserve in Puerto Rico. The intended primary audiences of the digest are researchers and reserve managers who are starting work on permanent forest inventory plots, particularly in tropical regions. The digest may also be useful in training and educational activities based on inventory plots.

The digest is based on methods developed, tested and refined since 1987 within the Smithsonian Institution/MAB Biological Diversity Program, which was set up at the initiative of the Smithsonian Institution (SI). UNESCO has been pleased to be associated with this venture since 1987, particularly through providing financial and technical support to field training in such countries as Bolivia, Brazil, Ecuador, Guatemala, Panama, and Peru.

The digest has been compiled and written by researchers involved in the SI/MAB Biodiversity Program.

Francisco Dallmeier is the Director of Smithsonian Institution/Man and the Biosphere Biological Diversity Program (SI/MAB), co-ordinating international research and training activities on biodiversity monitoring for the SI/MAB international biodiversity plot network. Margo Kabel is a computer specialist at the Smithsonian Institution and has developed the computer mapping program used to generate the vegetation maps for the biodiversity plots. John Mayne is a graduate student at the University of Florida (Gainesville) and assisted with data analysis and calculations for the data set on the Bisley Biodiversity Plot in Luquillo, Puerto Rico. Richard Rice, a natural resources economist at The Wilderness Society, has conducted field work establishing the international network of biodiversity plots. Charlotte Taylor, a botanist with the Missouri Botanical Garden, conducted field work and species identification for the Bisley Biodiversity Plot in Puerto Rico.

CONTENTS

SUMMARY

Forest inventory plots provide one approach to documenting and monitoring plant diversity and are one means for obtaining long-term data on the growth, mortality, regeneration, and dynamics of forest trees. Many forest plots have been set up over the last few decades, but their scientific and practical results have not been commensurate with the time and money invested in their establishment and maintenance. Reasons for shortfalls between expectation and performance have been several: difficulties in funding long-term studies and research infrastructures; absence of sound scientific problematique; inability to handle large amounts of data; absence of agreed methodologies for ensuring cross-site comparability of data; dislocation between functions of research, resources management, and building up of local capacities. However, in the last decade modern computer-based technologies have opened new possibilities for surveying and establishing forest plots, for inventories and monitoring of plants present in those plots, and for using the inventoried plots in research, training, and resource management efforts.

This digest describes methods used by the Smithsonian Institution/Man and the Biosphere Biological Diversity Program (SI/MAB) and the Biological Diversity in Latin American Program (BIOLAT) for establishing and maintaining permanent inventory plots in tropical forests, with emphasis on sites designated as biosphere reserves[1]. It begins with a brief

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1. The SI/MAB Program is part of the overall effort of the Smithsonian Institution and of UNESCO in inventorying and monitoring biological diversity in tropical forests. BIOLAT is a complementary initiative of the Smithsonian Natural History Museum that provides survey and inventory data for additional taxa in several of the South American research sites.

description of the research sites where long-term inventory plots have been established: Beni Biosphere Reserve (Bolivia), Manu Biosphere Reserve (Peru), Luquillo Experimental Forest and Biosphere Reserve (Puerto Rico), Virgin Islands National Park and Biosphere Reserve (US Virgin Islands) and Great Smoky Mountains in the Southern Appalachians Biosphere Reserve (USA).

The permanent plot methodology is used to document species diversity and tree composition in protected forest areas. The plot is designed as a zone encompassing 25 ha, divided into 25 plots of 1 ha. Each 1-ha plot is in turn subdivided into 25 quadrats 20 x 20 m in size, with the quadrats permanently marked. Each tree ≥ 10 cm dbh is mapped in relation to two adjacent corner stakes, tagged, and identified. The data generated from each plot are entered, stored, and analyzed in personal computers. Tree coordinates and preliminary species information are entered in the field on portable laptop computers and later transferred to desktop computers in the office or laboratory. Users' guides and field guides make available to reserve managers, students, and researchers, all the basic information gathered in the plots. Loose-leaf folders and flip charts facilitate continuous updating as more information becomes available.

The detailed description of recommended procedures for field work and data management (including suggestions on ways to improve these processes) is complemented in the second half of the digest by a case study of Luquillo Biosphere Reserve and the effects of Hurricane Hugo in September 1989 on the permanent plot that had been established and censused in 1988. Two subsequent censuses have provided comparative information on hurricane effects on standing trees and basal area and crown damage, while changes in relative density, frequency, and diversity give a measure of the·impact of the hurricane on species composition.

METHODS FOR LONG-TERM BIODIVERSITY INVENTORY PLOTS IN PROTECTED TROPICAL FOREST

Francisco Dallmeier, Margo Kabel and Richard Rice

Introduction

Overview

Scientists estimate that over the next 25 years, more than a million species of plants and animals will become extinct (Ehrlich and Wilson 1991; Mann 1991; Myers 1988; Solbrig 1991a, 1991b; Soulé 1991; Wilcove 1987, 1988; Wilson 1988). Most of these extinctions will occur in the tropics where the pressure of poverty and population growth and a lack of technical and scientific infrastructure make conservation efforts extremely difficult. Such efforts are often further hampered by the absence of basic information on the biological resources most in need of protection. Long-term forest inventories are one means of obtaining such information.

During the period 1987-1991, procedures for establishing permanent forest inventory plots were tested and refined at field sites in Bolivia, Peru, Puerto Rico, and the US Virgin Islands, as well as in Great Smoky Mountains National Park, as part of the Smithsonian Institution/MAB Biological Diversity Program (SI/MAB). SI/MAB researchers visited a number of research plots established by other institutions in several countries, including Brazil, Ecuador, Indonesia, Malaysia, Panama, Puerto Rico, and Venezuela. Changes in protocols for those sites were made to insure flexibility and maximum usefulness of the SI/MAB procedures under a variety of research conditions. The resulting protocol stems from many discussions with a number of researchers conducting plot work and from our own experience.

The goals of the SI/MAB Program are to: 1) facilitate a documented inventory of plant diversity; 2) provide long-term data on the growth, mortality, regeneration, and dynamics of forest trees; and 3) create an information base for research and education that will contribute to the conservation and management of biosphere reserves and other protected areas throughout the world (SI/MAB Biological Diversity Program 1991).

To conserve tropical forest diversity and promote sustainable use of forest resources, it is necessary to understand how forests change. The permanent plot inventory system provides a baseline distribution of tree species and describes habitats within a particular site. Monitoring changes, or lack thereof, in these plots over time enables an understanding of the impact of natural and man-made disturbances on species and communities composition. Data produced through monitoring can also be used to predict changes, based on our present understanding of the ecosystems. Small plots up to two ha in size and containing 1200 to 1400 trees ($\geq$ 10 cm dbh) within a protected area can provide a window on species diversity and allow relatively quick and accurate characterizations of the larger forest.

Long-term forest inventories can provide managers with important information needed to establish conservation priorities and serve as the base of future work. Without adequate inventories, managers cannot measure change over time, identify gaps in existing knowledge, or set priorities to fill these gaps. They have little idea of what and how management activities should be modified to ensure that conservation objectives are met. Simply put, good inventory data are key to successful research projects, conservation, and management. Permanent inventory plots can provide data that are otherwise unobtainable and that, when maintained and measured repeatedly, become more valuable over time (Curtis 1983).

Long-term inventories can also be used to help integrate management of protected areas with compatible development on surrounding lands. Data gathered from permanent inventory plots in temperate forests have long been used to project future growth and yields on managed timberlands (Curtis 1983), information that is critical in planning for sustainable logging. Similar information is needed to ensure that logging in tropical forests proceeds in a sustainable fashion.

This paper provides an opportunity for those who are starting work on permanent inventory plots to benefit from the accumulated experience of past researchers. It is also intended to promote a greater degree of consistency in the type of data collected at different locations and elicit a better

understanding of what data are avaliable for comparison with other research plots in the tropics. Analyses of plant diversity and forest dynamics within regions are badly needed to advance conservation objectives for large areas. Few individual researchers have data adequate for this purpose, and there is much to be gained by pooling data through the cooperative efforts of research workers and organizations - particularly in the context of formal, international designations such as biosphere reserves (Curtis 1983). This requires compatibility and comparable reliability in the data collected at different sites (Synnott 1979; Curtis 1983).

Good biodiversity inventory data are key to successful research, conservation, and management. When these data are integrated with long-term inventory plots, they can provide data that are otherwise unobtainable and that, when maintained and measured repeatedly, become more valuable over time.

In addition, it can be expected that in the future the data generated by permanent plots will be analysed by many researchers and often for purposes not anticipated by the initial investigators. Objectives and procedures change with time, and there can be no guarantee that the procedures and analyses foreseen when the plots were established will be those deemed appropriate at a later date. Data and procedures in long-term inventories should therefore be as complete and general as possible; it is usually worth the added time and effort to obtain accurate readings on a wide range of measurements. Shortcuts should be avoided, as they may limit the usefulness and reliability of the data for subsequent researchers.

Portions of the text may appear at first to be mere repetitions of the obvious. Experience has shown, however, that some issues become obvious only at the analysis stage - when it is too late to return to the field and correct mistakes. Although an in-depth treatment of sampling design

is beyond the scope of this contribution, some discussion of sampling is included in the description of plot installation and measurement, with a view to providing field personnel with a better understanding of why certain procedures are recommended and how they might be modified to accommodate particular circumstances.

Site descriptions

Five sites have been used since 1986 to test the permanent plot methodology in a variety of field situations. Each site is located in a different biosphere reserve. Together, the reserves represent a wide variety of forest types, ranging from moist tropical forest in the Amazon Basin of Peru and Bolivia to deciduous hardwood forest in the eastern United States. Brief descriptions of the reserves follow.

Beni Biosphere Reserve

Bolivia's Beni Biosphere Reserve is located in the provinces of Ballivian and Yacuma within the department of Beni (14°38'S, 66°18'W) (Fig. 1). The reserve is 135,000 ha in size and consists primarily of flat land with some poorly drained areas. The higher zones of the reserve range from 220 to 235 m in elevation. The mean annual temperature is 27°C; mean annual precipitation is 1800 mm, with a dry season between April and October. The reserve contains a variety of habitats, including seasonally dry tropical forest, gallery forest, swamp forest, forest islands, and savanna. In relation to biological diversity, Beni Biosphere Reserve is an important representative of the eastern Bolivian lowlands. Biodiversity plots were set up at Beni in 1987 and 1988. Censuses were conducted in 1990 and 1991.
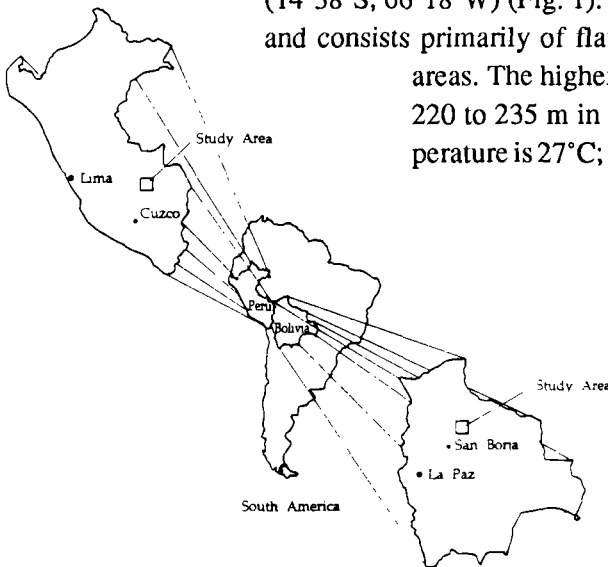

Figure 1. Location of study areas in Beni Biosphere Reserve, Bolivia, and Manu Biosphere Reserve, Peru.

Manu Biosphere Reserve

The Manu Biosphere Reserve lies in the Upper Amazon Basin of Peru northeast of the old Incan capital of Cuzco (Fig. 1). The reserve is located in the provinces of Manu and Paucartambo in the departments of Madre de Dios and Cuzco (11°19'-13°02'S; 71°07'-72°26'W). Manu includes part of the easternmost mountain ranges of the Andes and the lowland region of Amazonia. The protected area comprises 1,881,200 ha of land that ranges from 240 to 4000 m in elevation. The area contains nearly all of the ecological zones of eastern Peru, including humid forest, humid subtropical forest, very humid subtropical forest, and very humid low montane forest. It also holds one of the highest levels of biological diversity found in protected areas in the world (e.g. for birds, see Terborgh *et al.* 1990). SI/MAB and BIOLAT biodiversity plots were established in 1987 and 1988. A census was conducted in 1991.

Luquillo Biosphere Reserve

Luquillo Reserve, in the Luquillo Mountains of eastern Puerto Rico approximately 35 km from the city of San Juan (18°21'N, 65°45'W) (Fig. 2), contains 11,340 ha that range in altitude from 150 to 1080 m. Four vegetation types are generally recognized in the area - subtropical wet forest, subtropical rain forest, palm brake, and elfin woodland (dwarf forest) that is found only at the highest elevations. The reserve is unique in that it has been the site of ecological studies for the past 40 years. The resulting extensive database provides guidelines for managing similar but more intensively used areas in the Caribbean. Luquillo's SI/MAB biodiversity plot was
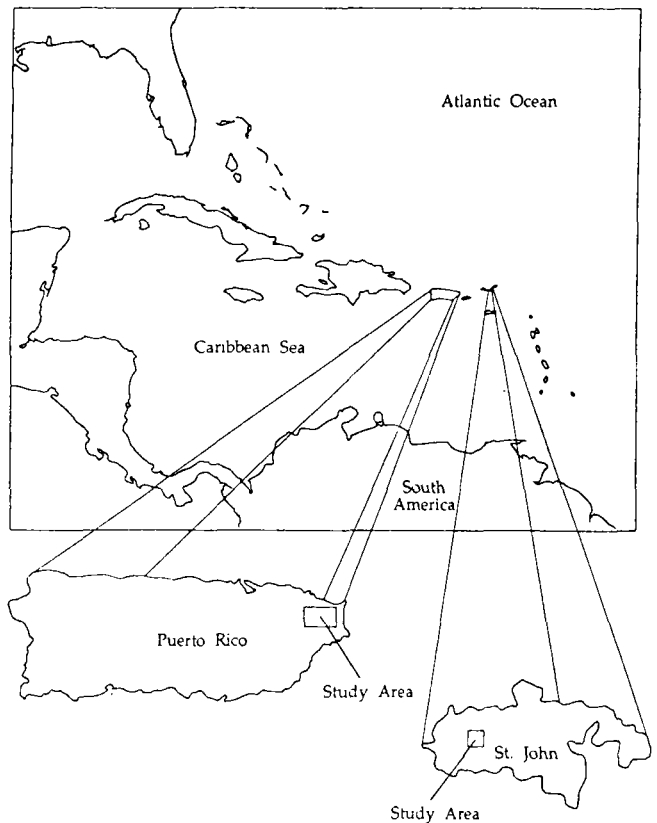

Figure 2. Location of study areas in the Luquillo Biosphere Reserve, Puerto Rico, and the US Virgin Islands National Park and Biosphere Reserve on the island of St. John.

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established in 1988 and 1989. Censuses are being conducted yearly to assess the effects and damage caused by Hurricane Hugo in 1989.

Virgin Islands National Park and Biosphere Reserve

The island of St. John in the US Virgin Islands (88 km east of Puerto Rico) is the home of the US Virgin Islands Biosphere Reserve (18°21'N, 64°44'W) (Fig. 2). The reserve contains 6127 ha that vary in altitude from sea level to 389 m. Subtropical dry forest and brush cover 70-85% of the total island, with subtropical moist forest in higher elevations and protected valleys. The dry forest of St. John has regenerated for a period of about 100 years following extensive sugar cane cultivation that ended in the late 1800s. The park is thus an excellent area for observing dry forest regeneration and for planning restoration and management in similar ecosystems throughout the Caribbean region. The SI/MAB biodiversity plot was established in 1991. Mapping of the plot vegetation is scheduled for 1992, and censuses will be conducted in 1995 and 1996.

Great Smoky Mountains National Park

The Great Smoky Mountains National Park forms part of the Southern Appalachians Biosphere Reserve of eastern Tennessee and western North Carolina (United States) (Fig. 3). It covers 209,000 ha of mountainous terrain in the Great Smoky Mountains, and its land base ranges in altitude from 259 to 2025 m. Vegetation changes with elevation, slope, and soil moisture patterns; the major forest types include northern hardwood forest, mixed oak forest, pine oak forest, cove forest, and spruce-fir forest.
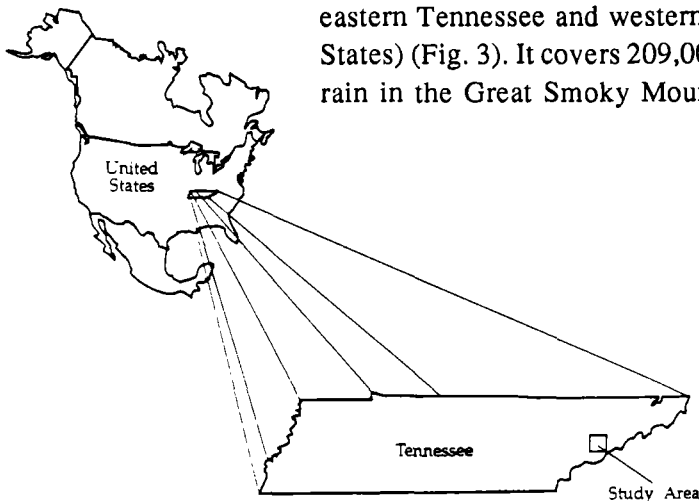

Figure 3. Location of study area in the Great Smoky Mountains National Park and Biosphere Reserve, Tennessee, USA.

Once a Pleistocene refuge with 30% of its vegetation in primary forest, the area is now recognized as one of the most important living laboratories of biodiversity in the United States. A SI/MAB biodiversity plot was set up in the reserve in 1989. Censuses will be conducted in 1992 and 1993.

Locating and describing the permanent plot

Plots are expensive to establish. They are also expected to be permanent. Thus, location is not a decision to be made lightly. It is very helpful for a qualified field ecologist to visit potential sites and define the most representative areas for setting the plots.

Site location should be based on cartographic information, aerial photographs, and field verification. It is important to describe both the site and the plot at the time the plot is being established. At least one permanent geological marker (locateable) for each plot is recommended. Significant elements of the description include: 1) detailed data on the location, access to the plot and how the plot was demarkated, to help subsequent researchers find the area; 2) careful recording of slope, aspect, soil types, geology, and local climate (because vegetation growth and productivity are often influenced by local topographic characteristics, it is necessary to describe these characteristics as precisely as possible); 3) a history of past land use in the area; and 4) general information about the site's flora and fauna.

Our experience in the SI/MAB Biodiversity Program has been that many plots in lushly carpeted tropical forests where undergrowth quickly regenerates are lost to researchers within three to five years because of a lack of precise location data. For this reason, the location of access trails to the plots must be accurately noted on topographic maps (if available) and clearly delineated in the field with permanent markers. At the same time, researchers should minimize disturbances that may result in making the plot too conspicuous or in altering its species composition. Therefore, whenever possible the information on plot location should refer to conspicuous natural landmarks such as rock formations and creek intersections. In some cases, trees tagged from past studies might serve this purpose.

Sampling overview and plot design

The permanent plot methodology is used to document species diversity and tree composition in protected forested areas. The plot is designed as a zone of 25 ha (Fig. 4) that allows for simultaneous study of a number of topics (e.g., nutrient dynamics, invertebrate diversity, forest regeneration). It also provides the framework for the consistency needed in comparing data collected at different sites. Such a protocol will not accommodate all research interests. But it does make possible a number of highly beneficial activities, including the gathering of reliable biodiversity data over a relatively short period of time for use in comparative studies and the means to educate people about the diverse and numerous plant species in protected forested areas.

These benefits are due largely to the methodology, which relies 1-ha plots within the 25-ha zone. The smaller plots (the size of which can be expanded if desired) help create a more manageable framework for research: inventories. can be completed more rapidly, and species can be monitored over time with a greater degree of certainty. The site-specific data that can be garnered from the plots should make excellent educational tools for future researchers and for reserve managers who must arrive at or carry out management decisions. In addition, the tree diversity and composition information from plots can be readily analyzed and incorporated into users' manuals and field guides (Dallmeier *et al.* 1991*b*, 1991*c*, 1991*d*, 1991*e*) within a year after a plot is established. The system thus provides an opportunity to prepare and distribute useful information in a
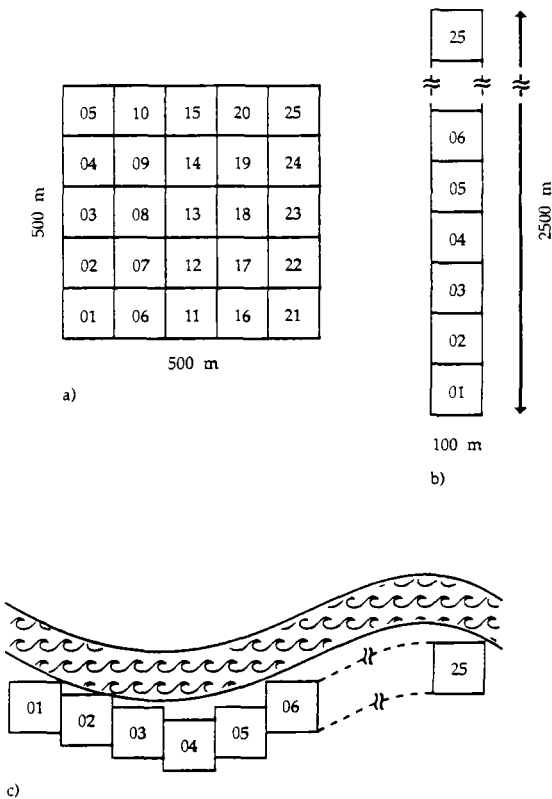
Figure 4. Variation on the layout of a 25-ha zone. a) 25-ha grid; b) 25-ha linear plot; c) 25-ha plot following an ecological zone (example shown here: a river).

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timely fashion. Even smaller (and more numerous) plots may be set for short duration experiments in forests where access to a large number of small areas is relatively easy. In tropical forest ecosystems, however, it is often more efficient to increase the amount of data gathered in each plot and reduce the total number of plots. High labour costs and logistical problems can make it impractical to maintain a large number of small plots.

Determining the number of plots required for effective research clearly hinges on more than access and cost considerations. This decision is best reached after habitat variability is assessed. For example, four permanent plots in the Beni Biosphere Reserve represent four discrete managed and unmanaged habitats. Four years after initial establishment, researchers now estimate an additional 15 plots are needed to represent most of the habitats or plant communities in the reserve.

In order to help ensure that data gathering, processing, and interpretation will be comparable among the network sites, we recommend the standard 1-ha size and measurement guidelines described below. This methodology can be quickly adapted to existing experimental plots in many protected tropical forest areas or conservation areas. The hectare is a standard measure in international use and is easily converted to other units (e.g. acres).

Selection and surveying of the plot should be done with additions in mind to accommodate future research objectives. For example, a 50-ha area is considered the minimum needed to obtain statistically significant samples of a large number of species for use in analyses of tropical forest dynamics and demographic change (Hubbell and Foster 1983; Manokaran *et al.* 1990).

To gain an understanding of the magnitude of the data that this system produces, consider the following. The 1-ha plots established by SI/MAB at the five research sites each holds at least 420 to 610 individual trees $\geq$ 10 cm dbh. The plot on St. John Island, where trees $\geq$ 4 cm dbh were measured, contains approximately 3500 individual trees. In addition to the number and size of trees, the species and location of each tree in the plot is recorded. In Puerto Rico, information has been obtained on the amount of damage and mortality sustained by trees on the Luquillo site as a result of Hurricane Hugo and the amount of regeneration that is occurring. For the plots in the Amazon Basin of Bolivia and Peru, researchers have identified local uses of tree species. Thus, several data sets now exist, containing more than 40,000 independent observations that can be used to describe the forests. An important aspect of future work will be to maintain and manage these data with the twin goals of reducing errors and assuring high quality.

Surveying the plot

In the 25-ha configuration used by the SI/MAB Biodiversity Program, the zone is surveyed in a horizontal plane using a theodolite and then divided into 25 plots, each 1 ha in size. The 1-ha plots are each subdivided into 25 quadrats 20 x 20 m in size (Fig. 5; 20 m is generally the longest distance that can be accurately surveyed in a dense forest). The quadrats are permanently marked at each of their corners with aluminium or plastic stakes and numbered consecutively, starting at the baseline of the plot (the east/west line at the bottom of the plot).
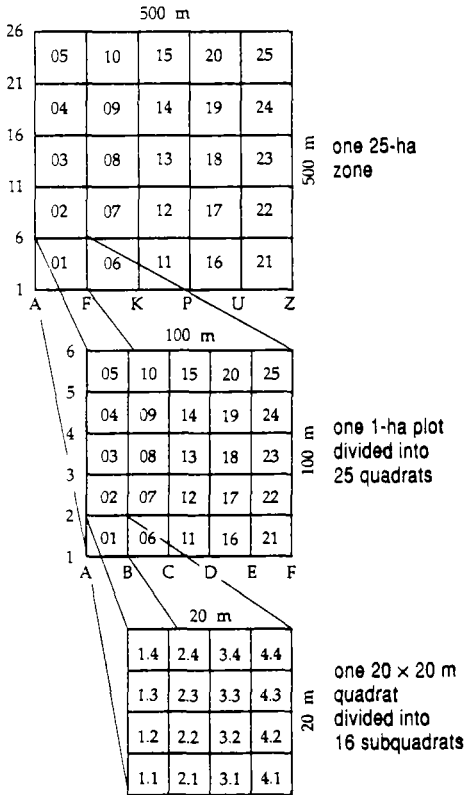
All stakes should protrude well above the forest floor to increase visibility. Red stakes are recommended for the corners of the 1-ha plots and white stakes for marking the 20-m quadrats. If fire is a problem (such as is the case for two plots at the Beni site), aluminium or iron stakes are preferred over plastic stakes for any study lasting longer than one year. Plastic stakes become too brittle when exposed to the heat of fires and are likely to melt or break. Also, in one of the Beni plots, cattle often snap off the plastic stakes; in the Great Smoky Mountains research area, rodents have been known to damage the plastic stakes.

Quadrats are the main organizational unit within the plot. Each marked tree is mapped in relation to two adjacent corner stakes that are measured precisely with a theodolite and then set. The stake in every quadrat corner is labelled with a letter and number to differentiate its location in the plot. It is recommended that during the survey of each quadrat, additional stakes be set every five meters (using a metric tape) to delimit 16 subquadrats (each 5 x 5 m) within the 20 x 20-m sampling unit. Setting the additional stakes at the same time the survey is

Figure 5. The 25-ha zone is divided into twenty-five 1-ha plots. Each plot is divided into 25 quadrats (each 20 × 20 m), and each quadrat into 16 subquadrats (each 5 × 5 m).

conducted eases the task of making necessary corrections for slope (see below). All 16 subquadrats are numbered consecutively, beginning with the number of the quadrat (Fig. 5).

Surveying to establish quadrat corners should proceed from the centre of the plot outward to minimize measurement errors. Quadrat corners should be built along the north-south centre line (Fig. 6); new corners are then added westward to the edge of the plot. The next step is to finish the centre row eastward before moving to other portions of the

a)

b)

Figure 6. a) Central quadrat of a 1-ha plot; b) direction of sighting that the surveying team followed in establishing the 1-ha plot.

The plot is surveyed in a horizontal plane using a tripod mounted theodolite which is leveled using a plumb-bob positioned over the center of the first corner stake. On sloping ground, the 20-m interval between corner stakes must be adjusted by a factor related to the degree of slope.

plot to establish the remaining corners. To begin the survey, researchers set up a tripod-mounted theodolite and level it using a plumb-bob positioned over the centre of the first stake. This stake serves as the arbitrary centre of the plot and as a common point from which all four corners of the first

quad can be established. In this way, any error introduced by moving the theodolite in establishing the first four corners is avoided.

After the tripod is in position, the instrument operator sights along a diagonal bearing to establish the first corner. Technician A goes down the line with a tape measure to reach a horizontal distance of 14.124 m-half of the diagonal distance of the 20 x 20-m quadrat (Fig. 6). A surveying rod is held vertically as a target over the 14.124-m mark to facilitate the determination of the true bearing. An additional person should be available to push aside branches or small stems so that the instrument operator has a clear line of sight and to keep vegetation from deflecting the tape. It is extremely important that the tapes be pulled snug to avoid sagging and, thus, distortions in measurements. Even a few centimetres, of discrepancy in initial measurements can result in much larger errors at the border of the plot. Periodic check measurements to compare new and past work are highly recommended; performed as often as possible, they will reduce the risk of accumulated error. In using the theodolite, it is also important to avoid taking measurements in close proximity to metal objects such as belt buckles, jewelry, glasses with metal frames, or wristwatches as they could cause errors in the magnetic readings.

Researchers in the field record (with pencil) the survey data in waterproof notebooks that are later transcribed into a permanent record book. Essential information includes: a) three different bearing measurements – the 'back' measurement (from the new set up point back to the previous stake on the same line), the 'check' measurement (to previous established stakes above and below the current line), and the 'new' measurement (to set the next stake on the current line); b) the coordinates of the corner stakes being surveyed and the direction of the survey; c) the angle along which the surveying is proceeding in relation to the horizontal; d) the vertical difference in height between the scope and the stake being surveyed; e) the distance being measured between the scope, the new point being surveyed, and the new slope-corrected distance (see below); and f) the elevation of each corner stake.

Slope correction[1]

On uneven terrain, the 20-m interval between quadrat corner stakes must be adjusted to account for slope. The purpose of this correction is to ensure that each quadrat contains 400 m^2 regardless of topography. As

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1. While the following discussion focusses on slope corrections in relation to establishing corner stakes, the same procedure is used to obtain slope corrected measurements for tree mapping.

shown in Fig. 7, the distance between two points measured along a slope is always greater than the corresponding horizontal distance. On sloping ground, the 20-m interval between corner stakes must there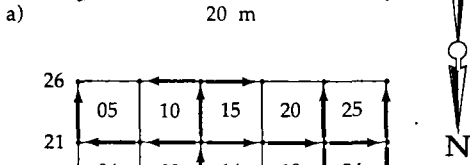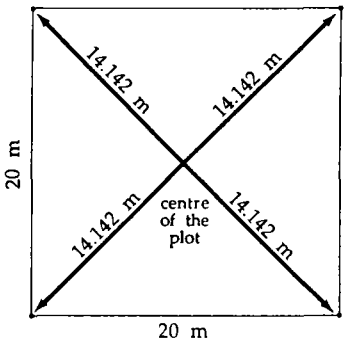fore be adjusted by a factor related to the degree of slope. The formula used to calculate this correction (Durr *et al.* 1988) is:

(1.0) Slope correction = 1/cos arctan (% slope/100).

Once it is figured, the correction factor is multiplied by 20 (m) to obtain a slope-corrected ground measure between quadrat corners.

The average angle of incline or decline is determined at a distance of 20 m from the surveyor. For example, to extend a survey line from established corner A to new corner B, the surveyor would first send a technician with a surveying rod 20 m along the correct bearing to the new corner. The surveyor would then use a theodolite or clinometer to determine the average slope between corner A and the technician standing 20 m away along the line to corner B. If the slope were found to be 25%, using the above formula, the correction factor would be:

1/cos arctan (0.25) = 1.031

The resulting slope-corrected ground measurement would be 20.62 m (1.031 x 20 m). Corner B would then be located by extending the tape an additional 0.62 m. A sighting should be taken at that distance to ensure that the stake is placed in the proper location. For greater accuracy, the final placement of all corner stakes should be made with the aid of a plumb-bob.

Figure 7. The distance between two points measured along a slope is always greater than the corresponding horizontal distance. On sloping ground, the 20-m interval between stakes must therefore be extended by a factor corresponding to the degree of slope.

In determining the angle of slope, it is important that the measurement be taken along a line of sight parallel to the average slope of the ground. In other words, the height of the instrument should be equal to the height of the target. Since the measurement begins at the eye level of the surveyor, it should end at an equal height on either the surveying rod or the body of the technician.
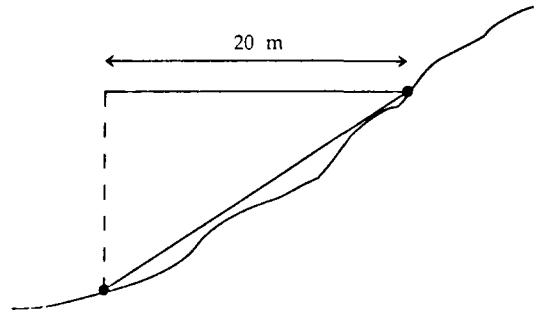
Occasionally, it is necessary to correct for slope using a two-step procedure. For example, if the crest of a steep hill falls along the line between two adjacent corners, it may not be possible to correct for slope with a single measurement. In this case, average slope should first be determined between the established corner and the crest of the hill and then used in conjunction with the corresponding taped distance along the slope to determine the planar distance between the two points. This distance should be subtracted from the total desired planar distance of 20 m. The residual planar distance, along with the average slope taken from the crest of the hill downward, should be used to establish the sloped distance corresponding to the residual planar distance. The formulae used for this procedure are presented below:

(1.1) Sa x Qa = Pa
(1.2) 20 m - Pa = Pb
(1.3) Qb x Pb = Sb
(1.4) Sa + Sb + St

where:

Sa = the sloped distance between the established corner and the intermediate point at the crest of the hill.
Qa = 1/cos arctan (% slope a/100), from (1.0) above.
Pa = planar distance corresponding to the sloped distance between the established corner and the crest of the hill.
Pb = 20 m - Pa (i.e., the residual planar distance).
Qb = 1/cos arctan (% slope b/100).
Sb = the sloped distance between the crest of the hill and the corrected corner location.
St = the total sloped distance between the crest of the hill and the corrected corner.

To facilitate slope correction in the field, a table of correction factors can be constructed using the formula 1/cos arctan (% slope b/100). As an alternative, a hand-held calculator can be programmed with prompts to accommodate both the one-step and two-step procedures outlined above. To facilitate measurements over steep terrain, it may be more practical to block out areas with the theodolite and fill in data using a compass and a hand clinometer. This allows stakes to be set more quickly so that the rest of the project can get started. Later, the team should return to examine the topography in greater detail. Sharp landslips and ravines that may fall even within 5-m blocks should be properly taken into account.
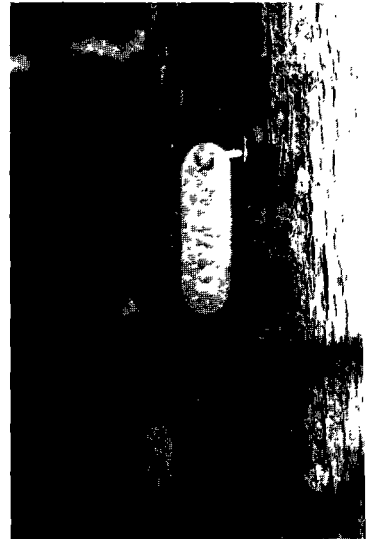
Materials

Several types of theodolites have been used in our survey work, including the Lietz TS20A scale reading theodolite, with a 30× magnification, and a smaller Ushita theodolite model – Tracon S-25. In some tropical forests, the 'high-tech' electronic distance-measuring theodolites do not perform well in high humidity or if handled roughly. In a 25-ha zone, 900 red plastic surveying stakes are necessary to mark the plot corners (Forestry Suppliers catalogue # 39503), and 11,025 white plastic stakes are needed to mark quadrat corners (Forestry Suppliers catalogue # 39501). At least two 30-m steel measurement tapes are needed for corner measurements, and different colours of flagging tape are used to mark the location of plot and quadrat corner stakes. Researchers carry a 2-m telescoping surveying rod that extends to 4 m, a clinometer, and two heavy rubber mallets to set the stakes in place.

Tree tagging, measurement, and identification

Once each plot has been surveyed, string is tied along the borders of each quadrat to facilitate general orientation during mapping. The string also makes it easier to determine whether individual trees are located within a given quadrat. All string is removed once mapping is completed. Tree tagging and identification can begin as soon as the corner stakes of the quadrats have been set and the strings tied. The process (Fig. 8) includes locating all trees ≥ 10 cm diameter at breast height (dbh; measured with a dbh tape at 1.3 m from the ground), placing a numbered aluminum tag facing outward toward the baseline and located above the 1.3-m level to avoid interference with dbh measurement, measuring dbh, marking the line of dbh measurement with red paint, and identifying the tree species.

In tagging the trees, the aluminium label should face outward, oriented toward the baseline of the plot and set with a nail a little more than 1.3 m from the ground. Each individual tree is tagged with a different number consisting of a sequence of four double digits.

To accomplish these tasks, a team of three individuals walks the quadrat, starting at the left corner baseline in concentric circles of decreasing size to the centre of the plot. One person sets the tag in place; another records dbh and paints the trees; the third identifies the trees (Fig. 9). In some cases, subsequent visits by a botanist are required to complete species identification. Smaller
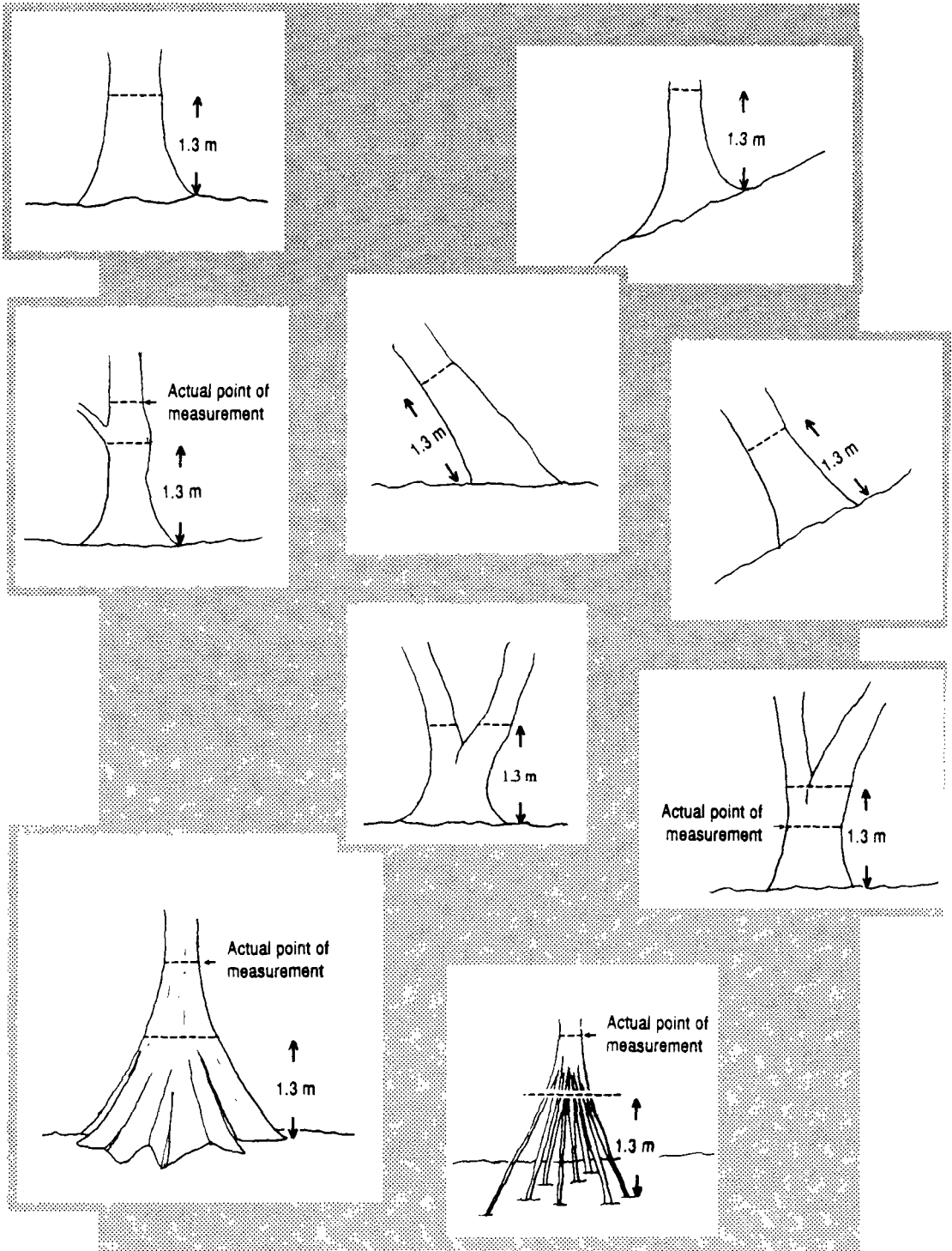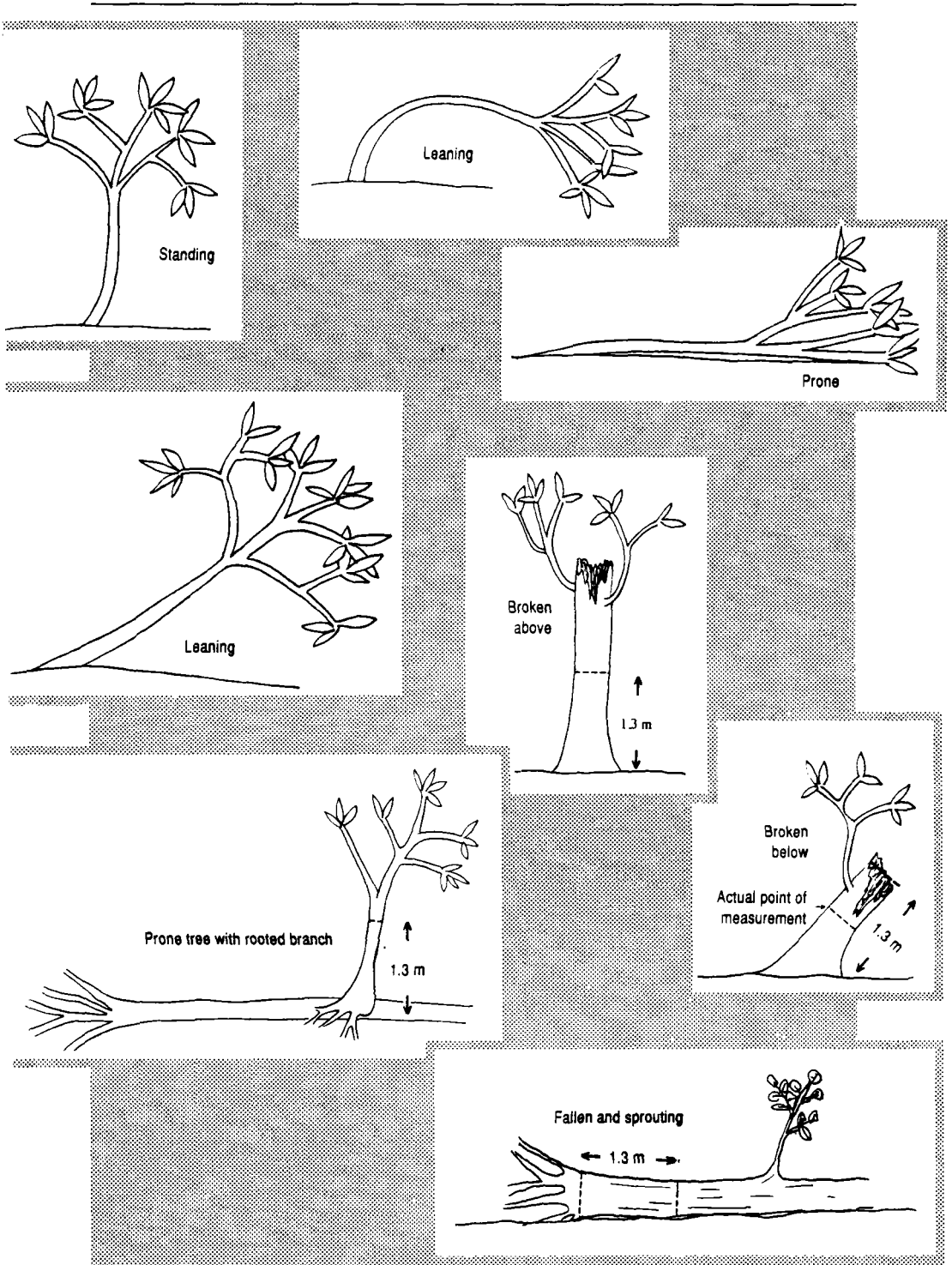
Figure 8. Methods used for measuring trees.

Figure 9. Classification of irregular trees.

trees can be measured with calipers; this has been done only at the St. John plot, where intensive studies are planned. Aluminum nails work best to set the tags, although steel nails may be needed for extremely hard wood. The nail should be driven to angle down and just far enough in so that it will not fall out when pulled or if bark should fall off, leaving enough room for the tree to grow before 'eating' the tag. For young, fast-growing trees ≤ 10 cm dbh, grafting tape or commercial electrical cable ties should be used to set tags, allowing the tree room to grow. However, these materials melt quickly, and over time may become brittle and break. If the possibility of fire exists and the trees are not large enough to hold nails, it is necessary to wire the tag to the base of the tree. A note to that effect should be recorded on the data sheet.

Since 1989, when SI/MAB researchers began painting the point of dbh measurement, the accuracy of the observations has improved considerably. Inconsistent measurements are still found, however, usually because certain trees (such as figs) have high-

Diameter at breast height (dbh), should be measured with a dbh tape at 1.3 m from the ground, avoiding any protrusions of the trunk. Smaller trees are measured with calipers.

ly irregular surfaces or because of vines or other vegetation growing along the bark. When such problems are encountered, a note is made on the data sheets. Other errors when measuring dbh include incorrect determination of the point of measurement, misreading the dbh tape, and faulty recording of information either in the field or later when the data are transferred to a computer. Each individual tree is tagged with a different number consisting of a sequence of four double digits. Using 01-13-24-09 as an example, the first two numbers (01) designate the 25-ha zone, single habitat, or plant community. The second set of numbers (13) corresponds to the 1-ha plot in the zone. The third pair (24)

identifies the quadrat, and the last two numbers (09) represent an individual tree in the quadrat. No other tree receives this number. The tree numbers start at 01 in each quadrat and continue until the last tree is labelled. The average number of trees per quadrat in SI/MAB's South American plots ranges from 17 to 39. At the US Virgin Islands plot, the number of trees ranges from 140 to 160 per quadrat. As discussed earlier, the large number of trees recorded for the US Virgin Islands plot is a result of tagging all trees ≥ 4 cm dbh, rather than only those trees ≥ 10 cm dbh.

At the SI/MAB plots, all trees are examined by qualified botanists, and voucher specimens are collected for herbarium identification and preparation of high resolution plant photocopies - or 'mini-herbariums' - for inclusion in users' guides to the plots. On average, more than 60% of the trees are identified during the first year of field study, increasing to 80% once the sample herbarium specimens are verified and to 96% following a second visit to the plot. When the set of field and herbarium corrections is finished, near complete identification is accomplished for all tagged trees, with a final estimated error of < 2%. Common errors in identifying trees include selecting the wrong leaves for study, determining two or more separate species as one, splitting one species into two or more, having insufficient knowledge of the species' field characteristics, relying on identifications and common names used by local residents, and making clerical mistakes.

Tree conditions

Several categories of tree conditions have been assigned at the Puerto Rico plot where damage from Hurricane Hugo is being assessed. The categories are (a) high damage for trees with no branches remaining after the hurricane, (b) medium damage for trees with one to three branches remaining, and (c) low damage for trees with four or more branches remaining. To facilitate data manipulation and analysis, the following categories have also been recognized: alive standing, alive broken, alive fallen, dead standing, dead broken, dead fallen, and not located. Researchers at other sites may find it helpful to develop similar categories for use in recensuses or following cataclysmic events such as Hurricane Hugo.

Materials

The following materials have been used to measure and tag trees at the research plots: aluminium and steel nails 7 cm in length; aluminium tree tags

SI/MAB researchers map each tree to the nearest cm. The mapping software can be run on any IBM compatible computer with 256K RAM, a hard drive, and an MCGA graphics or better capability. SI/MAB recommends laptops in the field because they are lightweight and can be operated by batteries.

(67 x 25 x 1 mm) with a 5-mm hole at one end (purchased from National Band and Tag Co., Newport, Kentucky, USA); three hammers; 3000 cable ties; five rolls of grafting tape; two diameter tapes; two 50-m measuring tapes; clipboards; three calipers; several colours of flagging tape; red paint for the dbh marks; small brushes; field data sheets; pencils; blank tree tags; and hand-stamp steel dies to replace lost tags.

Tree mapping

In addition to measuring and identifying trees in the quadrats, each tree is mapped to the nearest centimeter. A mapping team of four to six people uses two 50-m measuring tapes and a dbh tape to accomplish this task. Each tree

It was necessary to assign several categories of tree conditions to trees at the Puerto Rico plot where damage from Hurricane Hugo is being assessed. The categories are: high damage for trees with no branches remaining after the hurricane, medium damage for trees with one to three branches remaining, and low damage for trees with four or more branches remaining.

is located by one person known as the 'tree locator'. Another person holds a pole with coloured flagging to mark the tree's location, while two additional people measure line A and two others measure line B. These lines denote the distance from a left quadrat corner (line A) to the tree being measured and from a right corner (line B) to the same tree (Fig. 10). For trees on slopes, the degree of slope of lines A and B are measured with a clinometer and recorded. Slope corrected measurements are automatically calculated by the software. This system allows measurements from any of the four sides of the quadrat. The coordinate corners are denoted by their intersecting boundary lines (quadrat boundary lines are numbered in clockwise sequence from one to four, starting at the baseline).

This information is recorded on data sheets where careful attention must be paid in order to avoid the two most common errors in mapping: switching lines A and B and incorrectly recording the line numbers. Researchers later enter the data into the SI/MAB computer program, which calculates by triangulation the X and Y coordinates of the tree, taking into account the dbh. The computer then generates a map of each quadrat, showing the exact location of each tree and its relative diameter.

A ground-truthing crew of three individuals verifies each quadrat map in the field to correct any mistakes. A set of 25 corrected quadrat maps, together with spread sheets, are prepared for each 1-ha plot (see Box 1). The accompanying spread sheets show the X and Y coordinates, dbh, genus, species, and tag number for each tree. These data are compiled in users' and field guides, such as those prepared for researchers working at Beni and Luquillo (Dallmeier *et al.* 1991a, 1991b, 1991c, 1991d).

This system, although designed for 20 x 20-m quadrats, is also practical for use in 5 x 5-m subquadrats where two people can map all
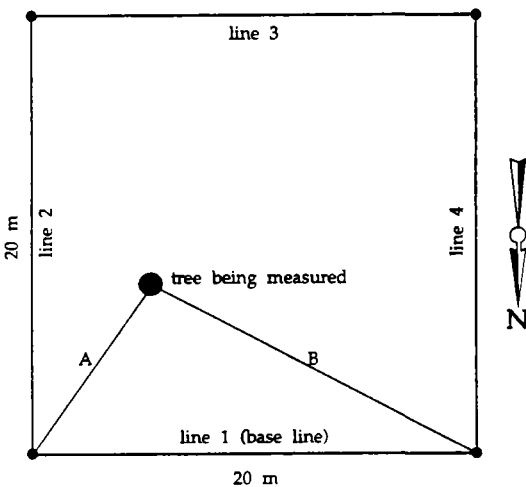

Figure 10. Trees within a quadrat can be measured from any two adjacent corner stakes. Line "A" is the diagonal distance from a left quadrat corner to the tree being measured, and line "B" is the diagonal distance between the right corner and the same tree.
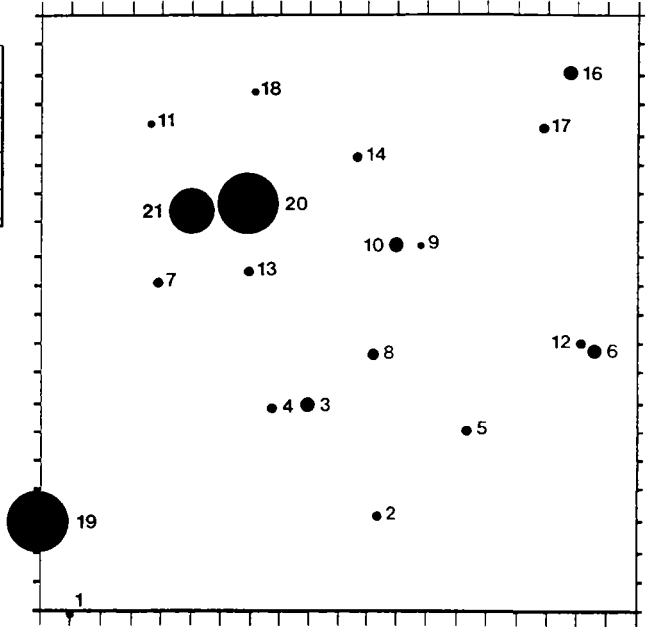
Box 1. Example of a quadrat map and spread sheet from a users' guide

BENI BIODIVERSITY PLOTS
SMITHSONIAN/MAB BIODIVERSITY PROGRAM
PLOT 0113 - QUADRAT 02 - 1990/91 CENSUSES
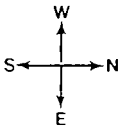
1- *Pithecellobium latifolium* (Leguminosae-Mim) PITLAT
2- *Brosimum lactescens* (Moraceae) BROLAC
3- *Scheelea princeps* (Palmae) SCHPRI
4- *Brosimum lactescens* (Moraceae) BROLAC
5- *Brosimum lactescens* (Moraceae) BROLAC
6- *Scheelea princeps* (Palmae) SCHPRI
7- *Brosimum lactescens* (Moraceae) BROLAC
8- *Scheelea princeps* (Palmae) SCHPRI
9- *Brosimum lactescens* (Moraceae) BROLAC
10- *Scheelea princeps* (Palmae) SCHPRI
11- *Brosimum lactescens* (Moraceae) BROLAC
12- *Heisteria nitida* (Olacaceae) HEINIT
13- *Brosimum lactescens* (Moraceae) BROLAC
14- *Brosimum lactescens* (Moraceae) BROLAC
16- *Scheelea princeps* (Palmae) SCHPRI
17- *Brosimum lactescens* (Moraceae) BROLAC
18- *Brosimum lactescens* (Moraceae) BROLAC
19- *Cupania cinerea* (Sapindaceae) CUPCIN
20- *Salacia -1* (Hippocrateaceae) SAL-1
21- *Salacia -1* (Hippocrateaceae) SAL-1

[*Source* : Dallmeier *et al.* 1991c ©]

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Box 1. (Contd.)

BENI BIODIVERSITY PLOTS
SMITHSONIAN/MAB BIODIVERSITY PROGRAM
PLOT 0113 - QUADRAT 02 - 1990/91 CENSUSES

	TREE GENUS	SPECIES	COMMON NAME	CODE	X	Y	DBH	(multiple-stem) NOTES
1	Pithecellobıumlatifolium		Pacaysillo	PITLAT	1.02	0.07	0.090	
2	Brosimum	lactescens	Quecho	BROLAC	11.34	3.22	0.160	
3	Scheelea	princeps	Motacu	SCHPRI	9.00	6.85	0.502	
4	Brosimum	lactescens	Quecho	BROLAC	7.80	6.79	0.250	
5	Brosimum	lactescens	Quecho	BROLAC	14.41	6.04	0.202	
6	Scheelea	princeps	Motacu	SCHPRI	18.52	8.73	0.377	
7	Brosimum	lactescens	Quecho	BROLAC	3.87	11.01	0.156	
8	Scheelea	princeps	Motacu	SCHPRI	11.24	8.59	0.302	
9	Brosimum	lactescens	Quecho	BROLAC	12.83	12.22	0.084	
10	Scheelea	princeps	Motacu	SCHPRI	12.08	12.15	0.417	
11	Brosimum	lactescens	Quecho	BROLAC	3.62	16.26	0.100	
12	Heisteria	nitida	Coto	HEINIT	18.42	9.05	0.190	
13	Brosimum	lactescens	Quecho	BROLAC	6.96	11.46	0.257	
14	Brosimum	lactescens	Quecho	BROLAC	10.63	15.19	0.175	
16	Scheelea	princeps	Motacu	SCHPRI	17.82	17.91	0.437	
17	Brosimum	lactescens	Quecho	BROLAC	16.91	16.16	0.190	
18	Brosimum	lactescens	Quecho	BROLAC	7.12	17.36	0.123	
19	Cupania	cinerea	Sama blanca	CUPCIN	0.12	2.78	0.260	/.350/.490/.530/.530
20	Salacia	-1	Guapumo (hoja grande)	SAL-1	7.07	13.64	0.650	/0.700/0.670 check for flowers
21	Salacia	-1	Guapumo (hoja grande)	SAL-1	5.35	13.38	0.610	/0.700 check for flowers

vegetation $\geq$ 1 cm dbh. In addition, the system can be used to map areas along a transect or trail where stakes are located every 20 m. It even allows mapping of irregular areas such as a gallery forest. The areas can be laid out as a series of quadrats in a single or double file or other irregular sequence. For example, in a protected forest in Venezuela, a transect of 20 x 20-m quadrats is planned that covers an estimated 17 ha, starting at sea level and rising in elevation to 2000 m. Eventually, each quadrat can be divided into smaller subquadrats that, when staked and mapped, will provide the bases for more detailed demographic studies.

One advantage to setting up 5 x 5-m subquadrats is that their size provides a practical means for mapping the much larger number of trees in small diameter classes. For example, reducing the diameter limit from 10 cm to 4 cm in the Virgin Islands increased the number of trees mapped by sevenfold. Even greater increases can be expected if the diameter limit is reduced to 1 cm. It is impractical to map such a large number of trees using the methodology outlined above. An alternative method that has proven quite accurate involves locating the trees by eye in a 5 x 5-m subquadrat, pencilling in their location on a map, and later entering the data into a computer using a digitizing tablet (see Hubbell and Foster 1986).

Materials
Research teams need the following material to locate trees in the field for mapping: 50-m steel measuring tapes marked to centimeter, one dbh tape, a pole with coloured flagging, water-proof notebooks, and pencils.

Tree mapping software
The software used to produce the tree maps has two components: compiled Dbase III Plus programs and compiled BASIC programs. This software can be run on any IBM-compatible computer with 256K RAM, a hard disk drive, and MCGA graphics capability. Menu and data retrieval functions are handled by the Dbase programs, and numeric calculation and map creation tasks are performed by the BASIC programs. The interface between these programs is transparent to users through menus, allowing users to manipulate the files of data, which are organized by quadrat. The system menu includes the following options: create a new file for tree data, add new tree data, edit existing tree data, and generate maps of the trees in a specific quadrat with or without slope. Users may also print out all the data for a given quadrat. Further details are presented in Boxes 2 and 3.

Box 2. Tree mapping software instructions

Main menu options
The main menu is the first screen displayed. Most of the menu options described below can also be executed from the function keys, thus bypassing the main menu.

CREATE new database
The first step in using this system is to create a separate file for all tree data from a single quadrat. A database named 'QUAD' is the default. To CREATE a new database, enter 'C' from the main menu. Then enter the name of the database you want to create. The naming convention for quadrats is ZONE# + PLOT# + QUADRAT#: the name is thus composed of three two-digit numbers. The program automatically supplies a '.dbf' extension to the file. All of the main menu options (including CREATE) display a '.' prompt when execution is completed. Once the '.' prompt is displayed, the user can select another option.

SWITCH databases
The SWITCH option is used to open an existing data file. It is not possible to switch to a database that has not been created.

ADD records
The ADD option appends blank records to the end of the data file currently in use. The name of the current file is always displayed on the main menu screen. The fields used are LINENO, TREENO, DBH, A, B, SLOPE A, SLOPE B, X, Y, STATUS, FAMILY, GENUS, SPECIES, and NOTES. You must enter data for LINENO, TREENO, DBH, A, B. Coordinates X and Y are calculated by the computer when the map is generated. Entering data in the remaining fields is optional. The STATUS field is used to note any tree condition previously defined; for example, dead broken, dead standing, or alive broken.

NOTES is a 40-character text field often used to record any additional information related to the tree in question; for example, tag is missing.

EDIT records
EDIT is designed to view selectively and change records in the current file. The PgUp and Pgdn keys are used to move through the records in the file to reach the point where editing is to be done.

LIST all records
This is an alternative way to add and edit records. LIST displays the records in the current database on the screen in a columnar format. New records are added by moving the cursor past the last field in the last record. Records are edited by typing over the existing data.

MAP tree data
The X and Y coordinates are generated using either of the following two map options: the w/o slope option produces maps that lack topographic definition; the w/slope option reads the slope correction for each tree and generates maps indicating topographic planes. This greatly increases the accuracy of the maps on sloped terrain.

Tree data can be mapped even if only one record exists in a file. Press P at the main menu (or F5). The system will exit dBase and call up the mapping program in BASIC, then read in the data from the current database.

Bad data (usually incorrect A or B measurements) will cause an error message to appear; the tree to which the bad data pertain can not be mapped, but all other trees in the database can; or, you may return to the main menu to correct the problem. One clue to the existence of bad data is that the sum of the fields A, B, and dbh must always be ≥20 m. If not, it is usually the case that the tree in question lies on or very close to the line between the stakes. This error can nor-

mally be avoided if the recorder in the field totals the measurements when they are taken.

A hard copy of each map and the data screens can be made by pressing SHIFT + PrtSc. Tick marks will appear around the perimeter of the map, indicating 1-m distances. Trees are represented by circles in proportion to their diameters. An abbreviated menu line at the bottom of the screen (P1/P2/D/M) allows users to draw the map with letters next to the trees (P1) or without letters next to the trees (P2). The latter option is useful if a number of trees are grouped closely on the map or several trees are located near a line. Including letters under these circumstances can make the map difficult to read. Choosing D produces a map that displays all the entered data in addition to the calculated values of X and Y. Option 'M' returns the user to the main menu.

PRINT records from current file
This option produces a hard copy record of each tree and includes the family, genus, species, and field notes. These data fields are not printed out under the PLOT option.

QUIT
Always exit the system using the QUIT option. Data may be lost if the power is turned off before properly exiting the system.

Box 3. Tree mapping glossary

BASELINE
The bottom of the 1-ha plot.

DBH
Diameter at breast height (the diameter of a tree as measured 1.3 m from the ground).

LINE NUMBER
The side of the quadrat used in taking 'A' and 'B' measurements. The baseline of the plot is always line number 1. Line numbers 2, 3, and 4 are numbered clockwise from the line 1 (baseline).

PLOT
One of 25 contiguous 100 x 100-m areas in a zone.

QUADRAT
One of 25 contiguous 20 x 20-m areas that make up a plot.

STAKE NUMBER
The corners of plots and quads are marked by stakes placed 20 m apart in the plots. The numbers on the stakes are in the form of coordinates, with A-Z across the horizontal X axis and 1-26 on the vertical Y axis. For example, stake numbers along the top edge of five plots read from A1 to Z1.

TAG NUMBER
An eight-digit number stamped on tags attached to all trees in the plots.

TREE NUMBER
The last two digits of a tree tag number.

ZONE
An area of land distinguished from adjacent areas by distinctive vegetation or topography. SI/MAB delineates 25 ha in establishing research sites.

The maps represent a planar view of the forest from above, with the trees indicated in cross section. The relative diameters of the trees are shown on the maps. Tick marks around the perimeter of the map mark 1-m distances. For quick reference, data about the trees in the mapped quadrat are printed on the same sheet. To accommodate steep slopes, the program allows the user to correct field measurements for topographic relief. The default setting calculates the X and Y coordinates with no degree of slope, but if the slope, expressed in percent, is entered, the software will adjust the coordinates accordingly. This feature greatly increases the accuracy of the maps on sites with topographic relief.

Preparing users' and field guides

Users' guides contain basic biological information about permanent plots at long-term research sites. The purpose is to assist in conducting more effective research and training. Studies over the period 1987-1991 have yielded sufficient information not only to produce the guides but also to begin in-depth analysis of forest diversity and dynamics. Each users' guide is accompanied by a complementary field guide containing a condensed version of information from the users' guide for use in the field (Box 4). Together, the two documents make available to students and researchers all the basic information gathered in the plots. They are designed for loose leaf holders to accommodate continuous updating as more information becomes available.

A consistent format has been followed in producing the users' guides. The first section provides a detailed explanation of the site ecology and gives a brief overview of the area's climate, topography, soils, vegetation, fauna and history. The second section details the methodology for establishing a permanent plot, presented in a readily understandable manner for researchers planning to use the same methodology in other areas. Section three consists of the

Box 4. Field guides for biodiversity plots: Samples from Beni

The field guides for diversity plots comprise double-sided 14 · 17.5 cm flip charts in plastic folders. One field guide is prepared for each 1-ha plot. Thus, four field guides have been prepared for the four Biodiversity plots at Beni (Dallmeier *et al.* 1991*b*).

Each guide contains a map showing the location of the plots, an overview of the reserve, a site description of the particular plot (including a list of trees), and a map and data sheet for each of the twenty-five 20 × 20-m quadrats making up the 1-ha plot.

LOCATION OF STUDY AREA
BENI BIODIVERSITY PLOTS

□ Biodiversity Plots
△ El Trapiche Campsite
○ Beni Biological Station (El Porvenir)
— — Road San Borja - San Ignacio

BENI BIODIVERSITY PLOTS
SMITHSONIAN/MAB BIODIVERSITY PROGRAM
PLOT 0313 - QUADRAT 07 - 1990-91 CENSUSES

List of Trees at Beni Biodiversity Plot 01

The following names are presented in alphabetical order, these are the trees 10cm dbh and larger from plot 01. The six-letter codes are used at the Beni Biodiversity Plots.

GENUS	SPECIES	FAMILY
		LEGUMINOSAE-MIM
Acacia	loretensis	
Ampelocera	ruizii	
Aspidosperma	rigidum	
Astrocaryum	macr...	
Brosimum	lac...	
Byrsonima		
Calycophyllum		
Copaifera		
Cordia		
Cupania		
Dryper...		
Euter...		
F...		

FIELD GUIDE TO
THE BENI BIOSPHERE RESERVE
BIODIVERSITY PLOT 03
BOLIVIA

Francisco Dallmeier
Robin B. Foster
Claudia B. Romano
Richard Rice
Margo Kabel

specific information gathered at the plot, providing a foundation for comparative analysis of the plot's vegetation. The users' guides include a complete set of maps for each 20 x 20-m quadrat in the plot, along with data sheets and a full size map of the plot. Whenever possible, the guides also include a "mini-herbarium" of three specimens, designed to help in identification (Box 5).

Data management and quality control

Because the data set generated by each plot can be quite large, quality control and data management are extremely important considerations. Data collection and computer entries are carried out by a number of people, followed by manipulation and cleaning of the data by yet more people in the office or laboratory. For these reasons, it is critical to devise uniform, detailed methods to handle and manipulate the plot data set and to give explicit instructions for recensus exercises (Box 6).

Computer equipment

The data generated from each plot are entered, stored, and analyzed in IBM-compatible personal computers. Tree coordinates and preliminary species information are entered in the field on portable laptop computers. Later, the information on the laptop diskettes is transferred to desktop computers in the office of laboratory. At least three backup copies of the data should be kept. SI/MAB recommends the use of laptops in the field because they are lightweight and can be operated with batteries. Diskettes and internal hard drives are prone to failure in the field; therefore, several backup copies of the data should be prepared daily to prevent major disappointments.

Box 5. Mini-herbarium of tree specimens

The Mini-herbarium is designed to help in identification.
It consists of high-resolution photocopies of dried pressed museum specimens and suffer the resulting limitations.
All photocopies are to the same scale. Species are arranged in alphabetical order by genus and species name.
Right is one specimen (*Guettarda viburnoides*) featured in the users' guide to Beni (Dallmeier *et al.* 1990c).
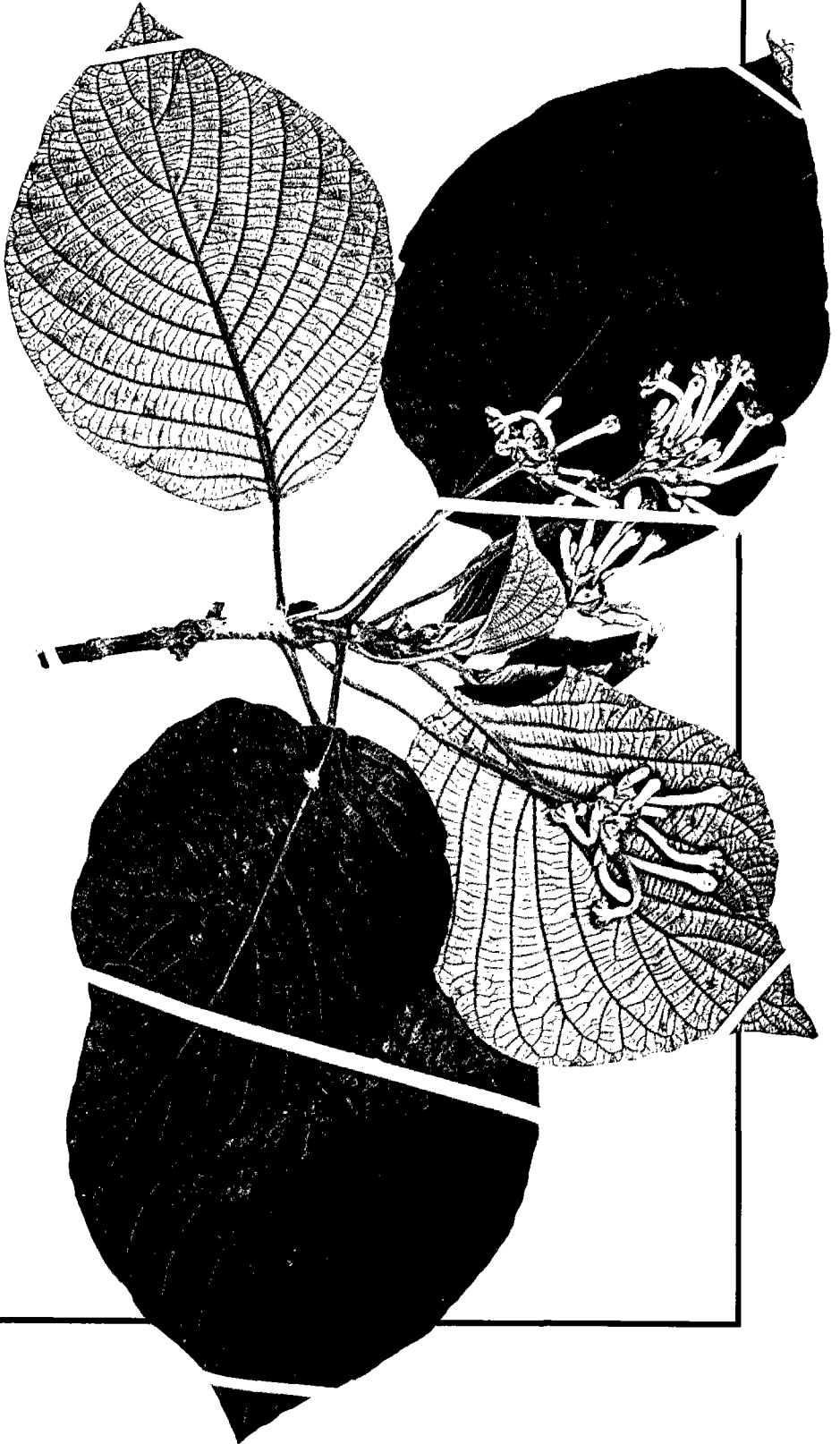
Data entry

While in the field, information from each field data sheet should be transferred to laptop computer files every night so that maps can be produced for ground truthing the following day. This procedure helps ensure that errors in measurement and data entry are discovered while researchers are still on site.

Budget for time and labour

Establishing and maintaining long-term biological inventory plots can be costly and labour intensive. The costs will vary from country to country and in relation to the level of professional expertise of the people involved in the process. The rough estimates that follow are based on SI/MAB's experiences in setting 1-ha plots. In surveying the plot, an experienced forest survey team can usually place 10 to 15 corner stakes per day. (At Beni Biosphere Reserve, the teams averaged 15; at the Bisley Biodiversity plot where the slopes are much steeper, the average was seven.) Thus, it takes approximately one week for a team of three people to set a 1-ha plot, or about 168 work-hours. Tagging trees and measuring their dbh with a team of three people should result in the completion of five 20 x 20-m quadrats per day. A plot with 25 quadrats should be finished in five days, requiring about 120 work-hours. In difficult terrain, it may possible to set only three quadrats per day.

A six-person mapping team should be able to map at least two quadrats a day and also complete ground truthing of the previous day's quadrats. The total plot can therefore be mapped in 13 days. Three extra days should be allocated for checking all maps in the field: mapping would then total 16 days per plot, or 768 work-hours.

SI/MAB estimates that an experienced botanist requires about 60 days, or 480 work-hours, to complete tree identification and prepare a mini-herbarium. Data entry and generation of the quadrat maps in the field takes 16 days at five hours a day for a team of two people, or 160 work-hours. Data maintenance and the final preparation of data sheets, maps, and final users' and field guides requires the time of two people over the course of six months per 2 ha or 1920 work hours. A rough total labour budget for setting a 1-ha plot (including data gathering, entry, species identification, and production of users' and field guides) is approximately 832 work-days, or 6832 work-hours. These general estimates do not incorporate associated costs of transportation, camp building and maintenance, worker training,

Box 6. Recensus instructions for biodiversity plots: Example of the 1991 recensus at Manu Biosphere Reserve

The 1991 recensus of biodiversity plots at Manu represents the second complete inventory for four of the permanent plots SI/MAB has established at that site. Mapping of the Manu plots began in 1987, and the first inventory was completed in 1988. The purpose of the 1991 recensus was to update the plot information, correct the quadrat maps, take new diameter measurements, and mark the point of measurement. Future censuses will be conducted at five-year intervals. Methods for taking diameter measurements and recording information from the plot have evolved considerably since 1987 and 1988, as necessitated by trial and error at the five research sites. Accuracy, consistency, and efficiency have increased considerably due the changes made in the protocol.

One of the most important changes for the 1991 recensus at Manu concerns measuring tree diameters. Based on censuses at the Puerto Rican, St. John, and Bolivian sites, diameters should be measured to the nearest millimeter and diameter measurements taken at 1.3 m from the ground. If abnormalities such as branches, bumps, or broken bark exist at the 1.3-m mark, the diameter should be measured at the smallest diameter between that mark and the ground. Every tree should be painted exactly where the measurement is taken for future reference.

In addition, researchers should organize their work sheets so that each field data sheet is accompanied by the most re-cent quadrat map and the spread sheet that contains the most up-to-date information for and status of each tree. The quadrat maps serve researchers in the field in three ways: 1) to assist in locating each of the trees previously mapped, 2) to mark changes in the location of any tree mapped incorrectly during the previous census, and 3) to denote the location of any new tree or any old tree not shown on the spread sheets. It is important to indicate the direction in which a tree has fallen with an arrow pointing from the base of the tree to the crown. In addition, any change in tree position from one quad, due to landslides or subsequent treefalls, to another should be marked as clearly as possible with arrows, dots, or numbers.

All plants recorded in the 1987-1988 data set of maps or spread sheets are included in the 1991 census. All new, free-standing trees with a principal stem ≥ 10 cm dbh at 1.3 m from the ground are also included. Plants excluded from the 1991 census are herbs, vines, epiphytes, hemi-epiphytes, and stranglers that will collapse if the host has died. The new census also excludes plants that are alive and were tagged in the original census but that do not meet the free-standing or diameter qualifications for new plants.

Researchers are expected to prepare replacement tags for all trees with missing tags and attach them the day following the discovery. Tags should be not removed from dead stems.

administration and coordination, or equipment and supplies. Note that computer equipment and facilities must be dedicated to the plot data set. A large amount of memory in the computer is necessary to accommodate all information as well as desktop publishing capability. The approximate cost of the computer equipment is US$18,000.

Acknowledgements

References

Curtis, O. 1983. *Procedures for Establishing and Maintaining Permanent Plots for Silvicultural and Yield Research*. General Technical Report PNW-155. Forest Service, Pacific Northwest Forest and Range Station, Olympia, Washington.

Dallmeier, F. 1991. Biological diversity conservation in Latin America: An uncertain perspective for the 1990s. Paper presented at First Venezuelan Congress of Ecology. Caracas (Venezuela), 15-19 April 1991.

Dallmeier, F., M. Kabel, C. Taylor, C. Romano & R. Rice. 1991a. *User's Guide to the Bisley Biodiversity Plots, Luquillo Biosphere Reserve, Puerto Rico*. Smithsonian Institution, Washington, D.C.

Dallmeier, F., M. Kabel, C. Taylor, C. Romano & R. Rice. 1991b. *Field Guide to the Bisley Biodiversity Plots, Luquillo Biosphere Reserve, Puerto Rico*. Smithsonian Institution, Washington, D.C.

Dallmeier, F., R. Foster, C. Romano, R. Rice & M. Kabel. 1991c. *User's Guide to the Beni Biosphere Reserve Biodiversity Plots*. Vol. I and II. Smithsonian Institution, Washington, D.C.

Dallmeier, F., R. Foster, C. Romano, R. Rice & M. Kabel. 1991d. *Field Guide to the Beni Biosphere Reserve Biodiversity Plots*. Vol. I, II, III, IV. Smithsonian Institution, Washington, D.C.

Durr, P.C., L. Richmond & C. Eagar. 1988. *Site Classification and Field Measurements. Methods Manual*. Science Division, Great Smoky Mountains National Park, Gatlinburg, Tennessee.

Ehrlich, P. R., & E. O. Wilson. 1991. Biodiversity studies: science and policy. *Science*. 253:758-762.

Hubbell, S.P. & R. Foster. 1986. Commonness and rarity in a neotropical forest: Implications for tropical tree conservation. In: M. Soulé (Ed.), *Conservation Biology, the Science of Scarcity and Diversity*, 205-234. Sinauer Associates, Sunderland, Massachusetts.

Mann, C. C. 1991. Extinction: are ecologists crying wolf?. *Science* 253:736-738.

Manokaran, N., J.V. LaFrankie, K.M. Kochummen, E.S. Quah, J.E. Klahn, P.S. Ashton & S.P. Hubbell. 1990. *Methodology for the Fifty Hectare Research Plot at Pasoh Forest Reserve*. Research Pamphlet No. 104. Forest Research Institute of Malaysia, Kepong.

Myers, N. 1988. Tropical forests and their species: Going, going,...? In: E.O. Wilson (Ed.), *Biodiversity*, 28-35. National Academy Press, Washington, D.C.

SI/MAB (Smithsonian Institution/Man and the Biosphere) Biological Diversity Program. 1991. *SI/MAB Biodiversity News Number 1 (Summer 1991)*. Smithsonian Institution, Washington, D.C.

Solbrig, O. T. 1991*a. Biodiversity: Scientific Issues and Collaborative Research Proposals.* MAB Digest 9. UNESCO, Paris.

Solbrig, O. T. (Ed.) 1991*b. From Genes to Ecosystems: A Research Agenda for Biodiversity.* International Union for Biological Sciences, Paris.

Soulé, M. E. 1991. Conservation: tactics for a constant crisis. *Science* 253:744-750.

Synnott, T.J. 1979. *A Manual of Permanent Plot Procedures for Tropical Rain Forest.* Tropical Forestry Papers No. 14. Commonwealth Forestry Institute, University of Oxford, Oxford.

Terborgh, J.; Robinson, S.K.; Parker, T.A. III; Munn, C.A.; Pierpont, N. 1990. Structure and organization of an Amazonia forest bird community. *Ecological Monographs* 60(2): 213-238.

Wilcove, D.S. 1987. From fragmentation to extinction. *Natural Areas Journal* 7: 23-29.

Wilcove, D.S. 1988. *National Forests: Policies for the Future.* Vol. 2. *Protecting Biological Diversity.* The Wilderness Society, Washington, D.C.

Wilson, E.O. (Ed.). 1988. *Biodiversity.* National Academy Press, Washington, D.C.

CASE STUDY OF SI/MAB BIOLOGICAL DIVERSITY PLOT RESEARCH METHODOLOGY:

Effects of Hurricane Hugo on the Bisley Biodiversity Plot, Luquillo Biosphere Reserve, Puerto Rico

Francisco Dallmeier, Charlotte M. Taylor,
John C. Mayne, Margo Kabel and Richard Rice

Introduction

The Puerto Rico permanent biodiversity plot is a cooperative project among the Smithsonian Institution/Man and the Biosphere Biological Diversity Program (SI/MAB), the Institute of Tropical Forestry (ITF), and the Department of Biology of the University of Puerto Rico, Río Piedras Campus (UPR). The plot is situated within the drainage basin of the Bisley Experimental Watersheds of the Luquillo Experimental Forest, also known as the Caribbean National Forest, in Puerto Rico (Fig. 1).

The permanent 25-ha research zone contains 25 one-hectare plots, which are further divided into 25 quadrats (20 x 20 m each) in a continuous grid. As of late 1991, only plot 13 had been established (Fig. 2). It was set up in 1988 by a cooperative team under the direction of the SI/MAB staff. Establishing the plot served to demonstrate the plot methodology and as a starting point for research. All trees in the plot have been mapped, marked, and identified. Two censuses have been conducted since Hurricane Hugo passed over the site in September 1989.

The plot area is not primary forest. The site was subject to selective logging and some agriculture until 1934 when it was purchased by the US Forest Service (Scatena 1989). Selective logging for valuable timber species was apparently not thorough, however, because some large, commercially valuable trees remain.

It is likely that charcoal-making had the greatest impact on the forest. Workers in this cottage industry selectively cut certain species; the downed trees were then burned *in situ*. One result was a significant

change in the vegetative composition (García 1991; Scatena 1989). Small portions of the plot area were also cleared for subsistence crops, most of which have long since disappeared, while larger portions were used to cultivate coffee, which was planted in the understorey of the native forest and can still be found in parts of the plot. The canopies of the altered areas were frequently enriched with certain native species (through the elimination of others), and the plot area seems to show these effects.

In these respects, the plot is typical of forests found for the last several centuries in Puerto Rico. Very little virgin forest remains, and what does is generally far removed from roads in the Luquillo Experimental Forest. Thus, the plot provides an excellent study site for gaining a greater understanding of present-day Caribbean wet forests. Human-induced changes aside, the dominant factor in the structure, species composition, and dynamics of Caribbean forests is the hurricane (Wadsworth and Englerth 1959; Weaver 1986, 1989). At Luquillo, hurricanes are predicted to strike approximately every 60 years and to pass close about every 10 to 20 years (Salivia 1972; Scatena 1989). Indeed, hurricanes passed very near the plot area in 1928 and 1956; one passed over in 1932 (Crow 1980; Scatena 1989). Damage
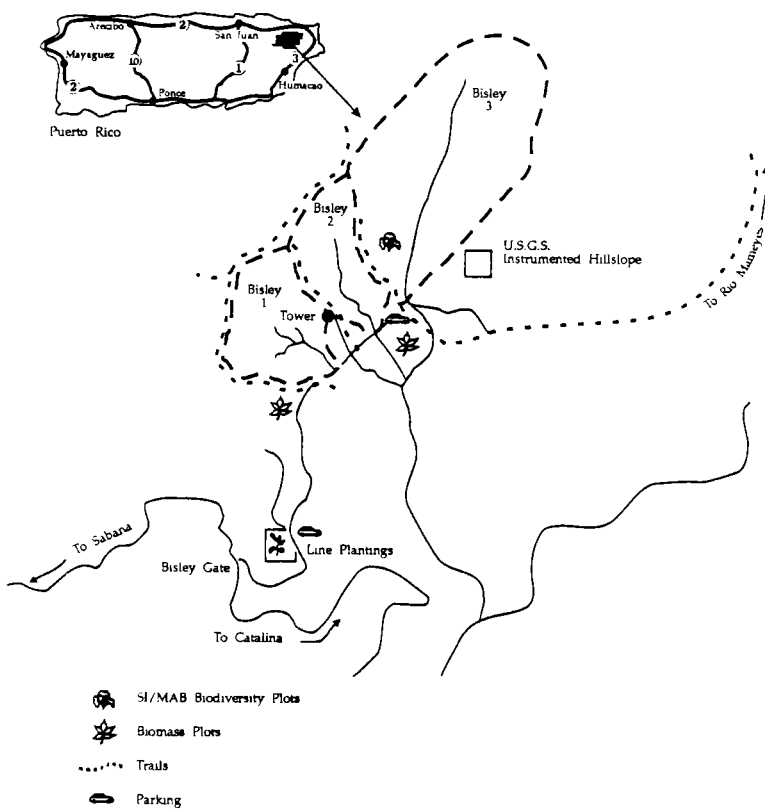

Figure 1. Map of study area.

done by these storms and subsequent regeneration greatly influence the vegetation that exists there today.

Data available from the spatial and long-term studies for which the plot was designed are augmented by the intensive monitoring of physical factors on the site as part of the ITF Experimental Watersheds project. For most tropical areas, long-term monitoring of a few environmental factors is available only under ideal conditions, while broad regional generalizations usually consist of only climate descriptions. But at Luquillo, 50 years of intensive study has occurred (Brown *et al.* 1983, Lugo 1986), and detailed data dating back several years are available. In addition, the Bisley project is directed at accurate measurements of temperature, rainfall, stream flow, erosion, and nutrient movements within the plot.

The research value of the biodiversity plot increased further - and quickly - due to the strike by Hurricane Hugo (a Class IV hurricane) on 19 September 1989. The eye of Hugo passed within 10 km of the plot. The hurricane carried sustained winds estimated at more than 120 miles (192 km) per hour with gusts as high as 200 miles (320 km) per hour. Hugo passed to the east and northeast of the Luquillo massif, the aspect on which the plot is located. The strongest winds of the hurricane struck from the north and northwest, and the mostly northwest-facing slopes of the plot thus received the full force of the storm.

Although many areas in the Luquillo forest have been studied and enumerated, the SI/MAB permanent plot is the only area in which all trees $\geq$ 10 cm in diameter at breast height (dbh) were marked adequately for relocation. The data from the plot represent a complete enumeration of hurricane effects and will serve as the basis for determining an estimate of error (through a count of trees completely missing or located only by inference under debris piles) for post-hurricane survey studies at other sites.

El Verde Field Station, administered by the Center for Energy and Environment Research (CEER), is also located in the Luquillo Experimental Forest. This field station was established in the early 1960s and has been the site of many intensive and long-term studies (Brown *et al.* 1983). El Verde sits on the western, somewhat drier side of the Luquillo massif. Long-term study areas have been established there, and new ones are being set up using methodology similar to that of the Hubbell and Foster Barro Colorado Island plot (Hubbell and Foster 1983). Comparisons between the SI/MAB plot and the El Verde study sites will offer a further dimension to forest research in Puerto Rico.

Methods

The methods used in establishing and censusing SI/MAB plots are described in the first part of this digest (Dallmeier *et al.* 1992). We refer the reader to that section for details about plot design and survey; tree tagging, measurement, identification, and mapping; computer software and data management and control; preparation of users' and field guides; and estimates of time and labour. The description of the methods below are limited to factors specific to the Bisley plot.

Specific plot location and description

The Bisley Biodiversity plot in Puerto Rico is located at approximately 18°18'N 65°50'W, ranging in elevation from 285 to 326 m (Fig. 1). It was set up in May 1988. Tree identification and map detail were checked in the field in January 1989. No voucher specimens were made because the tree flora of the Luquillo Forest is well known. Identifications were made by C.M. Taylor (UPR) and checked in the field for confirmation by I. Pérez (ITF) and C. Rivera (ITF). A mini-herbarium was prepared as
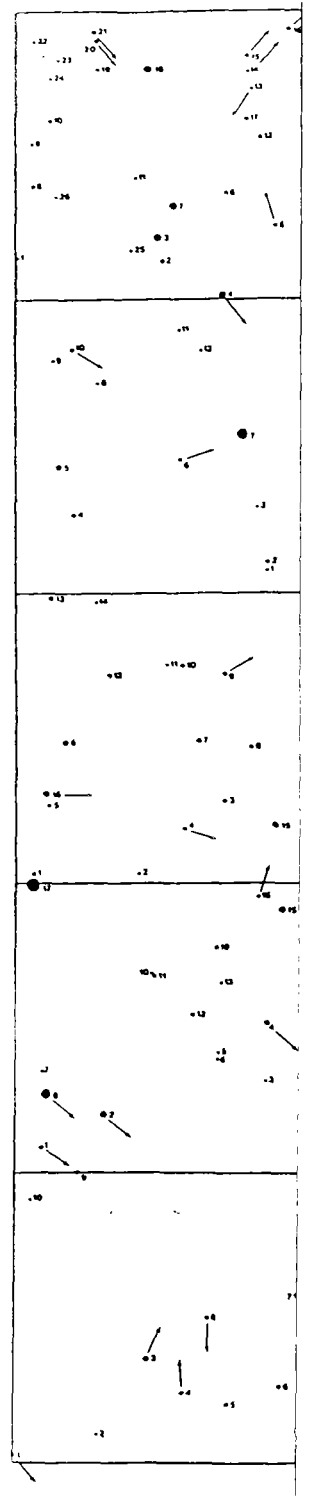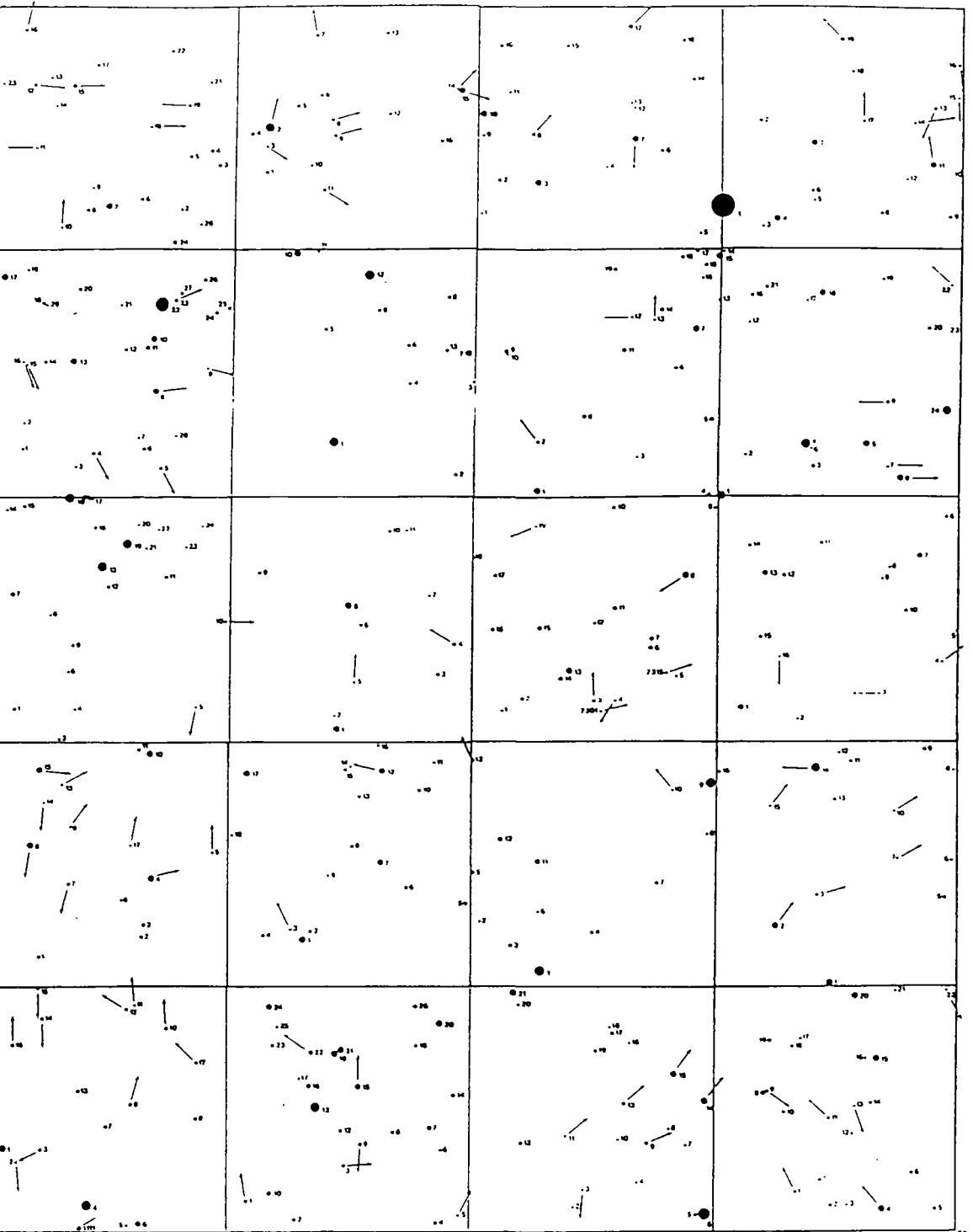
Figure 2. Map of Bisley Biodiversity Plot 0113, showing location of trees after Hurricane Hugo as censused in 1991. Circles mark standing tree trunk positions and are proportional to dbh. Arrows indicate direction in which trees fell and are not proportional to tree size.

part of the Bisley users' and field guides (Dallmeier *et al.* 1991*a*, 1991*b*). The plot was censused again in February 1990 and March 1991.

Data were recorded for each tree in the original (1988) census. In the 1990 and 1991 censuses, after Hurricane Hugo had passed over the site, diameters were measured again, and descriptions of the trees were made according to the following conditions: missing or located; in the same position or moved significantly; dead or alive; standing, leaning, or fallen; coppicing (showing regeneration from the trunk or base, including sprouting); and amount of damage to the crown, categorized as broken (the entire crown broken off at the trunk), heavy damage (most or all branches removed), medium damage (one to three major branches remaining), or low damage (four or more branches remaining). In the 1990 census, the degree of slope and aspect were recorded for each quadrat in the plot.

The Bisley plot is located in the subtropical wet forest zone (Holdridge 1971), or wet premontane forest zone (Ewel and Whitmore 1973). The climate is tropical, with an average annual temperature of 18 to 25°C and an average annual fluctuation of 5°C (Scatena 1989). Average yearly rainfall is approximately 3000 to 4000 mm (Brown *et al.* 1983, Scatena 1989). The site is drained by a stream that passes through the northeastern corner of the plot. Land near the stream is relatively flat, rising as one

The eye of Hurricane Hugo passed within 10 km of the plot on September 19, 1989. The hurricane carried sustained winds estimated at more than 120 miles per hour with gusts as high as 200 miles per hour. Here we can see the effects of the hurricane five months later in February 1990.

moves from the stream to increasingly steep slopes, normally 60 to 70% but exceeding 100% in some places. The aspect of the plot is generally north-northwest. Landslides are frequent, and several are found within the plot. The soils are derived from acidic volcano-clastic substrate and classified as ultisols. They have a high clay content and are near saturation much of the year (Scatena 1989; Ewel and Whitmore 1973).

The site is covered throughout with secondary native forest. Vegetation has been regenerating undisturbed since the 1940s, although it shows some signs of human alteration as discussed above. Vegetation at the research site is typical of wet Antillean forests. It is classified as *tabonuco* type (Beard 1949; Ewel and Whitmore 1973), with *tabonuco* (*Dacryodes excelsa*, Burseraceae) among the typical co-dominant species. The canopy includes some secondary species (*Cecropia schreberiana*, Moraceae, *Didymopanax morotoni*, Araliaceae) mixed with species characteristic of mature forests. Tree species found on the site are presented in Table 1.

Tree species in the plot were initially classified by successional status, as found in Ewel and Whitmore (1973). *Khaya niasica* (Meliaceae), an

This photo shows the regeneration of the Luquillo forest in March 1991. Hurricanes, unlike loggers, perform a more or less uniform thinning on site without regard to tree species or diameter size class.

Table 1. List of trees at Bisley Biodiversity Plot 0113, Puerto Rico[1]

Alchornea latifolia Sw., ALCLAT (Euphorbiaceae)

Alchorneopsis floribunda (Benth.) Muell. Arg., ALCFLO (Euphorbiaceae)

Andira inermisAndira inermis (W.Wr.) HBK, ANDINE (Leguminosae)

Buchenavia capitata (Vahl) Eichl., BUCCAP (Combretaceae)

Calycogonium squamulosum Cogn., CALSQU (Melastomaceae)

Casearia arborea (L.C.Rich.) Urb., CASARB (Flacourtiaceae)

Cecropia schreberiana (*peltata*) Miq., CECSCH (Moraceae)

Chrysophyllum argenteum Jacq., CHRARG (Sapotaceae)

Cordia borinquensis Urb., CORBOR (Boraginaceae)

Cordia sulcata DC., CORSUL (Boraginaceae)

Dacryodes excelsa Vahl, DACEXC (Burseraceae)

Dendropanax arborea (L.) Decne. & Planch., DENARB (Araliaceae)

Didymopanax morototoni (Aubl.) Decne. & Planch., DIDMOR (Araliaceae)

Drypetes glauca Vahl, DRYGLA (Euphorbiaceae)

Guarea glabra Sleumer, GUAGLA (Meliaceae)

Guarea guidonia (L.) Sleumer, GUAGUI (Meliaceae)

Inga fagifolia Willd., INGFAG (Fabaceae)

Inga vera Willd., INGVER (Fabaceae)

Khaya niasica, KHANIA (Meliaceae)

Laetia procera (Poepp. & Endl.) Eichl., LAEPRO (Flacourtiaceae)

Manilkara bidentata (A.DC.) A. Chev., MANBID (Sapotaceae)

Meliosma herbertii Rolfe, MELHER (Sabiaceae)

Nephelea portoricensis (Spreng.) Tryon, NEPPOR (Cyatheaceae)

Miconia prasina (Sw.) DC., MICPRA (Melastomaceae)

Ocotea globosa Schlecht. & Cham., OCOGLO (Lauraceae)

Ocotea leucoxylon Mez, OCOLEU (Lauraceae)

Pouteria multiflora (A.DC.) Eyma, POUMUL (Sapotaceae)

Prestoea montana (R. Graham) Nicols., PREMON (Palmae)

Pterocarpus officinalis Jacq., PTEIND (Leguminosae)

Sapium laurocerasus Desf., SAPLAU (Euphorbiaceae)

Sloanea berteriana Choisy, SLOBER (Elaeocarpaceae)

Tetragastris balsamifera (Sw.) Ktze., TETBAL (Burseraceae)

Trichilia pallida Sw., TRIPAL (Meliaceae)

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1. The above lists genus, species, species code, and family. Trees of these species with diameters of at least 10 cm at breast height have been identified at SI/MAB's Bisley plot 0113.

introduced species of African mahogany, was excluded from analyses of successional status. Analyses related to structural damage caused by Hurricane Hugo were completed both with and without the inclusion of palms (*Prestoea montana*) and tree ferns (*Nephelea portoricensis*, Cyatheaceae) because of their ability to regenerate quickly. For example, most individuals of the palm *Prestoea montana* were classified as having

sustained low damage, even though in the majority of cases their fronds had been stripped from the stems by the force of the hurricane's winds. Nearly all of these plants refoliated soon after Hugo; classifying them in the high crown damage category would have been misleading.[1]

Formulas used to calculate the basal area, relative density, relative dominance, frequency, relative frequency, relative diversity, and the important value index (IVI) are as follows[2] (Balslev *et al.*, 1987):

Basal area (b.a.)   =   area occupied at breast height

$$\text{Relative density} = \frac{\#\ \text{individuals of a species}}{\text{total } \#\ \text{individuals of all species.}} \times 100$$

$$\text{Relative dominance} = \frac{\text{combined b.a. of a single species}}{\text{total b.a. of all species}} \times 100$$

Frequency   =   number of quadrats in which a species is found

$$\text{Relative frequency} = \frac{\text{frequency of one species}}{\text{sum of all frequencies}} \times 100$$

$$\text{Relative diversity} = \frac{\#\ \text{of species in one family}}{\text{total } \#\ \text{of species}} \times 100$$

Importance Value Index (IVI)   =   sum of relative density, relative dominance, and relative frequency

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1. The relatively small amount of damage suffered by the palm *Prestoea montana* compared to dicotyledonous tree species is most likely due to its growth form. These palm trees have a single unbranched stem, with the two to six leaves produced in a group at the top. The leaves of most surviving palms were all damaged and many of the stems were completely defoliated, but new leaves quickly appeared. Most of the palms censused were relatively short, reaching only the tall understory or lower sub-canopy. The response of these palms to Hugo's wind damage may provide a clue to the origin of the large pure stands of palms that characterize the wetter, more exposed forest zones in Puerto Rico.
2. **Basal area** = the basal area (m^2) of individuals of a particular species as a proportion of the total basal areas of all species.
   Relative density = number of individuals of a particular species as a proportion of the total number of individuals of all species.
   Relative dominance = the combined basal area of a single species as a proportion of the total basal area of all species.
   Relative frequency = the frequency of a given species as a proportion of the sum of frequencies for all species.
   Relative diversity = number of species in one family as a proportion of the total number of species.
   Importance Value Index (IVI) = the sum of relative density, relative dominance, and relative frequency.

Table 2. Basic statistics from Bisley Biodiversity Plot 0113 before and after Hurricane Hugo

	1988 CENSUS	1991 CENSUS
Area of plot (m^2)	10,000	10,000
Families represented	17	17
Species represented	33	31
Total number of trees	434	440
Live trees	434	332
standing	434	251
fallen	—	60
broken	—	21
Dead trees	—	108
standing	—	19
fallen	—	71
broken	—	18
Percentage survivorship	100	74.8
Sprouting trees	—	81
fallen sprouting	—	60
broken sprouting	—	21
Total basal area		
live standing trees $(m^2\,ha^{-1})$	28.23	17.20
Trees with undetermined status	0	4

The IVI follows Curtis and McIntosh (1951). A score of 0 in this index indicates absence of a species; a score of 300 indicates a single species in a stand.

Results and discussion

Overall changes

A description of the vegetation in the Bisley plot before the impact of Hurricane Hugo is presented in Tables 1, 2, 3, and 4. None of these initial parameters is unusual for the area or for the type, age, and history of this forest. Slope and aspect were measured only after the hurricane, but little additional land movement was observed in the recensusing. Thus, these data are likely very similar to pre-hurricane conditions.

Table 3. 1988 pre-Hurricane Hugo data, by tree species, from Bisley Biodiversity Plot 0113

Species	Number of stems	Average dbh (m)	Basal area	Relative density	Relative dominance	Relative frequency	IVI
Alchornea latifolia	3	0.22	0.16	0.69	0.57	1.59	2.85
Alchorneopsis floribunda	11	0.40	1.97	2.53	6.98	4.23	13.75
Andira inermis	2	0.17	0.05	0.46	0.18	1.06	1.70
Buchenavia capitata	1	0.86	0.58	0.23	2.05	0.53	2.81
Calycogonium squamulosum	1	0.13	0.01	0.23	0.04	0.53	0.79
Casearia arborea	2	0.16	0.04	0.46	0.14	1.06	1.66
Cecropia schreberiana	8	0.36	0.94	1.84	3.33	3.17	8.35
Chrysophyllum argenteum	9	0.20	0.36	2.07	1.28	3.17	6.52
Cordia borinquensis	1	0.10	0.01	0.23	0.04	0.53	0.79
Cordia sulcata	1	0.19	0.03	0.23	0.11	0.53	0.87
Dacryodes excelsa	39	0.42	6.93	8.99	24.55	9.52	43.06
Dendropanax arborea	2	0.17	0.03	0.46	0.11	1.06	1.63
Didymopanax morototoni	16	0.28	1.20	3.69	4.25	5.29	13.23
Drypetes glauca	1	0.20	0.03	0.23	0.11	0.53	0.87
Guarea glabra	3	0.15	0.06	0.69	0.21	1.59	2.49
Guarea guidonia	19	0.41	3.25	4.38	11.51	5.82	21.71
Inga fagifolia	42	0.23	2.35	9.68	8.32	10.58	28.58
Inga vera	5	0.21	0.21	1.15	0.74	2.65	4.54
Khaya niasica	4	0.14	0.06	0.92	0.21	1.59	2.72
Laetia procera	2	0.22	0.09	0.46	0.32	0.53	1.31
Manilkara bidentata	13	0.34	1.48	3.00	5.24	4.76	13.00
Meliosma herbertii	2	0.20	0.08	0.46	0.28	1.06	1.80
Nephelea portoricensis	4	0.13	0.06	0.92	0.21	1.59	2.72
Miconia prasina	1	0.14	0.02	0.23	0.07	0.53	0.83
Ocotea globosa	1	0.20	0.03	0.23	0.11	0.53	0.87
Ocotea leucoxylon	3	0.14	0.05	0.69	0.18	1.59	2.46
Prestoea montana	135	0.17	3.83	31.11	13.57	13.23	57.90
Pouteria multiflora	2	0.11	0.02	0.46	0.07	1.06	1.59
Sapium laurocerasus	17	0.30	1.34	3.92	4.75	5.82	14.48
Sloanea berteriana	80	0.19	2.93	18.43	10.38	12.17	40.98
Tetragastris balsamifera	2	0.10	0.02	0.46	0.07	1.06	1.59
Trichilia pallida	1	0.11	0.01	0.23	0.04	0.53	0.79
Pterocarpus officinalis	1	0.70	0.38	0.23	1.35	0.53	2.11
TOTAL:	**434**		**28.23**			**99.47**	

The total number of trees in the 1988 census ≥ 10 cm dbh was 434 (Table 2). Only live standing trees were measured in this first census. The total number of trees in the 1991 census was 444. It appears that ten trees

Table 4. 1990-91 post-Hurricane Hugo data, by tree species, from Bisley Biodiversity Plot 0113

Species	Number of live stems	Average dbh(m)	Basal area	Relative density	Relative dominance	Relative frequency	IVI	Fre-quency
Alchnorneopsis floribunda	7	0.479	1.403	2.789	8.155	5.469	16.413	7
Alchornea latifolia	1	0.095	0.007	0.398	0.041	0.781	1.220	1
Andira inermis	2	0.161	0.041	0.797	0.238	1.563	2.598	2
Buchenavia capitata	1	0.825	0.535	0.398	3.110	0.781	4.289	1
Calycogonium squamulosu	0	0.000	0.000	0.000	0.000	0.000	0.000	0
Casearia arborea	1	0.145	0.017	0.398	0.099	0.781	1.278	1
Cecropia schreberiana	1	0.583	0.267	0.398	1.552	0.781	2.732	1
Chrysophyllum argenteum	3	0.160	0.070	1.195	0.407	2.344	3.946	3
Cordia borinquensis	0	0.000	0.000	0.000	0.000	0.000	0.000	0
Cordia sulcata	0	0.000	0.000	0.000	0.000	0.000	0.000	0
Dacryodes excelsa	33	0.413	5.396	13.147	31.365	14.063	58.575	18
Dendropanax arborea	1	0.096	0.007	0.398	0.041	0.781	1.220	1
Didymopanax morototoni	6	0.336	0.649	2.390	3.772	3.906	10.069	5
Drypetes glauca	1	0.129	0.013	0.398	0.076	0.781	1.255	1
Guarea glabra	1	0.119	0.011	0.398	0.064	0.781	1.244	1
Guarea guidonia	12	0.450	2.561	4.781	14.886	7.031	26.698	9
Inga fagifolia	17	0.215	0.824	6.773	4.790	8.594	20.156	11
Inga vera	1	0.168	0.022	0.398	0.128	0.781	1.308	1
Khaya niasica	2	0.152	0.041	0.797	0.238	1.563	2.598	2
Laetia procera	0	0.000	0.000	0.000	0.000	0.000	0.000	0
Manilkara bidentata	7	0.267	0.444	2.789	2.581	3.906	9.276	5
Meliosma herbertii	0	0.000	0.000	0.000	0.000	0.000	0.000	0
Miconia prasina	1	0.141	0.016	0.398	0.093	0.781	1.273	1
Nephelea portoricensis	2	0.107	0.018	0.797	0.105	1.563	2.464	2
Ocotea globosa	0	0.000	0.000	0.000	0.000	0.000	0.000	0
Ocotea leucoxylon	1	0.122	0.012	0.398	0.070	0.781	1.249	1
Pouteria multiflora	1	0.111	0.010	0.398	0.058	0.781	1.238	1
Prestoea montana	99	0.150	1.800	39.442	10.463	19.531	69.436	25
Pterocarpus officinalis	1	0.617	0.299	0.398	1.738	0.781	2.918	1
Sapium laurocerasus	7	0.334	0.661	2.789	3.842	4.688	11.318	6
Sloanea berteriana	38	0.217	1.923	15.139	11.178	13.281	39.598	17
Tetragastris balsamifer	3	0.204	0.147	1.195	0.854	2.344	4.393	3
Trichilia pallida	1	0.115	0.010	0.398	0.058	0.781	1.238	1
TOTAL	**251**		**17.204**					**128**

< 10 cm dbh grew to measurable size by the time of the 1991 census. (Scatena [pers. comm.] suggests these 10 trees may have been missed in the first measurement because the average increase in dbh per year is approximately 0.35 cm).

The number of plant families represented on the plot both before and after the hurricane was 17, but the number of species found on the site decreased from 33 before the hurricane to 31 afterward (Table 2). Each of the lost species - *Cordia sulcata* (Boraginaceae) and *Ocotea globosa* (Lauraceae) - was represented by only one individual in the 1988 census; both trees were killed by the hurricane.

In 1988, the total basal area occupied by all trees on the site $\geq$ 10 cm dbh was 28.2 m^2. Due primarily to mortality directly attributable to Hurricane Hugo, the occupied basal area decreased to 17.2 m^2 in 1991 (Table 2), or 60.9% of the occupied basal area in 1988.

The five species that represented the largest basal area in 1988 were *Dacryodes excelsa* (6.9 m^2), *Prestoea montana* (3.8 m^2), *Guarea guidonia* (3.3 m^2), *Sloanea berteriana* (2.9 m^2), and *Inga fagifolia* (2.4 m^2) (Table 3). Together, these five species represented 68.3% of the occupied basal area of the plot. After Hurricane Hugo, the basal areas of these five species dropped, respectively, to 5.4 m^2 (22% loss), 1.8 m^2 (53% loss), 2.6 m^2 (21% loss), 1.9 m^2 (35% loss), and 0.8 m^2 (65% loss). Together they occupied a total of 72.7% of the 1991 basal area (Table 4).

In the 1991 census, 251 live trees were standing, representing a decrease of 43% in live standing stems (Fig. 3). Seventy-eight fallen trees were alive and sprouting, 18 of which had broken trunks. However, none of the sprouts had grown to a stage where they could be assumed to have survived; more time must pass to assess their survival rate. Of a total of 108 dead trees found in the post-hurricane census, 19 were standing in March 1991, while 18 were broken and
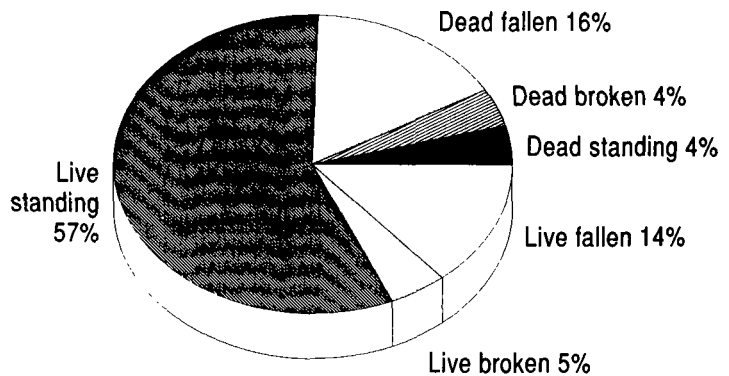

Figure 3. Status of trees in Bisley Biodiversity Plot 0113 after Hurricane Hugo, 1990 and 1991 censuses.

Dead fallen 16%
Dead broken 4%
Dead standing 4%
Live fallen 14%
Live broken 5%
Live standing 57%

Table 5. Status of all trees by species of Bisley Biodiversity Plot 0113, Puerto Rico, 1988 and 1991 censuses

Species	1988	1991					
	AS	AS	AB	AF	DS	DB	DF
Alchornea latifolia	3	1	0	1	0	0	1
Alchorneopsis floribunda	11	17	2	0	0	1	2
Andira inermis	2	2	0	0	0	0	0
Buchenavia capitata	1	1	0	0	0	0	0
Calycogonium squamulosum	1	0	0	1	0	0	0
Casearia arborea	2	1	0	0	1	0	0
Cecropia schreberiana	8	1	0	0	1	1	5
Chrysophyllum argenteum	9	3	0	3	0	1	1
Cordia borinquensis	1	0	0	1	0	0	0
Cordia sulcata	1	0	0	0	0	1	0
Dacryodes excelsa	39	33	1	1	0	1	3
Dendropanax arborea	2	1	1	0	0	0	0
Didymopanax morototoni	16	6	5	0	1	2	2
Drypetes glauca	1	1	0	0	0	0	0
Guarea glabra	3	1	0	1	0	0	1
Guarea guidonia	19	12	0	6	0	0	2
Inga fagigolia	42	17	4	12	2	0	7
Inga vera	5	1	1	1	1	1	0
Khaya niasica	4	2	0	2	0	0	0
Laetia procera	2	0	2	0	0	0	0
Manilkara bidentata	13	7	0	4	2	0	0
Meliosma herbertii	2	0	0	1	0	1	0
Miconia prasina	1	1	0	0	0	0	0
Nephelea portoricensis	4	2	0	0	1	0	1
Ocotea globasa	1	0	1	0	0	0	0
Ocotea leucoxylon	3	1	1	0	0	0	1
Pouteria multiflora	2	1	0	1	0	0	0
Prestoea montana	135	99	0	2	8	8	22
Pterocarpus officinalis	1	0	0	0	0	0	0
Sapium laurocerasus	17	7	1	3	2	0	1
Sloanea berteriana	80	38	2	20	0	1	19
Tetragastris bassamifera	2	3	0	0	0	0	0
Trichilia pallida	1	1	0	0	0	0	0

AS = alive standing   DS = dead standing
AF = alive fallen   DB = dead broken
NL = not located   DF = dead fallen

71 had fallen (Tables 5 and 6). The demise of these trees is believed to have been caused directly by Hurricane Hugo. Six trees were completely unaccounted for in the first post hurricane census (1990). They were most probably buried beneath debris piles and are presumed dead. Eighteen trees were not located in the 1991 census (Table 6), including the six

Table 6. Status of trees not located in Bisley Biodiversity Plot 0113 after Hurricane Hugo, 1990-91 censuses

Species	Quad	Tree	dbh	1990	1991
Prestoea montana	3	14	.14	NL	NL
Prestoea montana	5	17	.173	AS	NL
Inga fagigolia	6	3	.25	DF	NL
Sloanea berteriana	8	3	.116	AF	NL
Prestoea montana	10	19	.19	DB	NL
Presoea montana	10	21	.14	NL	NL
Prestoea montana	11	25	.14	NL	NL
Inga fagifolia	12	14	.14	DS	NL
Chrysophyllum argenteum	13	5	.137	AF	NL
Sapium laurocerasus	14	9	.273	DF	NL
Prestoea montana	18	5	.12	DF	NL
Sloanea berteriana	18	7	.28	DF	NL
Nephelea portoricensis	19	2	.10	DF	NL
Chrysophyllum argenteum	20	1	.10	NL	NL
Prestoea montana	20	2	.15	NL	NL
Inga fagifolia	24	23	.19	NL	NL
Prestoea montana	25	14	.123	AS	NL
Sloanea berteriana	18	3	.172	DF	NL

AS = alive standing   DS = dead standing
AF = alive fallen   DB = dead broken
NL = not located   DF = dead fallen

missing trees from the 1990 census. Eight of the additional missing trees were recorded as dead in the 1990 census and are still considered dead even though they were not located in 1991. The status of the four remaining missing trees is uncertain and will be verified in the next census.

The changes in relative density, dominance, frequency, and diversity, as well as in the importance value index for each species, give a measure of the impact of the hurricane on species composition in the plot and form a baseline from which to assess regeneration (Tables 3 and 4). Overall, the effects of the hurricane slightly increased the importance of some species and slightly decreased the importance of others. There were no striking impacts on any particular species except one - *Prestoea montana*, which suffered low damage and had a high survival rate.

The five species with the largest relative densities in 1988 were *Prestoea montana* (31.1), *Sloanea berteriana* (18.4), *Inga fagifolia* (9.7), *Dacryodes excelsa* (9.0), and *Guarea guidonia* (4.4) (Table 3, Fig. 4). These same five species showed the largest relative densities in 1991, although their abso-

lute densities and relative ranking had changed: *Prestoea montana* (39.4), *Sloanea berteriana* (15.1), *Dacryodes excelsa* (13.2), *Inga fagifolia* (6.8), and *Guarea guidonia* (4.8) (Table 4).

The five species with the largest relative dominance in 1988 were *Dacryodes excelsa* (24.6), *Prestoea montana* (13.6), *Guarea guidonia* (11.5), *Slonea berteriana* (10.4), and *Inga fagifolia* (8.3) (Table 3). The five species with the largest relative dominance in 1991 were *Dacryodes excelsa* (31.4), *Guarea guidonia* (14.9), *Sloanea berteriana* (11.2), *Prestoea montana* (10.5) and *Inga fagifolia* (4.8) (Table 4).

a) *Prestoea montana* (left) a) *Prestoea montana* (right)

b) *Sloanea berteriana* (left) b) *Sloanea berteriana* (right)

Figure 4. Maps showing distribution, before (left side) and after (right side) Hurricane Hugo, of the five species with the highest relative density in Bisley Biodiversity Plot 0113.

Again, the most dominant species remained the same after the hurricane, although their order of dominance was altered.[1]

The five species with the largest relative frequency in 1988 were *Prestoea montana* (13.2), *Sloanea berteriana* (12.2), *Inga fagifolia* (10.6), *Dacryodes excelsa* (9.5), and *Guarea guidonia* (5.8) (Table 3); the order of these species is the same as for relative density, although this is not necessarily always the case. In 1991, after Hurricane Hugo, the five species with the largest relative frequency were *Prestoea montana* (19.5), *Dacryodes excelsa* (14.1), *Sloanea berteriana* (13.3), *Inga fagifolia* (8.6), and *Guarea guidonia* (7.0) (Table 4).

1. The order of these species is the same as those for basal area, which is not surprising because calculation of relative dominance depends on basal area figures. These are the same five species that show the highest relative density, although their order differs due to differences in the diameters of the trees. If all trees of all species had the same dbh, then relative density would equal relative dominance. When the relative dominance of one species is greater than that of another species with a larger relative density, this indicates that the species with the greater relative dominance has fewer trees but more total basal area; i.e., fewer but larger trees.

c) Inga fagifolia
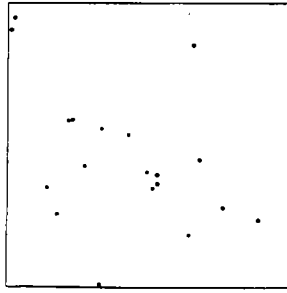
c) Inga fagifolia

d) Dacryodes excelsa
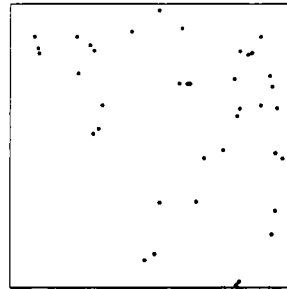
d) Dacryodes excelsa

e) Guarea guidonia
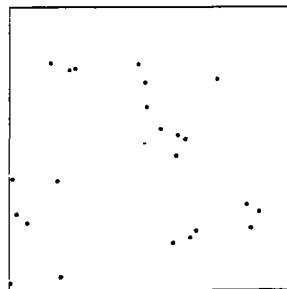
e) Guarea guidonia

The species composition and relative frequency found among the surviving trees is not significantly different from the composition of the plot before the hurricane. It is likely that gap specialist species will germinate and reach a canopy height before the regeneration of the mature forest species is complete, although they will not dominate as they would in a light gap area: the average size of trees was reduced by the hurricane, but it is still larger than that found in a nearby light gap. At Bisley, it is too soon to measure new individuals of gap specialist species in the 10 cm dbh size class.

Damage to individual species

All standing trees in the plot in 1988 sustained a degree of crown damage (Figs. 5 and 6). One hundred and twenty-nine trees, or 52% of the living trees still standing after the hurricane, sustained low crown damage; 35 trees, or 14%, sustained medium crown damage; and 82 trees, or 33%, sustained high crown damage. Most of the trees sustaining low crown damage were palms (*Prestoea montana*). When *Prestoea montana* was not included in the crown damage statistics, the percentage of trees sustaining low crown damage dropped to 23%, while the percentage of trees sustaining medium and high damage rose to 23% and 53%, respectively.

When crown damage was considered in relation to species, only four species other than *Prestoea montana* had enough individuals to make

meaningful any interpretation of the data (Fig. 7). More than 50% of the trees of the species *Sloanea berteriana, Guarea guidonia* and *Inga fagifolia* sustained high crown damage. In the case of *Dacryodes excelsa*, more than 40% of the trees sustained high crown damage.

When high and medium crown damage were combined into a single category called significant crown damage, 75% of the individual trees of *Slonea berteriana* qualified. For *Guarea guidonia*, 92.3% of the trees had significant crown damage; for *Inga fagifolia*, the amount was 83.3%; for *Dacryodes excelsa*, 61.3%.

Most of the trees on the plot (74%) and all but one individual of *Prestoea montana* fall into two diameter size classes - 0.100 to 0.149 cm and 0.150 to 0.199 cm. Crown damage by dbh class can only be considered for these two size classes, due to the paucity of individuals in other classes (see Fig. 8). No trend was observed in either of these size classes. Analysis of crown damage data for the 0.100 to 0.149 cm dbh size class showed that 58% of these trees sustained low damage, 7% sustained medium damage, and 37% sustained high damage (see first size class shown in Fig. 9). This is due in large part to the dominance of *Prestoea montana* in this size class
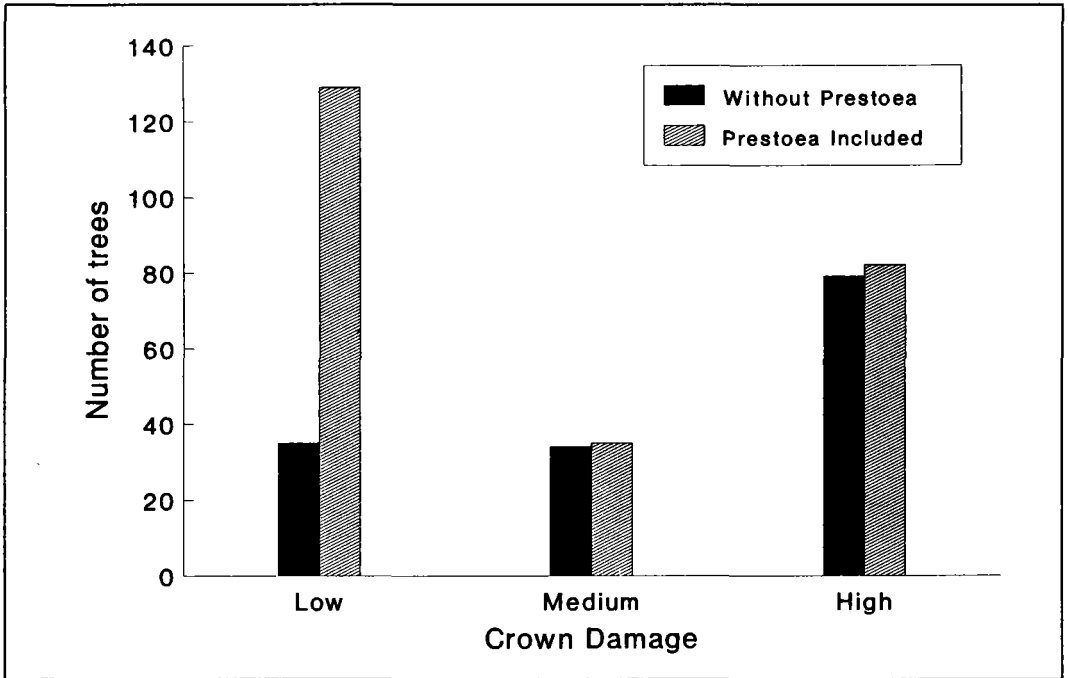
Figure 5. Number of trees, with and without *Prestoea montana*, sustaining low, medium and high crown damage in Bisley Biodiversity Plot 0113.
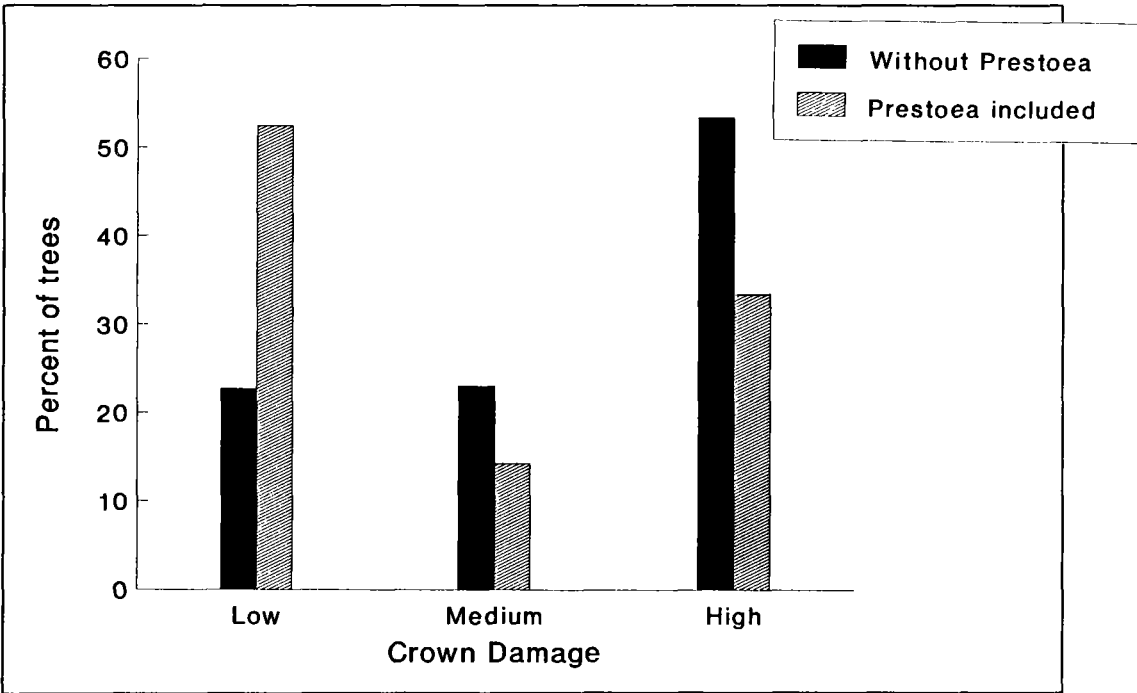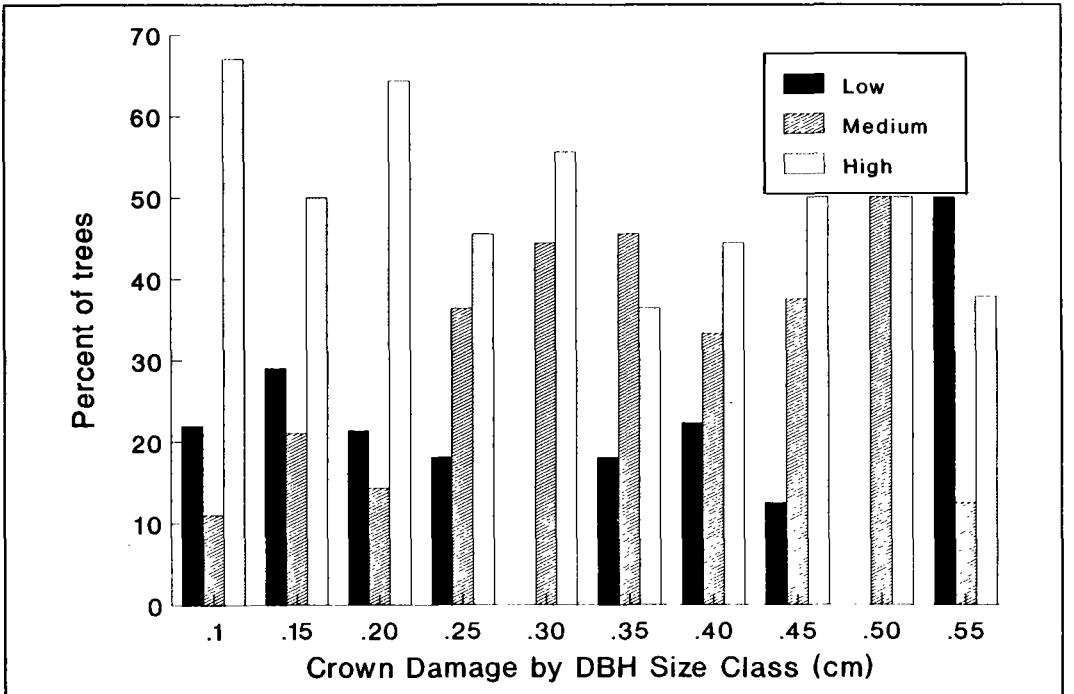
Figure 6. Percentage of trees, with and without *Prestoea montana*, sustaining low, medium and high crown damage in Bisley Biodiversity Plot 0113.
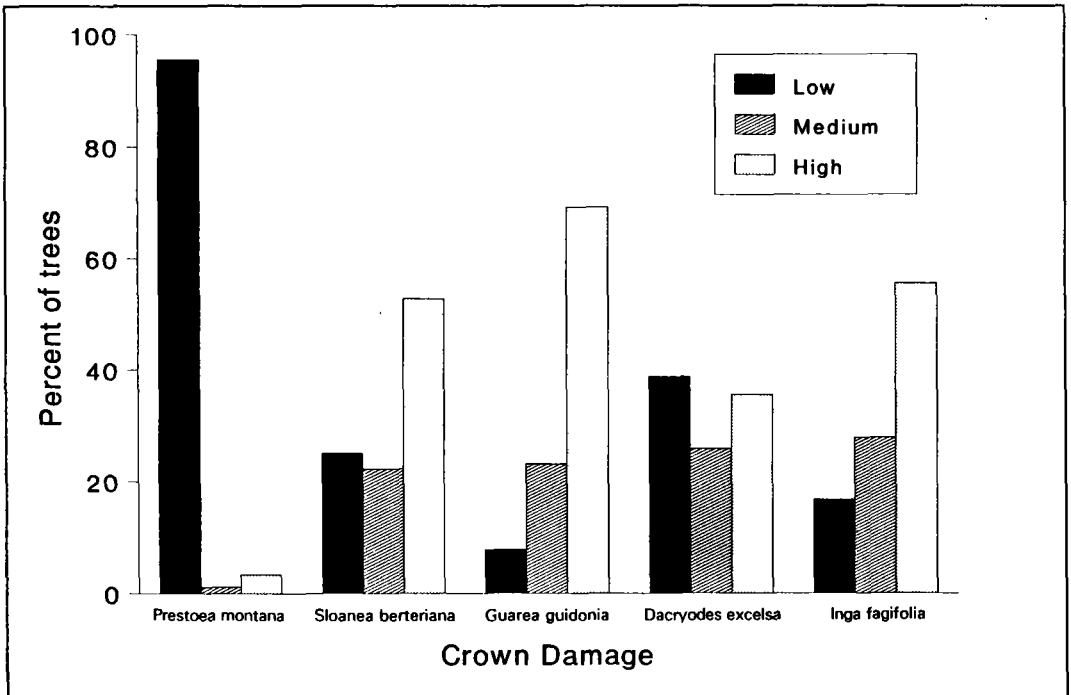
Figure 7. Percentage of trees sustaining low, medium and high crown damage in the five most prevalent species in Bisley Biodiversity Plot 0113.

(99% of the trees), the species which suffered much less damage than other species. If *Prestoea montana* is removed from consideration, the percentages of low, medium, and high crown damage in this size class change to 22%, 11%, and 67%, respectively (see first size class shown in Fig. 10).

With *Prestoea montana* included, crown damage in the second size class (dbh 0.150 - 0.199 cm)was as follows: 78% of the trees sustained low crown damage, 7% medium crown damage, and 18% high crown damage (see second size class in Fig. 9). When *Prestoea montana* is removed from the analysis, the damage estimates change markedly: 29% of the trees sustained low crown damage, 21% medium crown damage, and 50% high crown damage (see second size class in Fig. 10).

Apart from the higher survivorship and lower damage observed for *Prestoea montana*, no correlation was found between the amount of crown damage and species. This is probably due in part to the violent nature of the hurricane, but it may also be reflective of the small number of individuals of most species on the plot. In short, the sample may not be large enough.
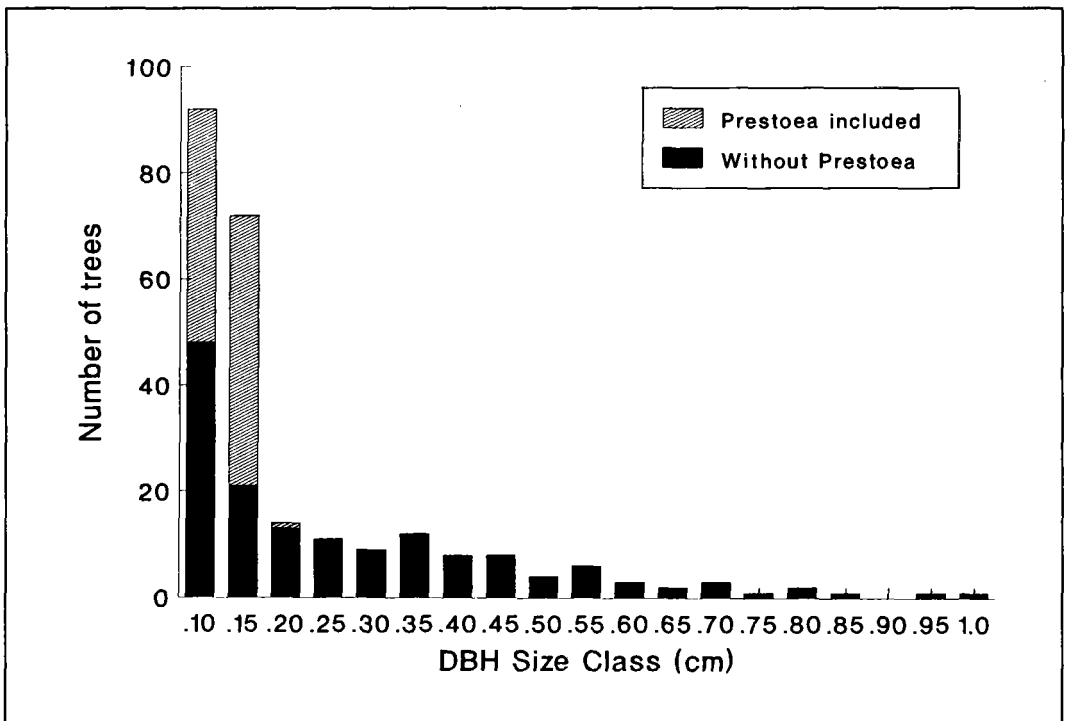
Figure 8. Number of trees by diameter size class, with and without *Prestoea montana,* in Bisley Biodiversity Plot 0113.
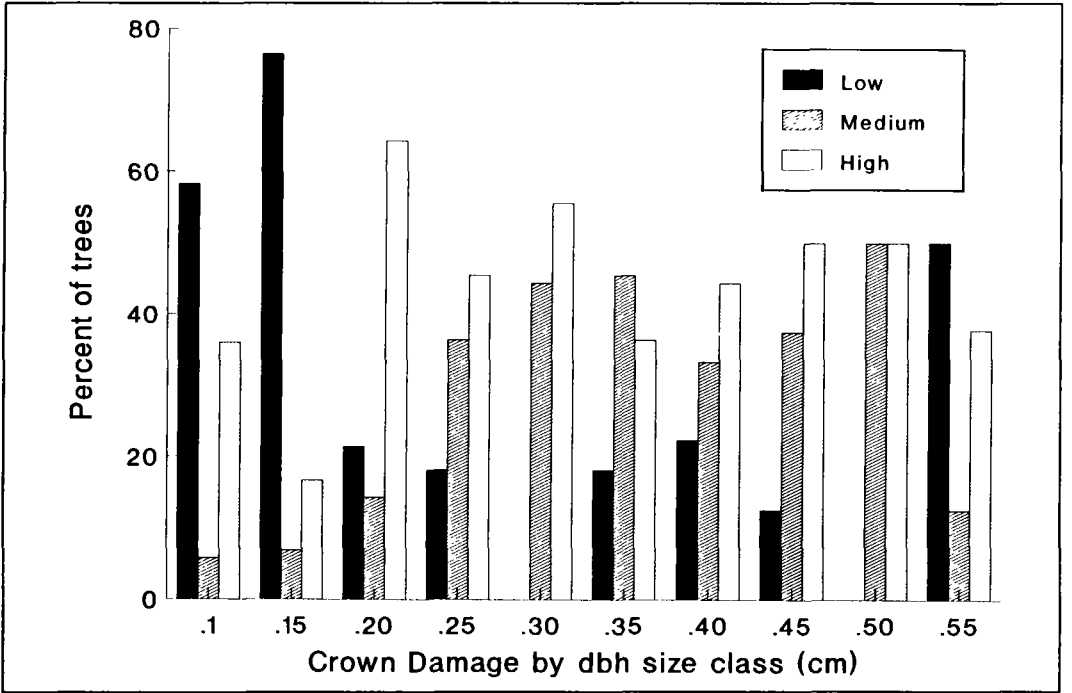
Figure 9. Percentage of trees in each diameter size class sustaining low, medium and high crown damage in Bisley Biodiversity Plot 0113.

Figure 10. Percentage of trees without *Prestoea montana*, in each diameter size class sustaining low, medium and high crown damage in Bisley Biodiversity Plot 0113.

Regeneration of the forest

Regeneration of damaged trees, in the form of sprouting, began before the plot was censused in February 1990. This initial growth will greatly influence the long-term regeneration and composition of the forest. The data gathered thus far are therefore considered preliminary and will form a baseline for future studies.

Coppicing is characteristic of many species on the plot. Palms (*Prestoea*) and tree ferns (*Nephelea*), however, are structurally different from dicotyledonous trees and, with only one terminal meristem, are not capable of sprouting.

The survival of many fallen and broken trees and their subsequent regeneration through sprouting distinguishes the disturbance effects of the hurricane from those related to other causes. Although severely damaged, many individual trees of species that are characteristic of mature *tabonuco* forest did survive, are now sprouting, or are already developing new crowns. Most previous studies of regeneration - even those conducted after hurricane disturbance - do not help predict the path of succession. The post-hurricane work of the past was restricted to the later stages of recovery and addressed the initial impact only through inference (notably, Crow 1980). Thus, the establishment of SI/MAB's Bisley plot before Hugo's strike provides an exceptional opportunity for long-term study of a successional pattern - from the beginning onward.

The post-hurricane forest setting in which the Bisley plot is located cannot be compared to a 'natural' forest gap. Nor can it be realistically compared to a forest where selective logging has allowed some trees to survive. Hurricane damage is a unique phenomenon that creates larger canopy openings than does selective logging. Hurricanes, unlike loggers, perform a more or less uniform thinning on site without regard to the tree species or diameter size class. In addition, there is no cleared portion after a hurricane - only a sparser forest that may or may not provide sites for seedlings of new species. Buried seed banks provide a large reservoir that is genetically and taxonomically diverse; it is from this reservoir that much of the regeneration in a cleared area arises. However, the survival and root-sprouting of trees after hurricanes may block the growth of many new seedlings from a buried storehouse and, thus, channel regeneration to existing plants.

The regenerative capacity of the Bisley plot and surrounding forest appears to lie with the large number of fallen, sprouting trees. Many of these

trees have vigorous, multiple sprouts. As time goes on, one or two sprouts will likely become dominant on each surviving tree and may ultimately reach the canopy. This strong advantage may diminish in importance, if these species are overtaken at least initially by the faster growing *Cecropia*, a short-lived secondary species that invaded the site after the hurricane with an estimated 66,000 seedlings per hectare (Scatena, pers. comm.).

It is too early in the regeneration of the forest to be able to predict which species will prevail on the site in the future. Still, it seems safe to say - in view of the fact that all species lost similar percentages of individuals - that the species composition in the years to come will be similar to that of the forest before Hurricane Hugo.

◆◆◆

In conclusion, the impact of hurricanes has long been credited with controlling the dynamics of the *tabonuco* forest (Beard 1947, Wadsworth and Englerth 1959). Long-term studies established at the time of Hurricane Hugo in an area as well-studied as the Luquillo Forest will allow documentation of the effects in finer detail than has been done to date. This information will be augmented by the permanent biodiversity plot, where the trees were fully enumerated before the advent of the hurricane.

Acknowledgements

References

Balslev, H., J. Luteyn, B. Ollgaard & L.B. Holm-Nielsen. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botánica* 92:37-57.

Beard, J.S. 1949. *The Natural Vegetation of the Windward and Leeward Islands*. Clarendon Press, Oxford.

Brown, S., A.E. Lugo, S. Silander & L. Liegel. 1983. *Research History and Opportunities in the Luquillo Experimental Forest*. Institute of Tropical Forestry Publication. General Technical Report, SO-44. USDA Forest Service, Southern Forest Experiment Station, New Orleans.

Crow, T.R. 1980. A rain forest: a 30 year record of change in structure and composition. El Verde, Puerto Rico. *Biotropica* 12:42-55.

Curtis, J.T. & R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476-496.

Dallmeier, F.; Kabel, M.; Taylor, C.; Rice, R.; Mayne, J. & Romano, C. 1991a. *User's Guide to the Bisley Biodiversity Plots, Luquillo Biosphere Reserve, Puerto Rico*. Smithsonian Institution, Washington, D.C.

Dallmeier, F.; Kabel, M.; Taylor, C.; Rice, R.; Mayne, J. & Romano, C. 1991b. *Field Guide to the Bisley Biodiversity Plots, Luquillo Biosphere Reserve, Puerto Rico*. Smithsonian Institution, Washington, D.C.

Dallmeier, F.; Kabel, M.; Rice, R. 1992. Methods for long-term biodiversity inventory plots in protected tropical forest. In F. Dallmeier (Ed.), *Long-Term Monitoring of Biological Diversity in Tropical Forest Areas: Methods for Establishment and Inventory of Permanent Plots*, 11-46. MAB Digest 11. UNESCO, Paris.

Ewel, J.J. & J.L. Whitmore. 1973. *The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands*. Forest Service Research Paper ITF-18. Institute of Tropical Forestry. USDA Forest Service, Southern Forest Experimental Station, Rio Piedras.

García, D. 1991. *Effect of Charcoal Making in the 1940's on the Species Composition of the Present-day Forest of the Bisley Experimental Watersheds*. Masters Thesis. University of Puerto Rico, Rio Piedras.

Holdridge, L.R., W.C. Grenke, W.H.T. Liang & J.A. Tosi Jr. 1971. *Forest Environments in Tropical Life Zones: A Pilot Study*. Pergamon Press, New York.

Hubbell, S.P. & R.B. Foster. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. In: S.L. Sutton, T.C. Whitmore & A.C. Chadwick (Eds). *Tropical Rain Forest: Ecology and Management*, 24-41. Blackwell Scientific Publications, Oxford.

Lugo, A.E. 1986. *Water and the Ecosystems of the Luquillo Experimental Forest*. Forest Service General Technical Report 50-63. USDA Forest Service, Southern Forest Experiment Station, New Orleans.

Salivia, L.A. 1972. *Historia de los temporales de Puerto Rico y las Antillas, 1492-1970.* Editorial Edil, Inc. University of Puerto Rico, Rio Piedras.

Scatena, F. N. 1989. *An Introduction to the Physiography and History of the Bisley Experimental Watersheds, Luquillo Mountains, Puerto Rico.* Institute of Tropical Forestry Report. USDA Forest Service, Southern Forest Experiment Station, Rio Piedras.

Taylor, C.M. & R.B. Waide. 1990. *New El Verde Plant Name Codes.* Terrestrial Ecology Division, Center for Energy and Environmental Research. University of Puerto Rico, San Juan.

Wadsworth, F.H. & G.H. Englerth. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. *Caribbean Forester* 20(1):38-51.

Weaver, P. L. 1986. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 22(1-2):53-70.

Weaver, P. L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia* 14(4):181-192.