HURRICANE DAMAGE AND RECOVERY IN THE MONTANE FORESTS OF THE LUQUILLO MOUNTAINS OF PUERTO RICO

PETER L. WEAVER

Southern Forest Experiment Station
Institute of Tropical Forestry
P.O. BOX 21390
Río Piedras, Puerto Rico 00928

ABSTRACT

Periodic disturbances caused by hurricanes constitute an integral phase of forest growth and development in the Caribbean region. The 35-year recovery in seven permanent plots in the Colorado Forest of the Luquillo Mountains in Puerto Rico covering the 14 through 49 year period after a major disturbance was characterized by: (1) ingrowth and mortality rates of 20 stems/ha/yr, or 1.1% yr of the initial number of stems; (2) shifts to larger tree diameters and heights; (3) a 3% decline in the number of trees in the intermediate and dominant crown classes and a 6% increase in the number of suppressed trees; (4) a 1.1% increase in the weighted mean specific gravity of all stems and a 2.6% increase for dicotyledons alone; (5) a change in species composition with the loss of pioneers, decrease in secondary species, and increase in the dominance of climax trees; (6) a decline in species richness from 88 to 83 species for the entire forest; (7) a decrease in diameter increment from 0.14 cm/yr in the years between 1946-51 to 0.09 cm/yr in the years between 1976-81 for all surviving stems; (8) an increase in standing stemwood and branch volume from 217 to 254 m^3/ha, with a net growth of 1.06 m^3/ha/yr; and (9) an increase in aboveground woody biomass from 122 to 145 t/ha with a net growth of 0.67 t/ha/yr. Patterns of disturbance and recovery appear to vary along elevational and topographic gradients within the Luquillo Forest. Windthrow is more common at lower elevations where there are large trees in valleys; breakage is more prevalent on slopes and ridges at higher elevations. In the Colorado Forest, biomass recovery appears linear. In the Tabonuco Forest below it, recovery is along a convex curve. In the Dwarf Forest at the summits, it may also be linear, but slower than in the Colorado Forest.

RESUMEN

Disturbios periodicos causados por huracanes constituyen una etapa integral en el crecimiento y desarrollo de los bosques en la Cuenca del Caribe. La recuperación durante 35 años de siete rodales permanents en el Bosque Colorado de la Sierra de Luquillo en Puerto Rico, entre el período de 14 a 49 años después de un disturbio mayor, se caracterizó per: (1) tasas de reclutamiento y mortalidad de 20 tallos/ha/año, ó 1.1Y. del número de tallos iniciales; (2) cambios a árboles con mayor dimetro y altura; (3) un descenso de 3% en el número de árboles en las clases de cops intermedio y dominante, y un aumento de 6% en el número de tallos suprimidos; (4) un aumento de 1.1 % en el peso especifico de todos los árboles combinados y un aumento de 2.6% en el peso especifico de los dicotiledones solos; (5) un cambio en la composición de especies con la pérdida de las pioneras, una reducción de las especies secundarias, y un aumento en la dominancia de árboles climax; (6) un descenso en la riqueza de especies de 88 a 83 en todos los rodales combinados; (7) una reducción

Carib. J. Sci. 22(1-2): 53-70(1986)

en el increment de diámetro de 0.14 cm/año durante los años 1946-51 a 0.09 cm/año durante los años 1976-81 en todos los árboles que sobreviveron; (8) un aumento del volumen en pie de los troncos y ramas de 217 a 254 m^3/ha con un increment neto de 1 y (9) un aumento en la biomasa maderera sobre el terreno de 122 a 145 t/ha con un increment neto de 0.67 t/ha/a Los patrones de disturbio y recuperación parecen variar según los gradientes ene elevación y topografia en la Sierra de Luquillo. La caida de arboles es mas común a baja elevación donde se encuentran árboles grandes en valles; la rotura es más prevalence en pedientes v cimas a elevaciones mayores. En el Bosque Colorado, la recuperación de biomasa aparece en la forma lihneal En el Bosque de Tabonuco localizado más abajo, la recuperación sigue en una forma convexa. En las cimas donde se encuentra el bosque enano, la recu puede ser lineal, pero más de despacio que en el Bosque Colorado.

INTRODUCTION

Hurricanes are recurrent phenomena in the Caribbean Basin. They occur mainly during the summer months of July, August, and September and cause damage to natural forests and plantations within the region. Records show that the effects of more than 70 storms have been felt in Puerto Rico since the early 1700's (Salivia 1972). Of these, 13 were classified as type A storms characterized by hurricane force winds that pass directly over the island (Fig. 1), Since 1766, the Luquillo Forest alone has experienced four type A hurricanes, The last was San Ciprian of 1932 with winds up to 150 km/hr. In addition to these storms, San Felipe, of 1928, a type A storm with winds up to 240 km/hr, passed about 45 km SW of the forest, and in 1931, San Nicolas, with winds up to 150 km/hr, passed offshore about 20 km N of the forest.

Wind speed, trajectory, and storm duration are critical factors that influence the destructive potential of hurricanes (Salivia 1972), The effects of hurricanes on forest structure have been documented, Observations of damage immediately after the passage of storms have shown considerable defoliation, breakage, and uprooting (Lugo et al. 1983; Wilkinson et al, 1978), In natural stands, windthrow has been correlated with soil depth and root development (Wood 1970; Wilson 1976), large crown-to-stem ratios (Wadsworth and Englerth 1959), and wet soils (Cremer et al. 1977), while breakage has been found on firm substrates such as limestone (Wadsworth and Englerth 1959). The abnormal production of seeds after storms (Bates 1929; King 1945; Webb 1958), regeneration in gaps of various sizes (Whitmore 1974), and the growth of secondary forests in patchy arrangements (Browne 1949) are features that enhance the survival of pioneer and secondary species within the natural forest.

Despite the numerous observations of hurricane damage and short-term vegetative response to disturbance, few studies of long-term changes in forests are available (Crow 1980). The purpose of the present study was to characterize the change in forest structure and species composition in the Colorado Forest which consists of Lower Montane Wet and Lower Montane Rain Forests, as described by Holdridge (1967), and Montane Rain Forest as described by Beard (1944, 1949); determine growth since the establishment of permanent plots in 1 946; and compare hurricane damage and recovery with the Dwarf and Tabonuco Forests located above and below the Colorado Forest (Wadsworth 1 951).

THE LUQUILLO MOUNTAINS

The Luquillo Mountains are located 8 km from the ocean in northeastern Puerto Rico and rise abruptly to 1075 m. The soils are mainly clays; silty clay loams and clay loams are also present. The soils are saturated most of the year and range in organic matter content from an average of 25 kg/m^2 (5%) at 600 m elevation to 40 kg/m^2 (14%) near the summits.

The abrupt elevational gradient from the coast to the highest summits profoundly affects the climate in the mountains, Rainfall near the windward border of the forest approaches 2300 mm/yr, with a mean annual temperature of 23°C. At the summits, rainfall averages about 4500 mm/yr with a mean annual temperature of 19°C. The upper slopes and ridges of mountains are usually enveloped in clouds that reduce solar insolation to 60% of that in coastal areas (Briscoe 1966). Moreover, intercepted cloud moisture yields an additional 500 mm/yr to the soil surface in the peak areas (Baynton 1968; Weaver 1972). Evapotranspiration decreases, and relative humidity and wind velocity increase with elevation (Briscoe 1966; Wadsworth 1951).

Ascending the Luquillo Mountains, the following forest types are encountered (Beard 1944, 1949): the Lower Montane Rain Forest, composed of the association called Tabonuco Forest, which extends from the forest border at 150 m to 600 m elevation; the Montane Rain Forest (the Colorado Forest Association), ranging from 600 to 900 m elevation; the Dwarf Forest (locally, Dwarf Forest), located on exposed peaks and ridges above 900 m; and Palm Brake (locally, Palm Forest) on steep slopes and in drainages above 500 m. The most recent classification of the vegetation of the Luquillo Mountains (Ewel and Whitmore 1973), using the Holdridge (1967) life zone system, recognized Subtropical Wet, Subtropical Rain, Lower Montane Wet, and Lower Montane Rain Forests. Hereafter, the local association names will be used.

The Colorado Forest is evergreen with two layers. The mean canopy height is about 15 m (Wadsworth 1949). Leaves are coriaceous and microphyllous. Stand volumes (stemwood and branchwood) average about 200 m^3/ha. Representative arborescent vegetation ≥ 10 cm in diameter on 4 ha showed 58 species and about 830 tree/ha, 96% of which were < 45 cm in diameter (Wadsworth 1951).

METHODS

In 1946, the seven permanent plots used in this study were established in Colorado Forest previously disturbed by hurricanes. The purpose was to determine tree diameter increment. Four plots were situated on slopes between 700 and 900 m elevation; one plot had both slopes and valleys and was located at 750 m; the remaining two plots were located in valleys at 650 m elevation. On each plot, all trees ≥ 4.1 cm at breast height (1.4 m above the ground) were identified to species, measured to the nearest 0.1 cm in diameter, and permanently tagged 15 cm below breast height to avert future errors in measurement that might be caused by swelling around the nails. Height was estimated visually to the nearest 0.5 m and checked occasionally using an abney level. Crown classes were also recorded as dominant, codominant, intermediate, and suppressed (Baker 1950). In 1951, 1956, and 1976, many of the plots were visited again, but tree measurements were incomplete. Height was not recorded, and ingrowth was partially recorded but never tagged. Detailed tree measurements were made again in 1981. This time, height was determined by an optical rangefinder to the nearest 0.1 m. Trees that did not contain tags were assessed by their diameter and Position in the stand as either residual trees that had lost their tags or as ingrowth. Any previously tagged tree that was missing was recorded as dead.

Tree diameter increments were statistically tested for differences among crown classes for species represented by sufficient numbers, and between years for all survivors, using Duncan's multiple range test. Tree volumes, including branches ≈ 2.5 cm in diameter, were determined using and existing equation derived for the construction of volume tables in the Colorado Forest (Wadsworth 1949). Aboveground woody biomass estimates were then attained by multiplying the individual tree volumes by their respective specific gravities. The latter were obtained from published sources (Little and Wadsworth 1964, Little et al. 1974), or from the Forest Products Laboratory in Madison, Wisconsin. A few small, rare, or endangered species were arbitrarily assigned a value of 0.6 g/cm^3, the weighted average for the forest.

Species trends were studied by following the survival and changes in numbers of stems and basal area of 'indicator' species that have a spectrum of roles in the Colorado Forest community. The species selected were (Little and Wadsworth 1964; Little *et al.* 1974): *Hedyosmum arborescens* and *Psychotria berterina,* small, short-lived, understory trees maturing at 10 cm in diameter and 6 m tall, found mainly in small openings in the forest; *Cecropia peltata* and *Didymopanax morototoni,* common, intermediate to large-sized pioneer trees, found in secondary forests and gaps in primary forests in the American tropics, growing to 30 to 50 cm in diameter and 15 to 20 m tall; *Miconia laevigata,* a small to intermediate-sized tree, reaching 15 cm in diameter and 8 m tall, widely scattered in the lower part of the Colorado Forest, found mainly in small openings: *Cyrilla racemiflora,* a long-lived, large, canopy tree, attaining sizes of 100 cm in diameter and 15 m tall, whose regeneration is tied to gaps in the mature forest; *Cordia borinquensis,* a common, shade tolerant, understory tree, to 15 cm in diameter and 7 m tall, capable of regenerating and growing under a canopy; *Prestoea montana,* a palm, a shade tolerant canopy tree reaching 15 m

tail, most common on steep, unstable soils and along drainages throughout the Colorado Forest; and *Micropholis chrysophylloides* and *M. garciniaefolia,* both shade tolerant, canopy trees reaching 50 to 60 cm in diameter and 15 m tall.

All species names mentioned in text were derived from the two volumens on trees of Puerto Rico and the Virgin Islands (Little and Wadsworth 1964; Little *et al.* 1974).

RESULTS

All information presented is based on changes occurring on the seven permanent plots during the 35-year period of measurement from 1946 to 1981. Because tree density for all plots combined was virtually the same in both 1946 and 1981, several direct comparisons of forest structure are possible. The results presented here are preliminary, and more detailed analyses are planned.

STAND CHANGES

Diameter Class Distribution. -Diameters were partitioned into classes as shown in Figure 2. The smallest diameter class showed a 15% change, declining from 2,975 to 2,525 stems. The 10.0 to 14.9 cm diameter class increased by 33%, or 285 trees. The remaining classes between 15.0 and 49.9 cm, with the exception of the 25.0 to 29.9 class, showed an increase in stem numbers ranging from 10 to 50 trees. From 50 to 134.9 cm, stem numbers declined to as many as four stems/class or remained about equal. In summary, many small- to intermediate-sized trees increased in diameter, and a few large trees suffered mortality.

Height Class Distribution. -Trees were grouped into 3-m height classes ranging from 0 to 2.9m through 21.0 to 23.9m tall (Fig, 3). The smallest two classes showed a decline in stems, particularly the 3.0 to 5.9 m class, where stems decreased by 55%, or from 2100 to 950. The remaining classes all showed increases in stem numbers ranging from 300 to 500/class except for the largest two classes which increased by only a few stems,

Crown Class Distribution. - The dominant and intermediate crown classes decreased by about 200 stems apiece, or 3%, from 1946 to 1981, while the suppressed crown class increased by about 500 stems, or 6% (Fig. 4). The codominant crown class remained virtually unaltered.

Specific Gravity Distribution. - Eight specific gravity classes were defined between 0.99 g/cm^3 (Fig. 5). In both 1946 and 1981, 35% of the stems were in the 0.65 class which ranged from 0.60 to 0.69g/cm^3. However, when basal area and volume were substituted for the number of stems, about 40% of the basal area and 43% of the volume were found in the 0.55 class in 1946. By 1981, both of these had declined to about 30%, but the 0.65 class had increased in both basal area and volume from about 28% to about 35%.

The weighted mean specific gravity for all trees on all plots combined increased from 0.563 to 0.574 between 1946 and 1981, despite an influx of palms, which have a low specific gravity. When palms were excluded, the weighted specific gravity for all dicotiledons, based on their respective volumes, increased from 0.608 to 0.632.

Ingrowth and Mortality. - The number of stems at the beginning and end of the study for all plots combined was virtually the same. The means and standard error of stem numbers/ha were: 1860 ± 73 in 1946 and 1858 ± 89 in 1981 (Table 1). Ingrowth averaged 20.0 ± 2.2 stems/ha/yr and mortality averaged 20.0 ± 0.8 stems/ha/yr. Annual flux for ingrowth and mortality averaged 1.1% of the original stem density.

When plot stem density for the 35-year period is considered on the basis of topography, the four slope plots combined declined by 6% while the two valley plots together increased by 9%. The plot with a mixed slope and valley topography also increased in stem density, but at a slower rate.

COMPOSITION CHANGES

Indicator Species. - All the *P. berteriana,* and 95% of the *H. arborescens* that were alive in 1946 had died by 1981 (Fig. 6). The 1981 total basal areas (growth on residual trees + ingrowth) ranged from 0 to 10% of the 1946 values. Regeneration of these species during the period of measurement amounted to only 20 and 10%, respectively, of the 1946 populations. Likewise, *C. peltata, D. morototoni,* and *M. laevigata* declined to 20% or less of their original 1946 populations. Regeneration of these species in the 35 years between measurements ranged from 0 to 10% of the 1946 populations. The 1981 total basal areas, however, were

higher than those of *P. berteriana* and *H. arborescens,* and ranged from 80 to 110% of the 1946 basal areas. This is due mainly to the larger size and longer survival of these tree species.

In contrast, survival of *P. rnontana, M. garciniaefolia* and *M. chrysophylloides,* ranged from 65 to 90% of their 1946 populations. When ingrowth was added to the original stem numbers, the 1981 populations of these climax species ranged from 100 to 120% of the 1946 populations. The 1981 total basal areas were also greater than in 1946, ranging from 125 to over 160% of the 1946 values for the dicotyledons. *Prestoea rnontana* only increased to 105%. of the 1946 value due to lack of diameter growth.

Mortality of *C. racemiflora* resulted in only 55% of the original 1946 population remaining in 1981. Regeneration during the period of measurement, however, resulted in a recovery to about 90% of the original population. Total basal area in 1981 was only 65% of that in 1946 due to the loss of several large trees. *Cordia borinquensis* showed a survival rate of 80% of its 1946 population. With regeneration, this species increased to 130%. of its original population. Total basal area in 1981 was nearly 130% of that in 1946 due to ingrowth and increment on residual stems.

The abundance of species by topography is also shown in Fig. 6. *Hedyosmum arborescens, C. racemiflora* and both species of *Micropholis* are more common on slope plots, whereas, *C. peltata, D. morototoni* and *P. montana* are found mainly on valley plots. The remaining species, *P. berteriana, M. laevigata,* and *C. borinquensis* are well represented on both topographic positions.

In summary, species requiring openings for germination and survival declined in numbers while total basal areas fluctuated widely depending upon tree size, growth rates, and longevity. In contrast, stem numbers and total basal areas of shade tolerant species either remained the same or increased.

Species Richness. -Variability in species richness among individual plots was considerable. The number of species ranged from 33 to 58/plot in 1946 and from 36 to 49/plot in 1981 (Table 2). On all seven plots combined, 88 species were found in 1946 and 83 in 1981.

The decrease in species from 1946 to 1981 ranged from 1 to 12/plot while increases from 3 to 9 (Table 2). For the entire forest, 11 of the species present in 1946 were lost and 6 species were gained by 1981. The greatest number of losses occurred on the valley plots at lower elevations.

GROWTH

Diameter Increment. -The most rapid diameter increments for 35-year survivors ranged between 0.20 and 0.30 cm/yr for dominant and codominant stems of *Tabebuia rigida, Ocotea spathulata, Haenianthus salicifolius, M. chrysophylloides,* and *Croton poeci/anthus* (Table 3). For all species combined, growth in dominants averaged 0.16, codominants 0.13, intermediates 0.09, and suppressed stems 0.05 cm/yr. Survivors showed a decline in diameter growth with the passage of time. Between 1946 and 1951, they averaged 0.14 cm/yr for all species regardless of crown class, and from 1976 to 1981, they averaged 0.09 cm/yr (Table 4).

Volume and Biomass Increment. -The mean volume for the seven plots increased from 216.7 ± 12.1 m^3/ha in 1946 to 253.8 ± 14.7 m^3/ha in 1981 (Fig. 7). Ingrowth including new stems and growth on residual trees averaged 117.9 ± 17.9 m^3/ha and mortality was 80.7 ± 9.1 m^3/ha. Net volume increase averaged 1.06 ± 0.5 m^3/ha/yr.

Net volume changes were positive on all but plot D (Fig. 7) where the mortality of large *C. racemif/ora* trees resulted in a 0.82 m^3/ha/yr decline. All four slope plots together averaged an increase of 0.18 m^3/ha/yr in volume, the mixed topography plot increased 2.10 m^3/ha/yr, and the valley plots averaged an increase of 2.31 m^3/ha/yr. When mortality (unharvested volume) was added to ingrowth to estimate volume growth, a similar pattern emerged (Fig. 7).

Aboveground woody biomas changes paralleled changes in volume. In 1946, the mean biomass for the seven plots averaged 121.4 ± 8.2 t/ha and in 1981, 145.0 ± 7.2 t/ha. Net biomass growth was 0.67 ± 0.25 t/ha/yr.

DISCUSSION

STAND CHANGES AND GROWTH

The changes in stand structure and species composition, accompained by positive volume and biomass accumulations during the period of measurement, are trends that can be attributed to recovery from past hurricane disturbance in the Colorado Forest.

Shifts in the distributions of diameter, height, crown, and specific gravity classes are all consistent with the steady trend of forest recovery. The loss of short-lived pioneer and secondary species with the increase in dominance of longer-lived, shade tolerant, climax species are trends that were also observed in the Tabonuco Forest (Crow 1980).

Diameter growth in the Colorado Forest is slow. In comparison, growth of 18 timber species in the Tabonuco Forest, measured during 20 years, ranged from 0.25 to 0.81 cm/yr (Crow and Weaver 1977), Elsewhere in the humid tropics, including 13 sites ranging from 20 to 2100 m in elevation with annual rainfalls between 1960 and 7500 mm (Leigh and Smythe 1978), diameter growth exceeded that of the Colorado Forest. In contrast, diameter growth in the Dwarf Forest is exceedingly slow, averaging only 0.03 cm/yr (Weaver 1983).

Estimated rates of net volume increase for other mature tropical moist forests are generally low, but greater than that of the Colorado Forest. In the Tabonuco Forest, independent estimates ranged between 2.26 and 4.35 m^3/ha/yr (Wadsworth 1957; Briscoe and Wadsworth 1 970). A partially cut rain forest in Malaysia yielded 1 to 3 m^3/ha/yr, a rain forest in Nigeria yielded 2 m^3/ha/yr, and a Dipterocarp forest in the Philippines yielded from 2.9 to 4.3 m^3/ha/yr (Johnson 1976). A tropical forest in Uganda appeared incapable of yielding more than 1.4 m^3/ha/yr for sawtimber under any polycyclic management system, nor more than 4.2 m^3/ha/yr under a monocyclic system (Dawkins 1959). These volume growth estimates could be doubled in managed tropical moist forests if more species and small dimension trees were included in the harvests. In contrast, net volume growth in secondary moist forests of the American tropics was considerably higher ranging from 7.7 to 33.8 m^3/ha/yr (Rosero 1979; Ladrach 1976),

Net above ground woody biomass growth for mature moist forests elsewhere in the American tropics is generally less than 2 t/ha/yr (Fig. 8). Again, growth in several secondary moist forests ranges up to 12 t/ha/yr.

Hurricane Damage and Recovery in the Luquillo Mountains

Information available from this study and others conducted in the Luquillo Mountains allows the formulation of an hypothesis regarding hurricane damage and recovery in each of the three major formations: the Tabonuco, the Colorado, and the Dwarf Forests.

The soils in the Luquillo Forest become wetter with an increase in elevation, notably so after the rather abrupt transition between Tabonuco and Colorado Forest (Wadsworth and Bonnet 1951). Presumably, they also remain saturated longer during the drier months in valleys at any particular elevation.

Tree size declines along the elevational gradient from Tabonuco through Colorado to the Dwarf Forest (Wadsworth 1951). In the upper forests, taper is more pronounced the crowns are lower on the stems, the proportion of branchwood is greater, and the roots are superficial (Wadsworth and Bonnet 1951). At any particular elevation in the Colorado and Dwarf Forests, trees are tallest in the valleys, intermediate in size on slopes, and smallest on the ridges. Tree density, however, is greatest on ridges. In contrast, the Tabonuco Forest has some of its largest trees on upper slopes and ridges. *Dacryodes excelsa,* the largest tree of the forest, commonly accounting for half the volume in mature stands (Wadsworth 1953), is one that grows preferentially on upper slopes and ridges (Crow and Grigal 1980).

Susceptibility to hurricanes is a function of tree species, tree size, rooting habit, density of stems, and topography, Damage is also related to storm intensity and possibly the interval between storms. In the Tabonuco Forest, where trees attain a large size, damage is by windfall, breakage, and defoliation. Windfall is most prevalent in valley areas where the soils are wet and the trees have large crowns whereas on slopes and ridges, trees suffer mainly breakage and defoliation (Wadsworth and Englerth 1959). It has been suggested that recurrent hurricanes in the Tabonuco Forest may have restricted the development of an emergent story (Odum 1970), resulting in small crowns that characterize the major forest dominants. Trees on slopes and ridges in the Colorado and Dwarf Forests are probably damaged mainly by breakage and defoliation, while trees in valleys suffer greater windthrow. The more common occurrence of *C. peltata,* and *D. morototoni* in valleys of Colorado Forest lends support to this idea, Smaller tree species common to openings, such as *P. berte-*

riana and *H. arborescens,* are more abundant in small gaps on slope topography.

Windthrow is less common and branch gaps diminish in size with an increase in elevation. The paucity of windthrow associated with hurricanes in summit areas may be surmized by the observation of a slow recovery on a recently disturbed site. In 1968, a plane wreck cleared an area on Pico del Este. After 16 years, it contains only a few small trees. If slow recovery characterizes the upper forest after hurricanes, we may assume that if a major windthrow occurred, it would be detectable long afterwards. Indeed, the formation of small "alpine meadows" in a few locations within the Dwarf and upper parts of the Colorado Forest may be related to landslides caused by high winds and heavy rainfall. Once formed, their recovery may span a couple of centuries.

The number of pioneers, their size, and their growth rates all decline with increasing elevation. Large pioneer species such as *C. peltata, D. morototoni, Alchorneopsis portoricensus* and *Alchornea latifolia,* along with several smaller trees of the Rubiaceae and Melastomataceae, rapidly invade disturbed sites in the Tabonuco Forest. In the Colorado Forest, *C. peltata* and *D. morototoni* are found along with the Rubiaceae (including *P. berteriana)* and Melastomataceae (including *M. laevigata).* In the Dwarf Forest, recovery is mainly by grasses and ferns. Pioneer and secondary trees are largely absent (Byer and Weaver 1977).

The result of the influx of pioneers and secondary species in the comparatively large opening of the Tabonuco Forest yields the greatest number of species 15 years after disturbance (Crow 1980). Closing of the stands eliminates those species that are dependent on openings for regeneration and growth. In the Colorado Forest, the influx of secondary species is lower due to the existence of fewer secondary species, as well as smaller openings and slower growth. In both forests, it is assumed that there is considerable local variation in species richness (Table 2) due to differences in stand conditions and disturbance at the time of hurricane passage. Hurricanes cause less damage in the Dwarf Forest, and tree species richness changes little during recovery.

The number of stems in the Tabonuco Forest peaks 15 to 20 years after the hurricane (Crow 1980) and then declines by 18% in the next 30 years due to competition among the survivors. In the Colorado Forest, recovery is slower due to fewer secondary species and slower growth. During the recovery period, the number of stems remains about equal for the forest as whole, although it declines on slopes and increases in valleys. In both forests, ingrowth results in a large number of stems in the smaller diameter and height classes. Continued growth and mortality of smaller stems due to competition shifts the distribution of trees into larger classes; this occurs more rapidly in the Tabonuco Forest than in the Colorado Forest because of faster growth. In the Dwarf Forest, stem density probably changes little because most damage is by breakage and defoliation.

The natural 'thinning' caused by disturbance increases the percentage of trees in the intermediate crown class. Through time, growth of the residual stems and ingrowth tends to close the stands, increasing the number of suppressed stems. This happens more rapidly in the Tabonuco than the Colorado Forest. In the Dwarf Forest, existing stems recover slowly, possibly by sprouting (Byer and Weaver 1977), with little ingrowth.

In Tabonuco Forest, two distinct periods of recovery were apparent: one from 1943 to 1951, when biomass growth was rapid, and a second from 1951 to 1976 when the stand approached steady state (Crow 1980), producing essentially a convex (that is, increasing at a decreasing rate) recovery of biomass). Because detailed intermediate measurements were lacking in the Colorado Forest, it was not possible to determine whether similar periods of recovery occurred. In an earlier work (Weaver 1983), it was suggested that volume recovery in the Colorado Forest was probably linear due to slower ingrowth and slower growth on residual stems. Volume recovery from breakage in the Dwarf Forest should parallel that of the Colorado Forest, but at a slower rate.

Acknowledgements

Dr. Carl Jordan of the Institute of Ecology, Athens, Georgia, and Dr. Peter G. Murphy of the Botany and Plant Pathology Department of Michigan State University, reviewed the manuscript and made valuable suggestions. Mr. Martin Chudnoff of the Wood Products Laboratory, Madison, Wisconsin, provided information on the specific gravities of trees not reported in the literature.

LITERATURE CITED

BAKER, F. S. 1950. Principles of silviculture. McGraw-Hill Book Co., Inc., NY. 414 p.

BATES, C. Z. 1929. Efectos del huracán del 13 de septiembre de 1928 en distintos árboles. Rev. Agric. P. R., 23:113-117.

BAYNTON, H. W. 1968. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of "Pico del Oeste. " J. Arn. Arb., 49:419-430.

BEARD, J. S. 1944. Climax vegetation in tropical America. Ecology 25(2):127-158.

_____ 1949. Natural vegetation of the Windward and Leeward Islands, Ox. For, Mere., 21: 1-192.

BRISCOE, C. B. 1966. Weather in the Luquillo Mountains of Puerto Rico. Inst. Trop. For. Res. Pap. ITF-3., Río Piedras, P. R., 250 pp.

_____, AND F. H. WADSWORTH 1970. Stand structure and yield in the Tabonuco Forest of Puerto Rico. p. 879-90. In H. T. Odum and R. F. Pigeon, eds., A tropical rain forest. USAEC, TID-24270.

BROWNE, F. G. 1949. Storm forest in Kelantan. Malayan For., 12:28-33.

BYER, M. D. AND P. L. WEAVER 1977. Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. Biotropica, 9(1);35-47.

CREMER, K. C., B. J. MYERS, F. VANDER DUYSANO I. E. CRAIG 1977. Silvicultural lessons from the 1974 windthrow in Radiata Pine plantations near Canbarra. Aust. For., 40:274-292.

CROW, T. R. 1980, A rainforest chronicle: a 30-year record of change in structure and composition at El Verde, Puerto Rico. Biotropica, 12(1):42-55.

_____, AND D. F. GRIGAL. 1980. A numerical analysis of arborescent communities in the rain forest of the Luquillo Mountains, Puerto Rico. Vegetatio 40(3):135-146.

_____, AND P. L. WEAVER 1977. Tree growth in a moist tropical forest of Puerto Rico. USDA For. Ser. Res. Pap. ITF-22. Rio Piedras, P. R., 17 pp.

DAWKINS, H. C. 1959. The volume increment of natural tropical high-forest and limitations on its improvements. Emp. For. Rev., 38:175-180.

EWEL, J. 1971. Biomass changes in early tropical succession. Turrialba, 21(1):110-112.

_____, AND J. L. WHITMORE 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. For. Serv. Res. Pap. ITF-18, Inst. Trop. For., Rio Piedras, P. R., 71 pp.

FOLSTER, H., G. DE LAS SALAS AND P. KHANNA 1976. A tropical evergreen forest site with perched water table, Magdalena Valley, Colombia. Biomass and bioelement inventory of primary and secondary vegetation. Oec. Plant., 11(4):297-320.

GOLLEY, F. B., J. EWEL AND G. I. CHILD 1976. Vegetation biomass of five ecosystems in north western Colombia. Trop. Ecol., 17:16-22.

HOLDRIDGE. L. R. 1967. Life zone ecology. Tropical Science Center. San José, Costa Rica. 206 pp.

JOHNSON, N. E. 1976. Biological opportunities and risks associated with fast-growing plantations in the tropics, J. For., 74:206-211,

KING H. C. 1945, Notes on the three cyclones in Mauritus in 1945: their effect on exotic plantations, indigenous forests and on some timber buildings. Emp. For, Rev., 24:192-195.

KLINGE, H. 1968. Litter production in an area of Amazonian terra firme forest. 1. Litter-fall, organic carbon and total nitrogen contents of litter. Amazonian, 1(4):287-301.

LADRACH, W. 1976. Rendimientos y comportamiento de la generación natural. p. 54-64. *In* ''Concesión forestal bajo Calima 1959-1975," Cartón de Colombia. Cali, Colombia.

LEIGH, E. G. JR. AND N. SMYTHE 1978. Leaf consumption, and regulation of folivory on Barro Colorado Island. p. 33-50. *In* G. G. Montgomery, cd., "The ecology of arboreal folivores. " Smith. Inst. Press. Washington, D.C.

LITTLE, E. L. JR. AND F. H. WADSWORTH. 1964. Common trees of Puerto Rico and the Virgin Islands, Agric. Handbook No. 249. USDA For. Serv., Washington, D.C. 548 pp.

_____, R. O. WOOOBURY AND F. H. WADSWORTH 1974. Trees of Puerto Rico and the Virgin Islands, Second Vol, Agric. Handbook No. 449. USDA For. Serv.. Washington, D. C. 1024 pp.

LUGO , A. E., M. APPLEFIELD , D. J. POOL AND R. B. MCDONALD. 1983. The impact of Hurrican David on the. forests of Dominica. Can. J. For. Res., 13(2): 201-211.

ODUM, H. T. 1970. Rain forest structure and mineral cycling homeostasis. p. H 1-52. In H. T. Odum and R. F. Pigeon, "A tropical rain forest. " USAEC, TID-24270.

ROSERO, P. 1979. Some data on a secondary forest managed in Siquirres, Costa Rica. p, 209-210. *In* G. de las Salas, ed. "Workshop agro-forestry systems in Latin America. " Turrialba, Costa Rica.

SALAS, G. DE LAS 1978. Carere-Opon el ecosistema forestal. Serie Técnica No. 8 CONIF. Bogotá, Colombia. 87 pp.

SALIVIA, L. A. 1972. Historia de los temporales de Puerto Rico y las Antillas, 1492 a 1970. Editorial Edil, Inc., UPR, Rio Piedras, P. R., 385 pp.

SNEDAKER, S. 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D thesis. University of Florida, Gainesville, Florida.

TANNER, E. V. J. 1980. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. J. Ecol., 68:573-588.

UHL, C. 1980. Studies of forest, agricultural, and successional environments in the upper Rio Negro region of the Amazon basin. Ph.D. thesis, Michigan State University, East Lansing, Michigan. 201 pp.

WASWORTH, F. H. 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. Ph.D. thesis, University of Michigan, Ann Arbor. 481 pp.

_____ 1951. Forest management in the Luquillo Mountains, I, The setting, Carib, For., 12(3):93-114.

_____ 1953. New observations of the growth in Tabonuco Forest. Carib. For., 14:106-111.

_____ 1957. Tropical rain forest. p, 13-23. *In* "FAO Forestry and Forest Products Studies No. 13", Tropical silviculture. Rome, Italy.

_____, AND J. A. BONNET 1951. Soil as a factor in the occurrence of two types of montane forest in Puerto Rico. Carib. For., 12:67-70.

_____, AND G. H. ENGLERTH. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. Carib. For., 20:38-51.

WEAVER, P. L. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. Carib. J. Sci., 12: 129-144.

_____ 1983. Tree growth and stand changes in the subtropical life zones of the Luquillo Mountains

of Puerto Rico. USDA For. Serv. Res. Pap. SO-190, New Orleans, Louisiana, 24 pp.

WEBB, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain-forest, North Queensland, Aust. J. Bot,, 6:220-228.

WHITMORE, T. C. 1974. Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. Inst. Paper No, 46, Common. For. Inst., Univ. Oxford, Great Britain. 77 pp.

WILKINSON, R. C., R. W. BRITT, E. A. SPENCE AND S. M. SEISER. 1978. Hurricane-tornado damage, and insect infestations of slash pine. S. J. App. For., 2: 132-134.

WILSON, H. H. 1976. The effect of the gale of August 1975 on forest in Canterbury. New Zeland J. For., 21(1):133-140.

WOOD, T, W. W. 1970. Wind damage in the forest of Western Samoa. Malayan For., 33:92-99.

TABLE 1.–Original stem densities, survival, ingrowth, mortality, and final stem densities for seven Colorado Forest plots from 1946 to 1981.

Plot[1]	Stem densities (stems/ha)				Survival[2]	Mortality		Ingrowth	
	1946	Mortality	Ingrowth	1981	%	Stems/ha/yr	%/yr[3]	Stems/ha/yr	%/yr[4]
A	2191	647	442	1986	70.5	18.5	0.84	12.6	0.58
B	1788	618	467	1637	65.5	17.6	0.99	13.3	0.75
C	1670	815	748	1603	51.2	23.3	1.39	21.4	1.28
D	1808	635	640	1813	64.9	18.1	1.00	18.3	1.01
Mean	1864	679	574	1760	63.6	19.4	1.00	16.4	0.88
E	1635	684	724	1675	58.2	19.5	1.19	20.7	1.27
G	1939	721	904	2122	62.8	20.6	1.06	25.8	1.33
H	1988	788	968	2168	60.4	22.5	1.13	27.7	1.39
Mean	1964	754	936	2145	61.6	21.5	1.10	26.7	1.36
Mean[5]	1860	701	699	1858	62.3	20.0	1.09	20.0	1.09

[1]Plots A through D are slopes; plot E is slope and valley; plots G and H are valleys,

[2]Survival % = (1946 density - mortality)/1946 density.

[3]Mortality % = (Mortality/1946 density)/35 Years.

[4]Hngrowth % = (lngrowth/1946 density)/35 years.

[5]Mean for all plots combined.

TABLE 2.–Changes in number of species by plot and for the entire Colorado Forest between 1946 and 1981.

Plot	Number of species		Species[1]	
	1946	1981	Lost	Gained
A	35	37	1	3
B	46	43	6	3
C	40	40	7	7
D	33	40	2	9
E	36	36	5	5
G	58	49	12	3
H	48	45	12	9
Entire forest	88	83	11	6

[1]Lost = species present in 1946 but missing in 1981; gained = absent in 1946 but present in 1981.

TABLE 3.–Diameter growth of 35-year survivors of select species by crown class on seven plots in the Colorado Forest.

Species	Mean ± SE[1] by crown class: Dominant (n)[2]	Co-dominant (n)	Intermediate (n)	Suppressed (n)
Calycogonium squamulosum	0.12[a3] ± 0.027(9)	0.11[a] ± 0.008(56)	0.10[a] ± 0.004(170)	0.06[b] ± 0.002 (278)
Croton poecilanthus	0.12[ab] ± 0.040(2)	0.26[b] ± 0.022(41)	0.18[b] ± 0.009(131)	0.08[a] ± 0.006 (113)
Cyrilla racemiflora	0.12[a] ± 0.019(54)	0.14[a] ± 0.020(25)	0.09[a] ± 0.023(21)	0.12 ± 0.039(4)
Haenianthus salicifolius	0.26[a] ± 0.026(28)	0.19[b] ± 0.017(32)	0.16[b] ± 0.023(29)	0.08[c] ± 0.016(23)
Magnolia splendens	0.11[a] ± 0.019(26)	0.06[a] ± 0.016 (9)	0.078[a] ± 0.010 (17)	0.04[b] ± 0.009(24)
Micropholis chrysophylloides	0.20[a] ± 0.021(33)	0.18[a] ± 0.013(56)	0.12[b] ± 0.006(130)	0.05[c] ± 0.005 (108)
Micropholis garciniafolia	0.14[a] ± 0.013(58)	0.11[b] ± 0.007 (135)	0.07[c] ± 0.004 (178)	0.04[d] ± 0.003 (173)
Ocotea spathulata	0.28[a] ± 0 (1)	0.09[b] ± 0.019(11)	0.05[c] ± 0.010(31)	0.02[d] ± 0.003(66)
Tabebuia rigida	0.30[a] ± 0.087 (4)	0.20[ab] ± 0.035 (8)	0.16[b] ± 0.027(17)	0.05[c] ± 0.009(20)
Remaining species	0.14[a] ± 0.015 (170)	0.13[a] ± 0.014 (164)	0.06[b] ± 0.004 (307)	0.04[c] ± 0.002 (517)
All species combined	0.16[a] ± 0.008 (385)	0.13[b] ± 0.006 (537)	0.09c ± 0.001 (1032)	0.05[d] ± 0.001 (1326)

[1]SE = Standard error.

[2]n = number of individuals.

[3]Means not followed by the same letter are significantly different at the 95% level according to Duncan's multiple range test

TABLE 4.–Comparison of diameter growth of surviving trees by crown class between 1946-51 and 1976-81 on four Colorado plots that were measured on both occasions.

Crown class[2]	Diameter growth (cm/yr ± SE)[1]: 1946-51(n)[3]	1976-81(n)
Dominant	0.15 ± 0.011 (219)	0.12 ± 0.12 (141)
Codominant	0.14 ± 0.009 (256)	0.16[*4] ± 0.010 (309)
Intermediate	0.14 ± 0.006 (550)	0.09[*] ± 0.004 (674)
Suppressed	0.12 ± 0.005 (620)	0.05[*] ± 0.004 (521)
Total	0.14 ± 0.004 (1645)	0.09[*] ± 0.004 (1645)

[1]SE = Standard error,

[2]Palms excluded from the calculations.

[3]n = number of trees.

[4]Significant differences at the 95% level are indicated by an asterisk.

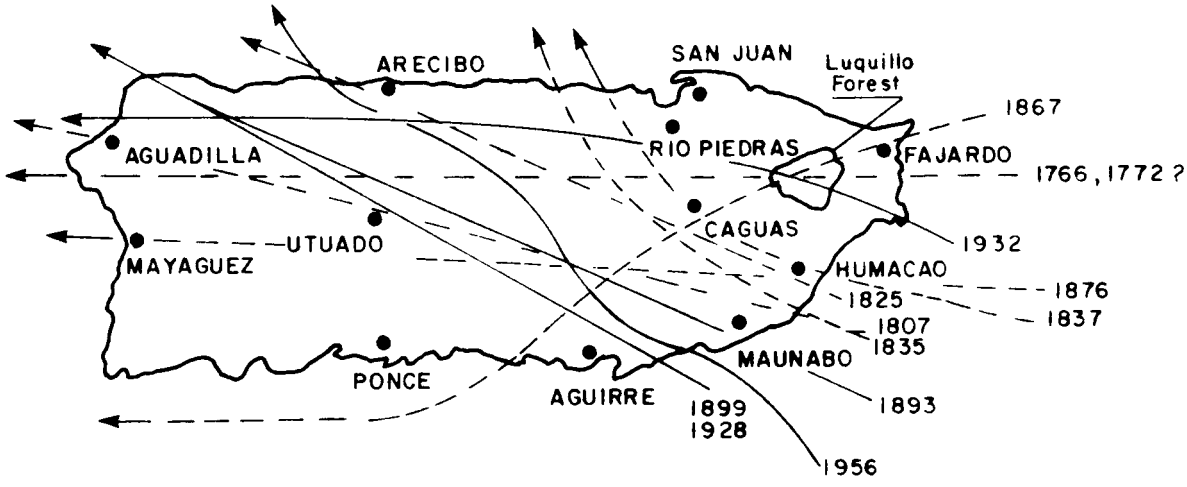

FIGURE 1.–Trajectories of type A hurricanes over Puerto Rico from 1700 to 1970. Solid lines are known hurricane paths and dashed lines are assumed paths based on descriptions.

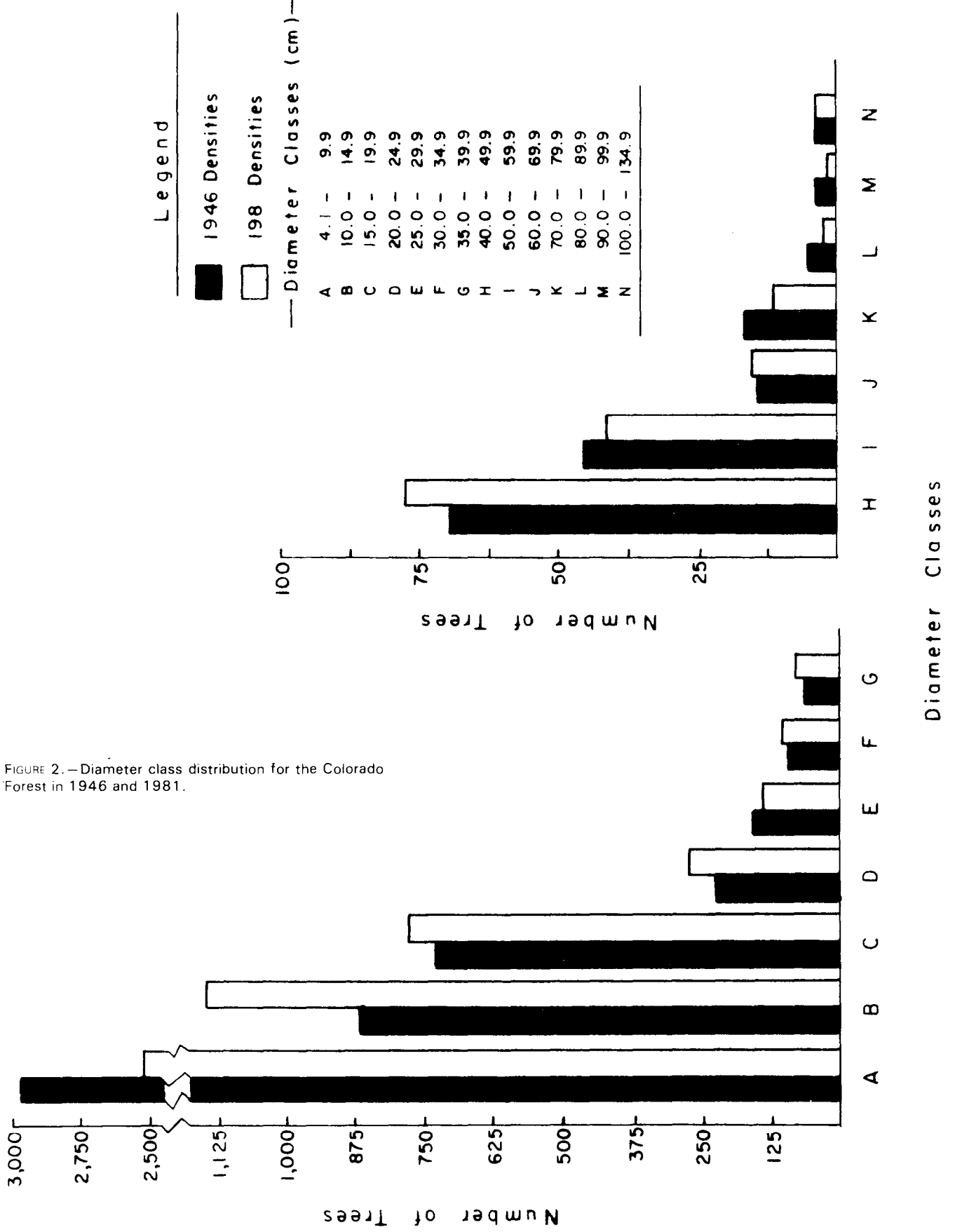

FIGURE 2.—Diameter class distribution for the Colorado Forest in 1946 and 1981.

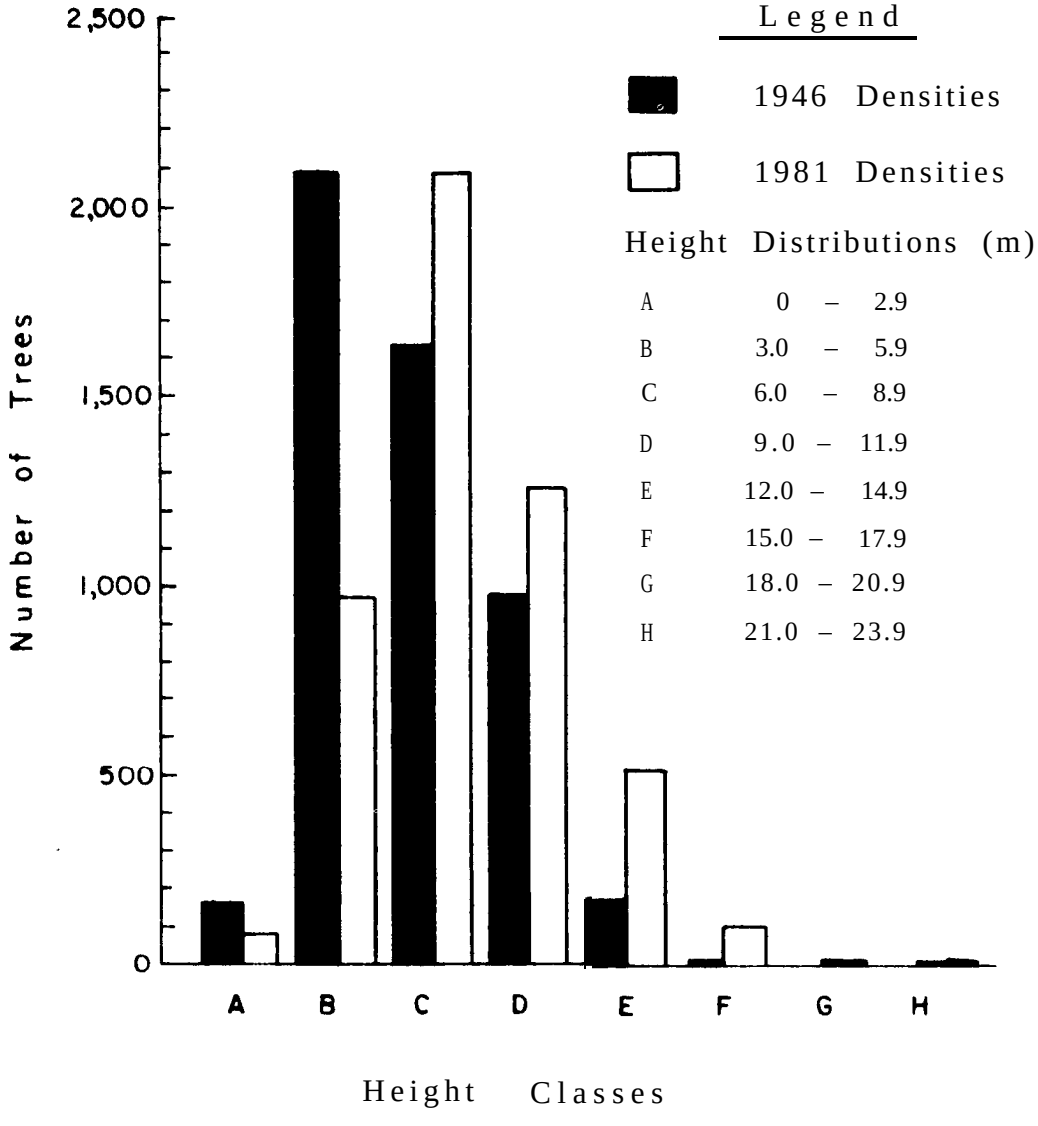

FIGURE 3.–Height class distribution for Colorado Forest in 1946 and 1981.

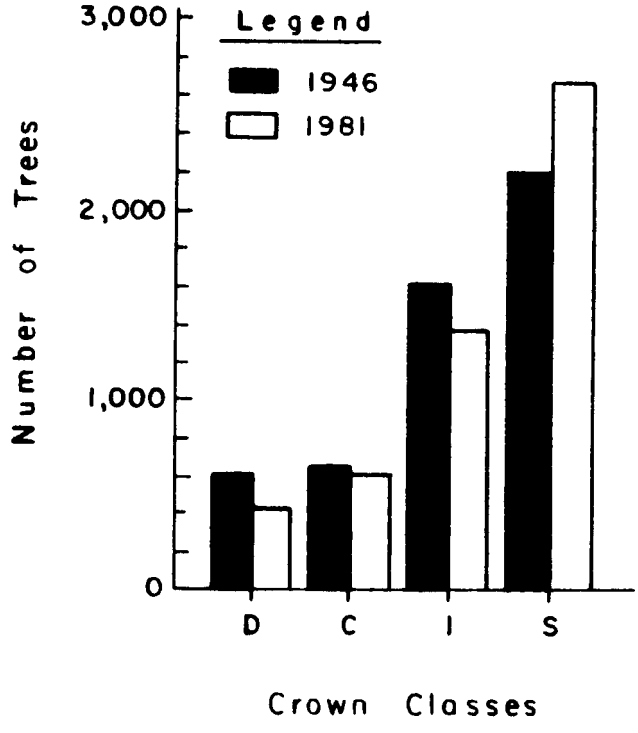

FIGURE 4.–Crown class distribution for Colorado Forest in 1946 and 1981, Crown classes are: dominant (D), Codominant (C), intermediate (I), and suppressed (S).

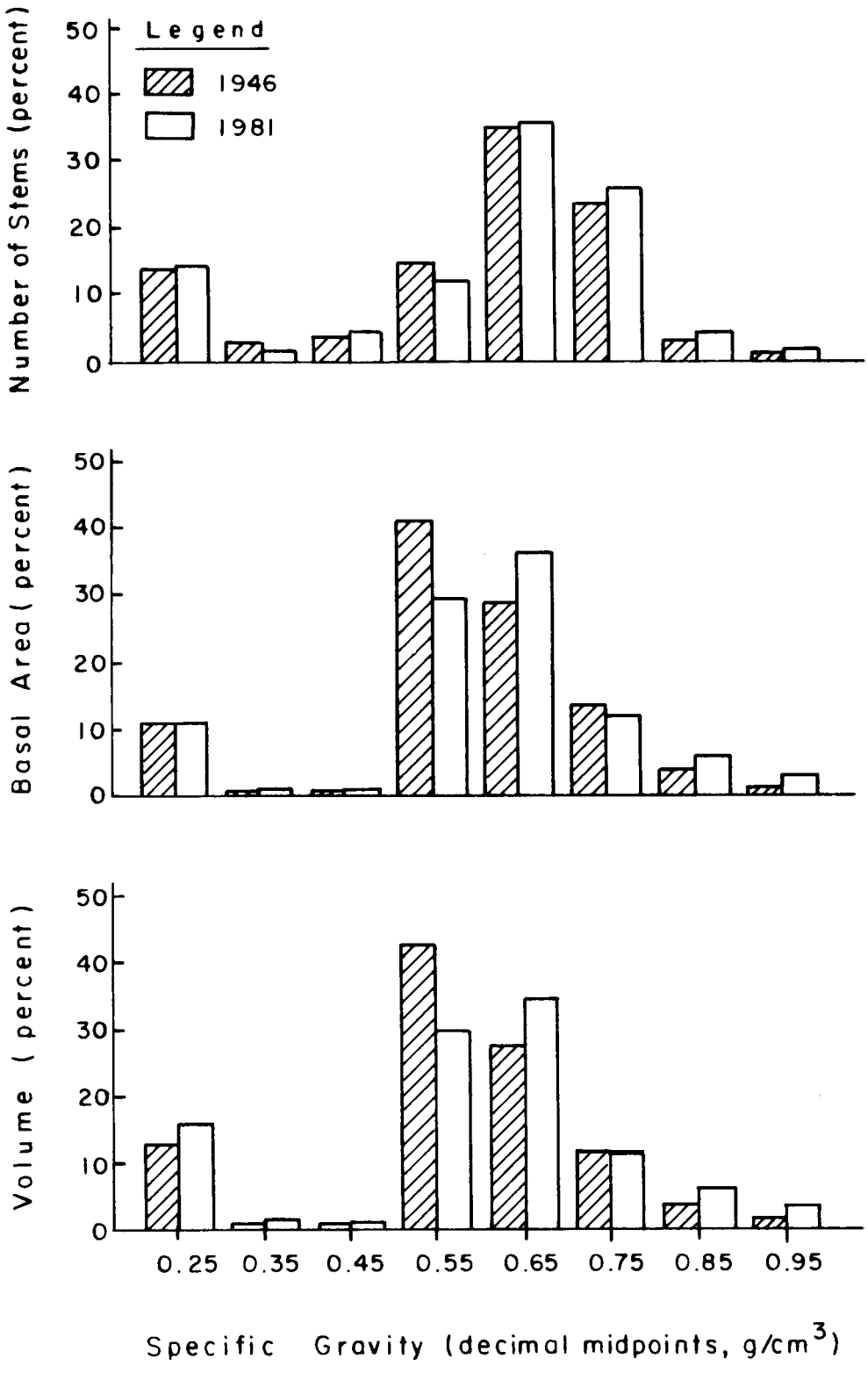

FIGURE 5.—Specific gravity groupings (0.25 = 0.20 to 0.29, etc.) for number of stems, basal area, and volume in 1946 and 1981 for the Colorado Forest.

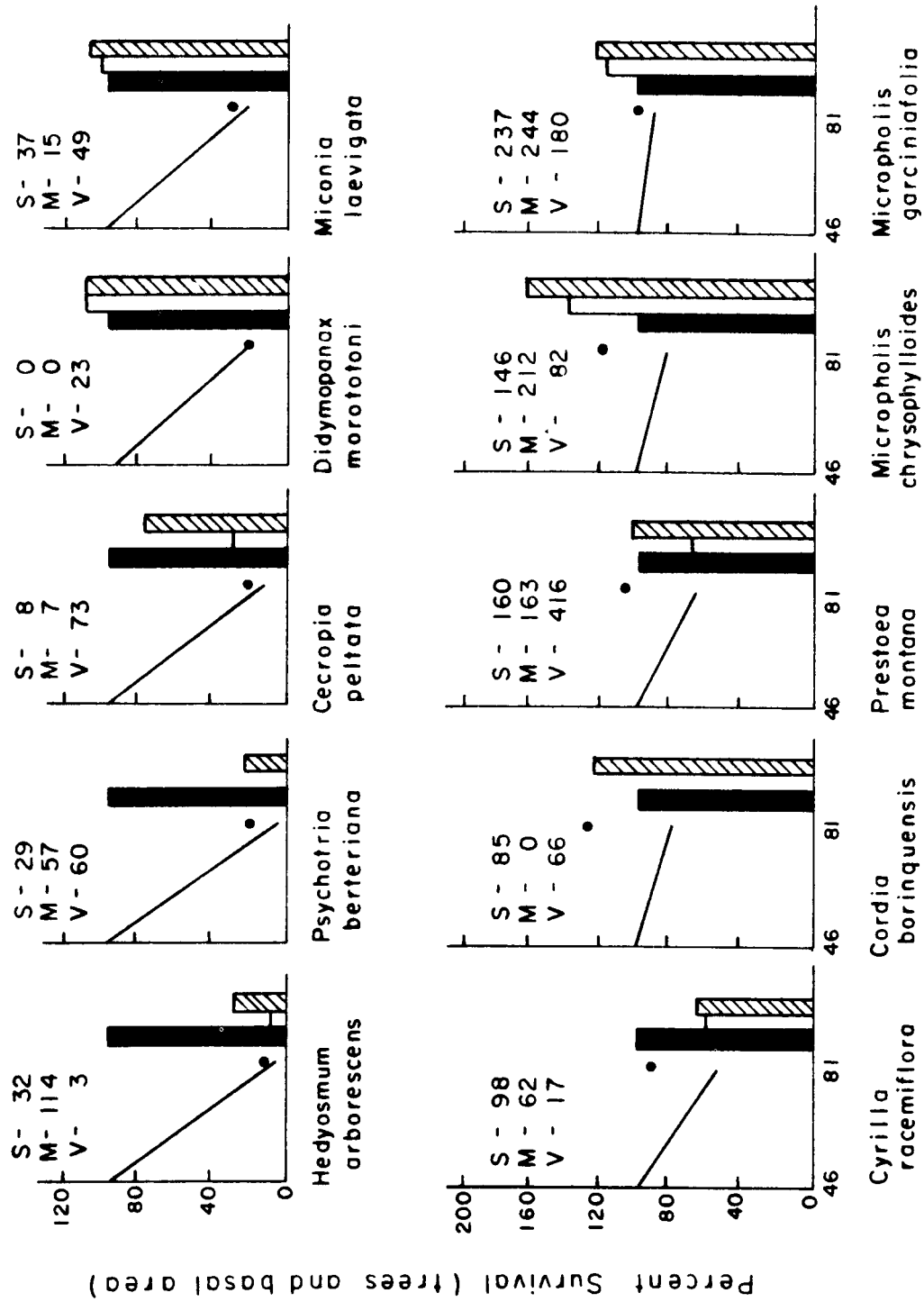

FIGURE 6.–Percent survival of indicator species in the Colorado Forest from 1946 to 1981, Lines indicate survival or original trees. Dot is 1981 population of trees (survival of original trees and ingrowth). Bars indicate basal area: 1946 basal area (shaded bars); 1981 basal area survival with growth on survivors (unshaded bars); and 1981 total basal area, growth of residual basal area and ingrowth (obliquely shaded bars), Number of trees/ha are indicated for slope (S), slope and valley (M) and valley (V) plots.

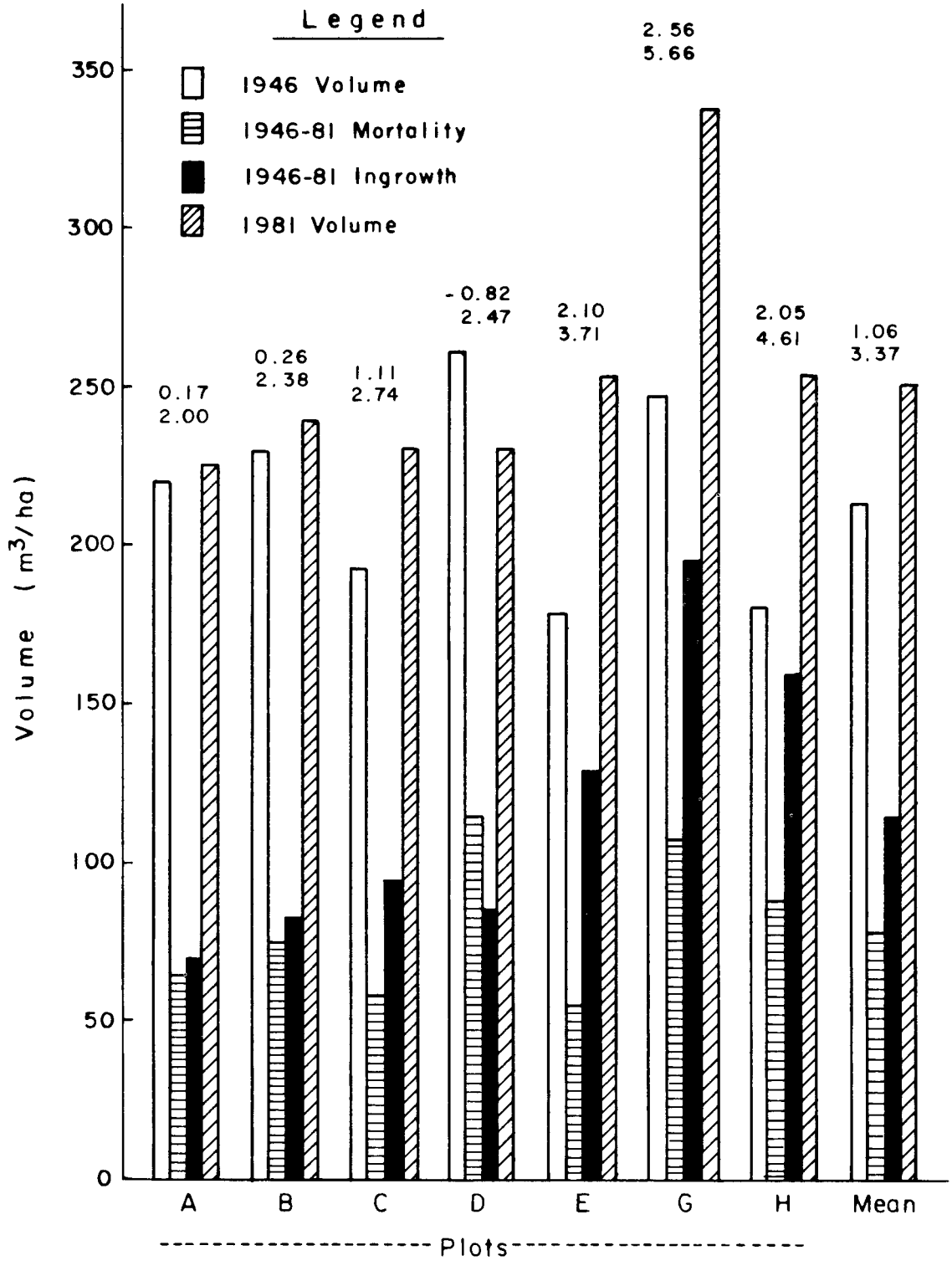

FIGURE 7.–Volume changes on seven Colorado Forest plots from 1946 to 1981. Mean is for all plots. Mean annual volume change (in m^3/ha) is shown above the bars. The top value represents net volume change. The bottom value includes mortality as growth (i.e., unharvested volume),

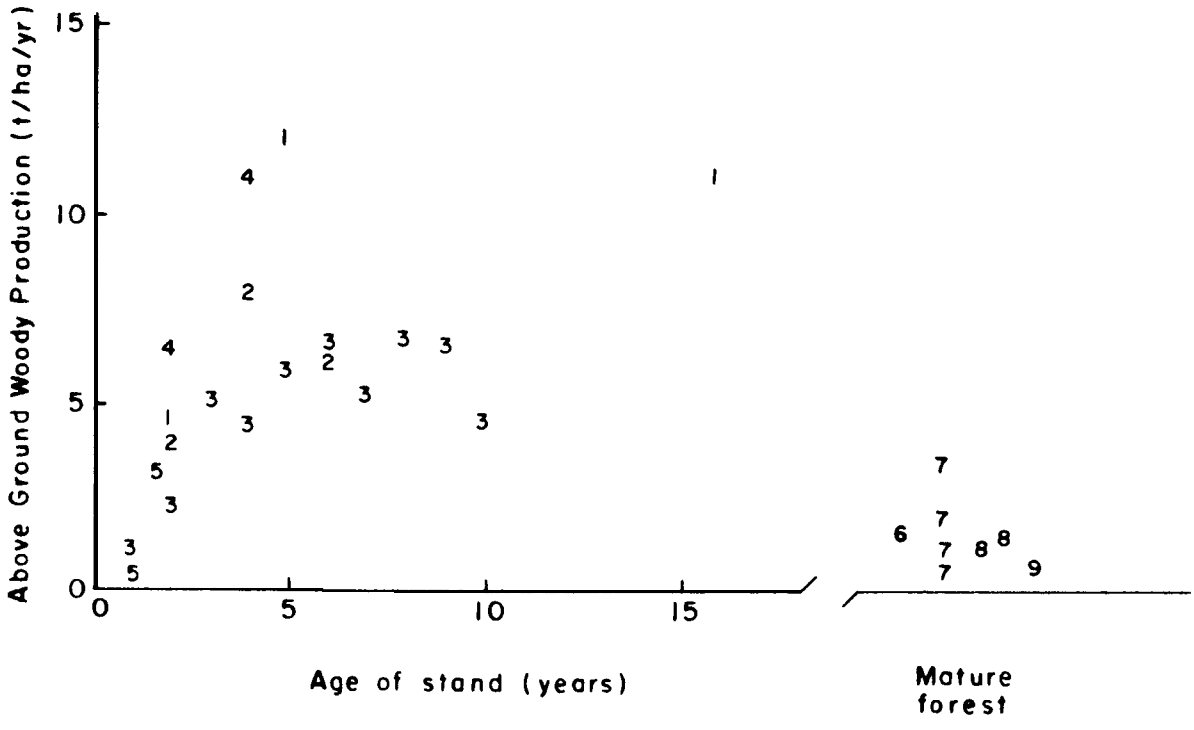

FIGURE8. Net biomass increase (aboveground, woody) for secondary and mature natural forests in the American tropics: (1) tropical moist forest (Salas 1978; Folster et al. 1976); (2) tropical moist forest (Ewel 1971); (3) subtropical moist forest Snedaker 1970); (4) tropical wet forest (Golley et al. 1976); (5) tropical moist forest (Uhl 1980); (6) subtropical wet forest (Crow 1980); (7) lower montane wet forest (Tanner 1980); (8) tropical moist forest (Klinge 1968); and lower montane wet forest -- Colorado Forest (this study). Forest formations are according to Holdridge (1967).