SLASH AND BURN IMPACTS ON A COSTA RICAN WET FOREST SITE[1]

JOHN EWEL, CORY BERISH, BECKY BROWN,
NORMAN PRICE, AND JAMES RAICH
Department of Botany, University of Florida, Gainesville, Florida 32611 USA

Abstract. Impacts of felling, mulching, and burning on budgets of C, N, S, P, K, Ca, and Mg; rates of CO_2 evolution from the soil; soil seed storage; and plant growth were evaluated. The felled tropical evergreen forest was 8–9 yr old, interspersed with patches of 70-yr-old forest and had a leaf area index of 6 and aboveground biomass of 5.2 kg/m².

Harvest of the largest trees removed 18% of the S, and >10% of all other elements except N. During the 11-wk mulching and drying period, 33% of the K and 13% of the P disappeared, but losses of other elements were <6%. Burn temperatures were >620°C in surface fuels, but soil temperatures were seldom >100°C at 1 cm or >50°C at 2 cm. The burn volatilized 1600 g/m² C, 49 g/m² N, and 13 g/m² S. Postburn wind and water erosion of ash, plus leaching, removed 34 g/m² N, 20 g/m² K, 1 g/m² P, 39 g/m² Ca, and 7 g/m² Mg, but insignificant amounts of C and S. After the burn and onset of the rains, 57% of the initial amount of N and 39% of the initial C still remained because of conservation of the organic-rich upper 3 cm of soil.

Soil CO_2 evolution was greater from beneath the 11-wk-old slash (3.6 gC·m⁻²·d⁻¹) than from beneath the forest (2.5 gC·m⁻²·d⁻¹), probably because the slash conserved soil moisture better than the actively transpiring forest. After the burn both the burned field and forest soil evolved CO_2 at ≈4.5 gC·m⁻²·d⁻¹. At this rate, 154 d of decomposition and respiration would release as much C into the atmosphere as did the burn.

Soil seed storage dropped from ≈8000 seeds/m² (67 species) in the forest, to 6000 seeds/m² (51 species) after 11 wk of mulching, to 3000 seeds/m² (37 species) after the burn. The seeds not killed by the burn, the survival of mycorrhizal fungi, and the release of nutrients resulted in vigorous and diverse postburn regrowth.

Key words: carbon; carbon dioxide; cations; Costa Rica; fire; mycorrhizae; nitrogen; phosphorus; seeds; shifting agriculture; slash and burn; sulfur; tropical forests.

INTRODUCTION

Forest felling and burning are parts of the shifting cultivation cycle that supports millions of people throughout the tropics. These practices are also the precursors of permanent agriculture, pasture establishment, and plantation forestry. Tropical deforestation is of great current concern (e.g., United States Department of State and United States Agency for International Development 1978, Myers 1980, National Research Council 1980), especially because of its potential impacts on genetic diversity (Myers 1979) and on biogeochemical cycles.

The impact of tropical forest felling and burning is of special importance to the global C cycle because of its relationship to world climate (Bolin 1977, Wong 1978, 1979, Woodwell 1978, Woodwell et al. 1978), although some feel that the role of tropical deforestation has been exaggerated (Broecker et al. 1979). It may also affect global S budgets. Tropical forest felling and burning have important local impacts on nutrient cycles, soil organisms, and stored propagules, all of which can have long-term effects on site quality and recovery.

Despite the ecological and economic implications of the slash and burn cycle, there have been few studies

of the changes in total standing crop of nutrients and organic matter from forest through felling and burning. One such study (from Ghana) was reported in two parts: one dealing with preburn soil and vegetation (Greenland and Kowal 1960), and the other dealing with the soil after clearing and burning (Nye and Greenland 1964). De las Salas and Fölster (1976) conducted a similar study in Colombia.

In our study, a second-growth tropical forest was felled and burned as part of the site preparation done in conjunction with a longer term study of succession and agroecosystem design. We took advantage of our site manipulation to quantitatively evaluate felling, mulching, and burning impacts. Element budgets were monitored throughout the preburn, mulching, postburn, and rain-onset stages, and soil seed storage, impact on mycorrhizae, and rate of CO_2 evolution from the soil were monitored concomitantly. The objective of this study was to describe quantitatively slash and burn impacts on a tropical forest, and thereby to help clarify some of the issues of global and local importance concerning tropical deforestation.

METHODS

Study site

The study was conducted near Turrialba, Costa Rica, in the Florencia Norte Forest owned by the Cen-

tro Agronómico Tropical de Investigación y Enseñanza (CATIE). The site is located at 9°53'N, 83°40'W, and lies 650 m above sea level. Our study area included some of the same land where Harcombe (1977a,b) conducted earlier studies on second-growth vegetation and nutrients. Mean annual rainfall is ≈2700 mm, and the dry season extends from January through March. The site is in the Tropical Premontane Wet Forest life zone (Tosi 1969). Topography is lightly undulating (5–28% slopes). The soil is the Colorado sandy clay series, classified as an Andept Inceptisol by Aguirre (1971), but earlier referred to as a senile latosol by Hardy (1961). The vegetation consisted of 8–9 yr old second-growth that had regrown following Harcombe's studies and a later interplanting of timber trees by CATIE foresters, plus remnant patches of an old (≈70 yr) secondary forest dominated by *Goethalsia meiantha*. The successional vegetation on the site is floristically and physiognomically typical of regrowth on similar soils in the humid tropics of Central America.

The vegetation on three 33 m × 33 m plots was felled during the 1st wk in January 1979. Firewood (17.8 m³) was removed from the site, and the remaining vegetation was allowed to lie on the soil through the dry season until it was burned on 22 March 1979. Each plot was surrounded by a buffer strip ≥5 m wide consisting of the uncut original vegetation. The burn was quite complete, and left the site covered with a uniform gray-white ash.

Burn temperatures

Temperatures in the litter and upper layers of the soil were measured using temperature-sensitive paints (Tempilaq) with melting points of 38°, 66°, 93°, 121°, 177°, 232°, 288°, 399°, 510°, and 621°C. Sensor design was similar to that of Fenner and Bentley (1960). Each paint was applied in a thin band parallel to the long axis of a 5 cm × 7 cm mica sheet, which was then stapled to a sheet of asbestos of the same size. The temperature sensors were placed at 62 randomly selected locations (21 or 20 in each of the three plots). To install each temperature sensor, a slit was made in the soil with a machete, and the temperature sensor was placed vertically so that it extended approximately 1–2 cm above the soil surface. The position of the soil surface was indicated with a small notch in the side of the mica sheet. The temperature sensors were recovered after the burn and the distance from the top of each sensor to the depth of melting was measured for each temperature-sensitive paint band.

Aboveground sampling

Prior to the burn, biomass was harvested from four 3 m × 3 m plots located in the uncut vegetation surrounding the experimental plots. All vegetation in each plot was harvested and separated into leaves plus reproductive parts, stems, and dead (= standing dead plus litter). Three subsamples, ≈0.5 kg each, were taken from each compartment, oven dried for ≥24 h at 65°C and weighed for fresh mass–dry mass conversions and chemical analyses. Specific gravity of the firewood removed from the site was determined by oven drying wood samples at 70°C, weighing them, and measuring their volume. Leaf area was determined by sampling ≈100 g fresh mass of leaves of common species from around each of the four biomass harvest plots. The area of each sample was determined with a leaf area meter (Li-Cor LI-3000), and the leaves were then oven dried at 70°C. The area to dry mass conversion (186.7 cm²/g, $r^2 = .999$) was then applied to the biomass harvest data to determine leaf area index.

Eleven weeks after the vegetation was felled the slash was sampled on two randomly located 1.5 m × 1.5 m plots. All fuel was harvested as a single compartment because most leafy material had decomposed during the 11 wk that the slash was on the ground. Two subsamples, ≈0.3 kg each, were oven dried as above.

Ash was collected within 20 cm of each of the 62 temperature sensors. At each point we placed a porcelain crucible (3.1- or 4.6-cm diameter) or a 50-mL Pyrex beaker such that its upper rim was beneath the litter and flush with the soil surface. Ash was also sampled by randomly placing three 8.9 cm diameter Petri dishes beneath the litter on each plot prior to the burn. After the burn, the containers were collected and covered, then taken to the lab, opened, and oven dried to constant mass at 70°C. Bulk density of the ash (mass per unit of undisturbed volume) was determined by weighing the ash in those 33 ash collectors that were brim-full. Ash depth was determined by 300 regularly spaced measurements, 100 in each of the three plots. The total mass of ash on the site was then calculated by multiplying the bulk density by the average ash depth.

Belowground sampling

Roots were sampled from 0 to 3 cm depth in the undisturbed preburn vegetation, from beneath the slashed vegetation that had been on the ground for 11 wk, and from beneath the ash immediately following the burn. Sampling was done with a 5.4-cm diameter corer having a sharp leading edge. For each of the three conditions (undisturbed vegetation, slash, postburn), four locations were sampled and three cores were taken from within each location. The natural vegetation roots were sampled from the four biomass harvest plots, and the slash and postburn sampling points were located inside the larger burn plot, one near each biomass harvest plot. The cores were soaked in a 20-L tank fitted with an overflow spout. Water was circulated into this tank and the flotsam,

including roots, was collected on a 0.5-mm sieve beneath the overflow spout. Roots were separated from the other overflow material, air dried, and separated into two size classes: ≤2 mm diameter and >2 mm diameter. These clean root samples were then oven dried to constant mass at 70°C. Root biomass was determined individually for each of the 36 soil cores, but the three cores from each sampling location for each of the three conditions were pooled to obtain enough root material for chemical analyses.

Soil was sampled under four conditions: beneath the second-growth vegetation in the buffer strips surrounding the plots; beneath the slash that had been on the ground for 11 wk; immediately following the burn; and immediately after the first rains, ≈2 wk after the burn. Four soil samples were taken for each condition, and each sample consisted of a composite of 10 cores. Sampling depths were 0–3 and 3–8 cm. Each composite sample was well mixed, oven dried at 55°C to retard denitrification, ground, and passed through a 2-mm sieve. Soil sampling locations were the same as root sampling locations. Bulk density was determined at 0–3 and 3–8 cm by taking 12 volumetric cores, 5.4-cm diameter, and oven drying them at 100°C.

Chemical analyses

Duplicate chemical analyses were run on all plant material and soil samples.

Plant tissues (leaves, stems, trunks, litter, fuel, and roots) were ground fine in a Wiley mill. N in plant tissues was determined using a semimicro Kjeldahl technique (Muller 1961). Tissues destined for cation, P, and S analyses were digested using the nitric-perchloric (5:1 ratio) method of Johnson and Ulrich (1959). Ca, Mg, and K were determined by atomic absorption. S was determined by the turbidimetric method of Chesnin and Yien (1950). P was determined colorimetrically as described by Johnson and Ulrich (1959).

The 47 ash samples that were not contaminated with mineral soil were pooled prior to chemical analyses into seven groups depending upon the surface temperature recorded by the sensor located within 20 cm of each ash collector. The seven temperature groups, with the number of samples included within each group shown in parentheses, were: 93°–177°C (5); 177°–232°C (3); 232°–288°C (2); 288°–399°C (5); 399°–510°C (14); 510°–621°C (8); >621°C (10). An eighth composite was made from the contents of the nine Petri dishes. Each of the eight composite samples was then divided into three subsamples: one destined for cation and P analysis, one for S analysis, and one for N analysis. One ash sample was oven dried at 70°C and weighed, then re-ashed in a muffle furnace at 800°C and reweighed to determine the C content of the ash. Cations, P, S, and N were determined as described above for plant tissues.

Soil pH was determined in water and 0.01 mol/L $CaCl_2$ using a soil:liquid ratio of 1:2.5 volumes. Soil organic matter and total N were determined on subsamples that were ground to pass through a 0.25-mm sieve. Total N was determined by the semimicro Kjeldahl technique (Bremner 1965). Organic C in the soil was determined by the Walkley-Black (1934) wet digestion method as modified by Siaz del Rio and Bornemisza (1962). A ratio of C digested to total C present of 0.75 was used, based on the recent work on tropical Andepts by Bornemisza et al. (1979). Exchangeable cations in the soil were extracted using ammonium acetate at pH 7.0 (Bower et al. 1952), followed by analysis via atomic absorption. Available soil P was extracted using $NaHCO_3$ (Olsen and Dean 1965), followed by colorimetric determination. Available soil S was extracted with $Ca_3 (PO_4)_2$ (500 $\mu g/g$ P) and the analysis was done turbidimetrically (Fox et al. 1964). Total soil S was determined using an induction furnace (Leco 572-200) on single composite samples of four cores each, 0–3 cm, from the forest, the 11-wk-old slash, and the postburn field.

Plant material C was calculated as 46.3% of plant tissue (Levitt 1969:130) after subtracting our analytical results for N, P, K, Ca, Mg, S, plus an assumed 2.5% for other mineral elements.

Carbon dioxide evolution

CO_2 evolution from the soil was measured in two 24-h series: 1 on 19 March immediately before the burn, and the other on 6 April, ≈2 wk after the burn. Methodology was similar to that of Schulze (1967). Nine locations were randomly selected along the plot boundaries. At each location we selected two paired sampling points, one at least 4 m into the undisturbed vegetation, and the other in the study plot, either in the preburn slash or in the postburn ash. A wire stand 5 cm high was located at each point and used to support an uncovered Petri dish containing 25 mL of 1.0N NaOH. The stand and Petri dish were then covered with an inverted 4 L can enclosing 0.019 m². Every 3 h for a 24-h period the cans were removed, the NaOH was collected and stored in a film canister, and replaced with fresh NaOH. Every 3 h three blanks were run by pouring 25 mL of 1.0N NaOH into a Petri dish and immediately back into the canister. In the laboratory, each sample was titrated with 0.5N H_2SO_4 to phenolphthalein and methyl orange end points. The CO_2 content of the blanks did not vary over time, so total CO_2 absorption of each sample was determined by subtracting the mean blank value from each sample value.

Soil moisture plus surface soil and air temperatures were monitored as physical variables that might influence rates of CO_2 evolution. Soil moisture was determined by weighing, oven drying (>24 h at 105°C), and reweighing paired samples of surface soil (0–5 cm)
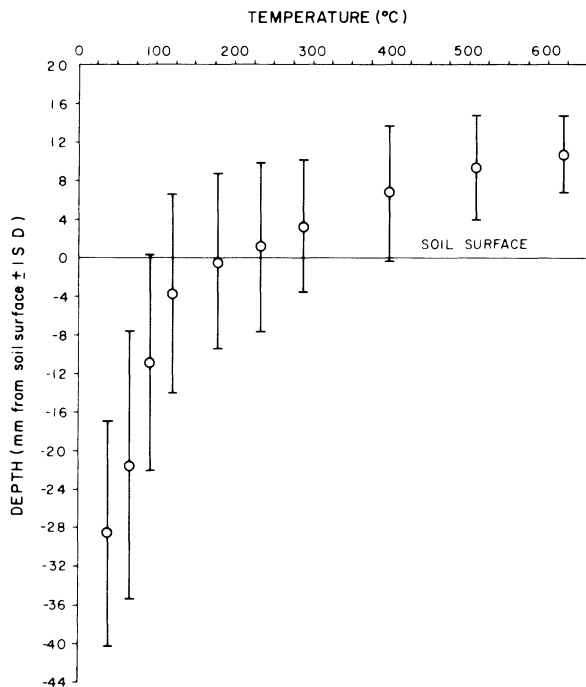
FIG. 1. Depth ($\bar{x} \pm$ SD) at which various soil and litter temperatures were reached during the burn.

from beneath the slash (or ash) and forest. Twelve pairs of samples were taken in conjunction with each diurnal, three at each of four times: morning, afternoon, evening, and end of diurnal (morning for preburn, afternoon for postburn).

At each 3-h sampling time temperature was recorded from three randomly located pairs of thermometers in the surface soil (1 cm) and two pairs in the air just above the soil surface.

Seeds in the soil

The impact of slashing and burning on seed storage in the soil was determined by germinating seeds from soil samples taken from the second-growth vegetation, from the 11-wk-old slash, and from the burned plots the day after the fire. Ten samples were taken from each of those three conditions at randomly selected points. The preburn samples from under the slash and the postburn samples were taken within 2 m of each other to permit paired analysis of the data. Each sample consisted of two cores of soil plus litter, 4 cm deep and 8.5 cm in diameter. Therefore, the surface area included in each sample was 113.5 cm² and the volume of each sample was 454 cm³. Each sample was spread to a depth of 1 cm over well-washed river sand. Six control flats containing only the river sand were used to monitor greenhouse contaminant seed inputs. All seedlings were counted and identified to morphospecies until 8 June (11 wk).

Plant growth

Soybeans were grown in nine samples of surface soil (0–3 cm) taken from each treatment: preburn slash, postburn, and forest. After 59 d all plants were harvested, and separated into leaves, stems, roots, and reproductive parts, prior to oven drying (70°C) and weighing. Roots were visually examined for nodules and stained with trypan blue in lactophenol prior to microscopic examination for mycorrhizal infection.

RESULTS

Numerical results are reported here as a mean, usually ±1 SD. Leaf area index of the felled second-growth was 6.0 ± 1.5 m²/m². The following values were determined as part of this study, and used for conversion of chemical concentrations to amount per unit area per compartment: bulk density of ash = 0.034 ± 0.016 g/cm³; specific gravity of firewood removed from site = 0.363 ± 0.011 g/cm³; and soil bulk density, 0–3 cm (including some surface litter), under uncut vegetation = 0.56 ± 0.08 g/cm³, under 11-wk-old slash = 0.49 ± 0.15 g/cm³, and postburn = 0.40 ± 0.09 g/cm³. Bulk density of 0.53 ± 0.05 g/cm³, for mineral soil surface to 7.6 cm, sampled beneath the forest, was used for 3–8 cm mass calculations and all mass balances in the Discussion section. Total soil S, 0–3 cm, under uncut vegetation = 0.072%, under 11-wk-old slash = 0.084%, and postburn = 0.049%. These S values are used for mass balance calculations in the Discussion section, and total soil S was assumed to be lost at the same rate after the burn and onset of the rains as was available soil S. Unburned wood was not measured but was estimated to be 20% of the preburn fuel and to have the same chemical concentrations as the harvested trunks.

Burn temperatures

Even though most of our burning consisted of back-fires, which are notoriously hot, the mineral soil was not exposed to excessively high temperatures (Fig. 1). The highest temperatures were reached in the dense fuel 1–2 cm above the soil surface, and average surface temperature was ≈200°C. Temperatures dropped markedly beneath the soil surface; the mean at 1 cm was ≈100°C, and at a depth of ≈3 cm the mean temperature was <38°C.

Temperatures varied considerably from point to point, depending upon fuel quality, amount, and moisture content. This variability is reflected in the standard deviations plotted around the means (Fig. 1). In general, the higher the temperature reached, the less variable was the depth at which it was achieved.

Chemistry

Soil changes, exclusive of element concentrations and bulk densities, are summarized in Table 1. Surface soil pH increased markedly through the decomposition

TABLE 1. Soil characteristics. C:N and cation exchange capacity (CEC) values are $\bar{x} \pm$ SD; pH values are mean (range); $n = 4$.

Depth (cm)	Status	pH (H₂O)	pH (CaCl₂)	Effective CEC (meq/100g)	C:N
0–3	Forest	5.0 (4.6–6.2)	4.9 (4.6–5.9)	43.6 ± 5.3	15.1 ± 1.3
	Slash	5.6 (5.3–6.2)	5.2 (5.0–5.5)	44.9 ± 4.8	13.6 ± 0.6
	Postburn	6.2 (6.0–6.6)	5.6 (5.4–5.9)	41.6 ± 2.8	12.5 ± 0.6
	Postburn and rain	6.0 (5.5–6.6)	5.6 (5.2–6.1)	47.0 ± 6.3	13.9 ± 1.3
3–8	Forest	5.3 (4.8–6.0)	4.7 (4.3–5.4)	40.3 ± 3.6	13.5 ± 1.1
	Slash	5.1 (4.8–5.8)	4.8 (4.5–5.3)	38.3 ± 2.2	12.6 ± 0.5
	Postburn	5.2 (5.0–5.6)	5.0 (4.8–5.3)	35.1 ± 0.8	13.0 ± 0.7
	Postburn and rain	5.2 (5.0–5.6)	4.9 (4.6–5.4)	43.7 ± 2.1	13.5 ± 1.0

interval and the burn, but the pH below 3 cm did not change. The ΔpH ($= pH_{H_2O} - pH_{CaCl_2}$) is negative under all conditions, indicating that the soil at the study site has a net negative charge, or positive cation exchange capacity. The cation exchange capacity was lowest immediately after the burn, which probably reflects the combustion of surficial organic matter. The C:N ratio in the surface 3 cm dropped during decomposition and the burn, indicating that C was released more readily than N, and/or that N accretion occurred. C:N ratios did not change significantly at 3–8 cm.

Mass and chemical concentrations are summarized in Table 2. The trunks, which were removed from the site and thus became a nutrient export, consisted of some 8–9 yr old *Cecropia, Ocotea,* and *Virola,* but were mostly remnant *Goethalsia* from the much older

secondary forest that covered the entire site prior to 1970. The biomass of the preburn vegetation, excluding trunks, (leaves + stems + roots = 3.2 kg/m²) is quite low, and may reflect the dominance of this regrowth by woody vines rather than trees and shrubs.

Carbon dioxide evolution

Rates of CO_2 evolution and changes in soil moisture were analyzed as a function of time of day, and no significant diurnal fluctuations were detected. Therefore, all CO_2 evolution and soil moisture data from each 24-h run were pooled (Table 3). Because fresh reagents were used for each of the two series, the differences in CO_2 evolution rates before and after the burn, and the absolute values, should be used with caution. Relative differences between soils sampled

TABLE 2. Mass and nutrient concentrations (percent dry mass) before and after the burn. Values are $\bar{x} \pm$ SD.

Compartment	Mass (g/m²)	N	P	K	Ca	Mg	S	C
Forest								
Leaves	318 ± 81	3.391 ± 0.434	0.10 ± 0.01	2.09 ± 0.27	1.51 ± 0.30	0.39 ± 0.06	0.36 ± 0.04	41.5
Stems	2615 ± 306	0.997 ± 0.164	0.033 ± 0.007	1.14 ± 0.30	0.93 ± 0.14	0.17 ± 0.03	0.17 ± 0.08	43.5
Trunks	2241	0.460 ± 0.116	0.016 ± 0.007	0.40 ± 0.22	0.44 ± 0.13	0.12 ± 0.06	0.21 ± 0.14	44.4
Dead	1610 ± 628	1.358 ± 0.330	0.030 ± 0.007	0.52 ± 0.26	1.27 ± 0.36	0.22 ± 0.02	0.23 ± 0.05	43.5
Roots ≤ 2 mm	183 ± 93	2.080 ± 0.354	0.045 ± 0.007	0.41 ± 0.44	1.38 ± 0.41	0.28 ± 0.03	0.37 ± 0.14	43.2
Roots > 2 mm	103 ± 105	1.476 ± 0.641	0.032 ± 0.012	0.75 ± 0.37	1.51 ± 0.44	0.44 ± 0.13	0.18 ± 0.10	42.7
Soil 0–3 cm	16 800 ± 2400	0.915 ± 0.120	$(4.2 \pm 0.4) \times 10^{-4}$	$(2.7 \pm 1.1) \times 10^{-2}$	0.15 ± 0.10	$(3.0 \pm 1.6) \times 10^{-2}$	$(7.5 \pm 2.3) \times 10^{-4}$	13.8 ± 1.9
Soil 3–8 cm	26 500 ± 2500	0.669 ± 0.075	$(2.6 \pm 0.7) \times 10^{-4}$	$(1.5 \pm 1.0) \times 10^{-2}$	0.10 ± 0.08	$(1.9 \pm 1.4) \times 10^{-2}$	$(2.7 \pm 0.8) \times 10^{-4}$	9.1 ± 1.6
Preburn slash								
Fuel	3850 ± 1266	1.193 ± 0.245	0.036 ± 0.010	0.62 ± 0.21	1.14 ± 0.15	0.21 ± 0.04	0.25 ± 0.06	43.5
Roots ≤ 2 mm	170 ± 70			Assumed same concentrations as postburn				
Roots > 2 mm	50 ± 68			Assumed same concentrations as postburn				
Soil 0–3 cm	14 700 ± 4500	1.028 ± 0.203	$(5.3 \pm 1.5) \times 10^{-4}$	$(4.1 \pm 1.0) \times 10^{-2}$	0.18 ± 0.07	$(4.0 \pm 1.0) \times 10^{-2}$	$(8.6 \pm 7.3) \times 10^{-4}$	13.9 ± 2.4
Soil 3–8 cm	26 500 ± 2500	0.644 ± 0.079	$(2.1 \pm 0.5) \times 10^{-4}$	$(1.8 \pm 0.5) \times 10^{-2}$	0.10 ± 0.05	$(2.0 \pm 0.9) \times 10^{-2}$	$(4.3 \pm 4.1) \times 10^{-4}$	8.1 ± 0.7
Postburn								
Ash	670 ± 206	1.427 ± 0.468	0.233 ± 0.120	2.83 ± 2.11	8.28 ± 4.10	1.59 ± 0.72	0.19 ± 0.07	25.7
Roots ≤ 2 mm	123 ± 86	2.166 ± 0.679	0.045 ± 0.004	0.27 ± 0.26	1.12 ± 0.21	0.27 ± 0.07	0.44 ± 0.18	43.1
Roots > 2 mm	30 ± 70	1.556 ± 0.668	0.023 ± 0.007	0.25 ± 0.20	1.66 ± 0.32	0.23 ± 0.06	0.43 ± 0.14	43.3
Soil 0–3 cm	12 000 ± 2700	0.898 ± 0.045	$(5.3 \pm 0.7) \times 10^{-4}$	$(4.3 \pm 0.9) \times 10^{-2}$	0.17 ± 0.04	$(4.5 \pm 1.0) \times 10^{-2}$	$(26.5 \pm 10.4) \times 10^{-4}$	11.2 ± 0.7
Soil 3–8 cm	26 500 ± 2500	0.580 ± 0.026	$(2.8 \pm 0.7) \times 10^{-4}$	$(1.4 \pm 0.1) \times 10^{-2}$	0.08 ± 0.03	$(1.7 \pm 0.4) \times 10^{-2}$	$(9.8 \pm 3.9) \times 10^{-4}$	7.6 ± 0.2
Postburn and rain								
Soil 0–3 cm	Assumed same as postburn	0.747 ± 0.074	$(6.2 \pm 1.0) \times 10^{-4}$	$(3.9 \pm 1.4) \times 10^{-2}$	0.16 ± 0.05	$(3.6 \pm 0.6) \times 10^{-2}$	$(20.4 \pm 6.7) \times 10^{-4}$	10.3 ± 0.4
Soil 3–8 cm	26 500 ± 2500	0.557 ± 0.058	$(2.8 \pm 0.5) \times 10^{-4}$	$(1.7 \pm 0.9) \times 10^{-2}$	0.07 ± 0.02	$(1.7 \pm 0.6) \times 10^{-2}$	$(10.5 \pm 3.0) \times 10^{-4}$	7.4 ± 0.7

TABLE 3. Carbon dioxide evolution from the soil, soil moisture, and soil and air temperatures before and after the burn. CO_2 and soil moisture values are $\bar{x} \pm$ SD; temperatures are means (range).

Status	CO_2 (g C·m^{-2}·24 h^{-1})	Soil moisture (%)	Temperatures (°C)	
			Soil	Air
Preburn				
Slash	3.62 ± 1.14	54.2 ± 14.4	21.4 (20.0–22.5)	22.5 (14.3–31.3)
Forest	2.52 ± 0.37	39.1 ± 7.2	20.4 (18.0–22.5)	21.7 (15.8–28.0)
Postburn and rain				
Ash	4.57 ± 0.47	62.5 ± 9.4	22.1 (20.6–24.8)	21.3 (19.6–25.0)
Forest	4.51 ± 0.77	52.9 ± 6.6	20.7 (19.3–21.8)	20.3 (19.1–22.3)

during the same 24-h run, however, can be used with confidence.

Before the burn, the rate of CO_2 evolution was significantly greater (paired t test, $\alpha < .05$) from soil beneath the slash than from forest soil. The soil beneath the insulating layer of slash was significantly wetter than soil beneath the actively transpiring forest. Both soil moisture and the abundance of dead plant material may be responsible for the greater CO_2 evolution beneath the slash. After the burn, however, there was no difference between the rate of CO_2 evolution from the soil beneath the ash and the forest.

Seeds in the soil

Substantially fewer seeds germinated from soil sampled from beneath the slash (≈ 6000 seeds/m^2) than from beneath the forest (nearly 8000 seeds/m^2), but the decrease was not statistically significant due to large point-to-point variability, especially in the forest (Fig. 2). The number that germinated after the burn (< 3000 seeds/m^2) was significantly less (ANOVA and LSD, $\alpha < .05$) than the number germinating from soil sampled from both forest and slash. Germination was quite rapid; at least two-thirds of all seeds that germinated over the 78-d period did so during the 1st 30 d.

The three germinated seed floras were remarkably diverse. The decrease in number of species followed a trend similar to that of the decrease in number of individuals: forest, 67 species; slash, 51 species; and postburn, 37 species. Of the total germinated flora of 104 species, 19 were common to all three treatments. The forest and slash had 28 species in common, and the forest and slash each had 21 species in common with the postburn field.

Plant growth

Soybeans grew equally well in soil taken from beneath the 11-wk-old slash, the forest, and the postburn ash. None of the plants became nodulated. Only 16 of 27 plants were infected with mycorrhizal fungi, and there were no significant differences in rate of infection among the three soils. Soybeans infected with mycorrhizae did not grow significantly larger than those that were uninfected. There were no significant differences in dry mass of leaves, stems, reproductive

parts, roots, or total biomass (overall mean = 6.7 g/ plant) among soybeans grown on any of the three soils.

Discussion

Burn temperatures

There are few other reports of temperatures recorded beneath burning tropical forest slash. Zinke et al. (1978), working in Thailand, reported temperatures as high as 650°C in the fuel 2 cm above the soil surface, dropping to 70°C 2–3 cm beneath the surface. Brinkmann and Vieira (1971) reported surface temperatures of 100°–150°C during their burn in Amazonian Brazil, and temperatures of 95°–125°C at 2 cm in the soil. Lal and Cummings (1979) recorded 74°C at a soil depth of 1 cm during a burn of forest slash in Nigeria. The temperatures reported from Brazil and Nigeria seem low, but soil temperatures stayed high for several hours. Uribe et al. (1967) reported no change in soil temperature below 5 cm during a burn in Colombia. Masson (1948) recorded temperatures beneath burning grasslands in Senegal, and found that soil temperature increased only ≈ 14°C at a soil depth of 2 cm.

Although the fire that races through the slash can be spectacular, its impact on the soil is really very moderate. This conclusion has been noted by others (Popenoe 1960, Nye and Greenland 1960, Seubert et al. 1977, Lal and Cummings 1979), but is often ignored in the rhetoric deploring the fires associated with tropical agriculture. Nye and Greenland (1960) point out that heating to 45°–50°C can increase soil fertility, perhaps through increased rates of N mineralization. Sertsu and Sanchez (1978) heated an amorphous Ethiopian soil, and found that fertility increased upon heating to 200°C because of increases in availability of N, P, Fe, and Mn. Temperatures >400°C, however, were detrimental because of organic matter destruction, fusion of clay particles, and reduced cation exchange capacity.

The effect of the burn is ameliorated by the insulation of the soil by the slash. Even though a slashed field is a blistering hot environment, the soil surface is well protected and soil moisture is conserved by this nontranspiring layer of dead plant material (Table 3). Thus in our study, the soil moisture not only buffered
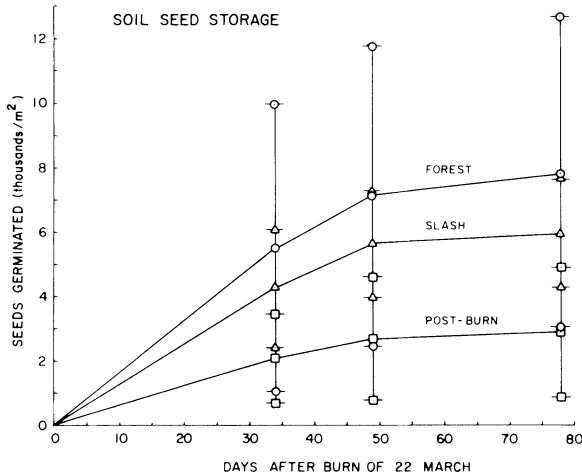
FIG. 2. Seeds germinated from soil sampled from the forest, the 11-wk-old slash, and after the burn. On each vertical bar, center symbol of each type shows the mean. Top and bottom symbols mark ± 1 SD. Circles refer to forest, triangles to slash, and squares to postburn.

temperatures during the burn, but enabled plants to initiate growth soon after the fire, even before the rains began 2 wk later.

Chemistry

Soil pH increases as a result of burning, and affects P and cation availability. Increases comparable to those at our site (Table 1) have been reported from Zaire (Laudelot 1954), Guatemala (Popenoe 1960), Ghana (Nye and Greenland 1964), Thailand (Zinke et al. 1978), Brazil (Brinkmann and Nascimento 1973), Peru (Seubert et al. 1977), and Nigeria (Lal and Cummings 1979). During the initial postburn phase, elements are readily available for plant uptake, but are also susceptible to leaching.

The amount of nutrient-rich ash deposited on our

site (670 g/m²) was substantially larger than the only other value in the literature: 400 g/m², measured by Seubert et al. (1977). We are confident that our large sample size ($n = 71$ ash collectors and 300 depth measurements) resulted in an accurate estimate of ash production and that the fire that produced it was representative of the intensity used by shifting cultivators. Within days after the burn, the dry season breezes had blown away substantial amounts of the uppermost fluffy white ash. After the onset of the rains, the less thoroughly combusted gray-white ash washed off the site or into the soil, leaving only charcoal fragments on the surface. Charcoal was still evident in the surface soil nearly 1 yr after the burn.

Three of the elements studied, Ca, Mg, and P, have sedimentary biogeochemical cycles, and are relatively immobile. The fates of these three elements at our site are summarized in Fig. 3. None of these elements was lost during the burn, but small amounts of Ca (2.6 g/m²) and substantial amounts of P (0.3 g/m²) were lost during the 11-wk decomposition period. Wood harvest removed 11–16% of the total stock of each of these three elements, but accounted for substantially less than the amount lost by postburn leaching, erosion, and wind (40–51%). After the burn and onset of the rains >40% of the Ca and Mg, but only 20% of the initial amount of P, remained in or above the surface 3 cm of the site. Much of the reduction in P probably resulted from fire-mediated conversion to forms not extracted by our technique. Fassbender (1975) heated seven tropical soils and found that there was a significant release of P as $H_2PO_4^-$, which then formed stable phosphates of Ca, Fe, and Al.

The other four elements monitored were much more mobile, either because they were readily leached (K), and/or because they were subject to physically or biologically mediated volatilization (C, N, S). One difference often cited as distinguishing temperate and tropical forests is that the nutrients in tropical forests
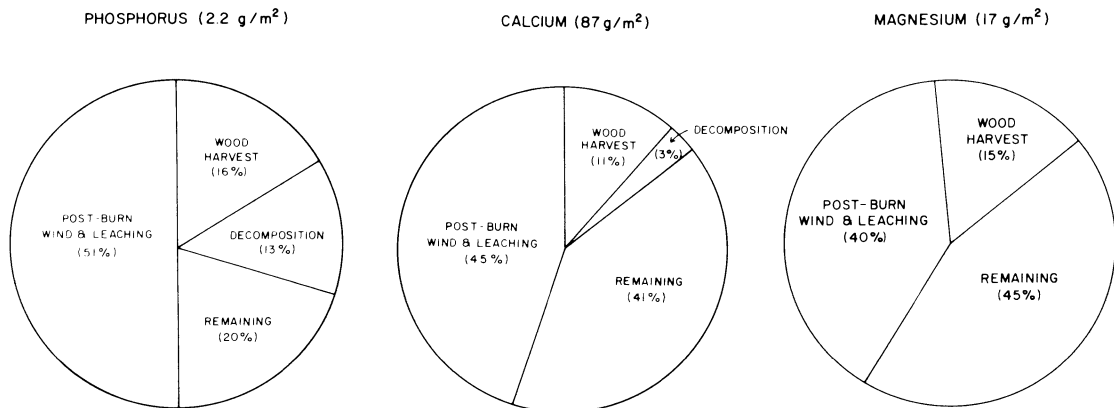

FIG. 3. Fates of the three most immobile elements: P, Ca, and Mg. Amount shown (g/m²) is the initial content of the preburn forest, including all aboveground biomass, plus soil and roots to 3 cm.

CARBON (kg/m²)

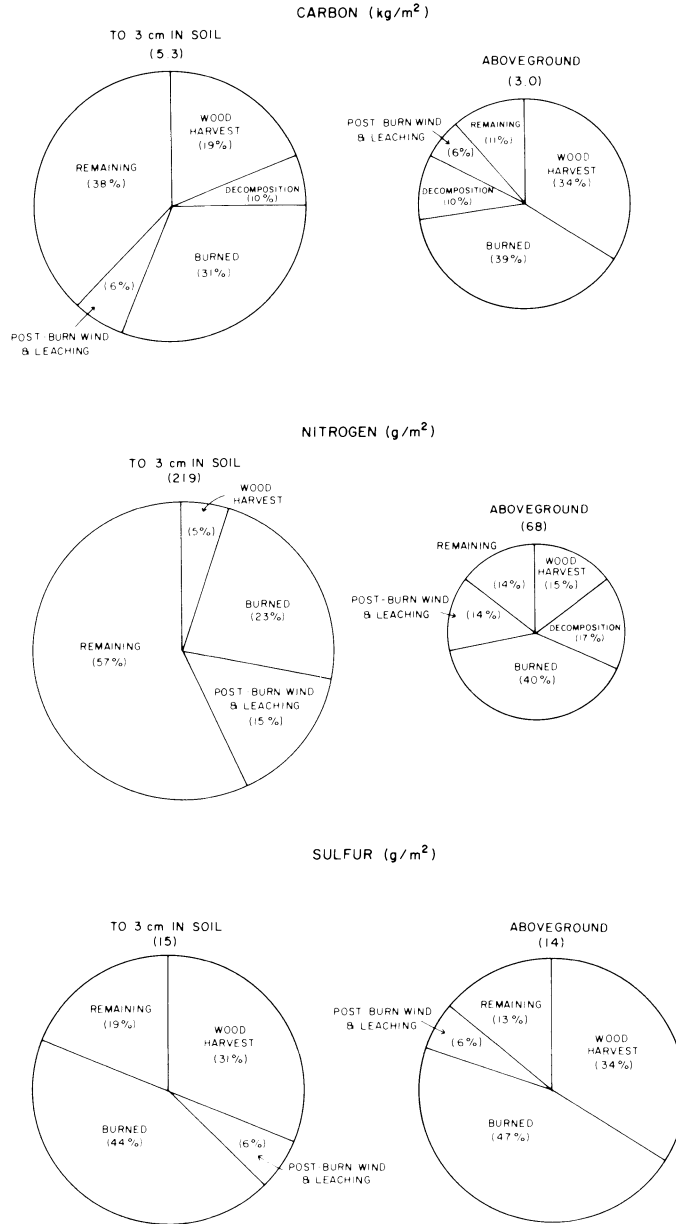NITROGEN (g/m²)

SULFUR (g/m²)

FIG. 4. Differences in fates of C, N, and S when budget includes only aboveground biomass or extends to soil depth of 3 cm. Amount shown (above pie diagram; kg/m² C or g/m² N and S) is the initial content of the preburn forest. There was some accretion of N and S during decomposition.

are primarily immobilized in aboveground biomass, whereas the bulk of the nutrients in most temperate-zone forests are in the soil. At our site this generalization is valid for P, Ca, Mg, and K, but not for C, N, or S (Fig. 4). Assuming that the ecosystem potentially affected by the burn extends from whatever is aboveground to a soil depth of 3 cm, we find that 43% of the C, 69% of the N, and 48% of the S (but only 10% of the K) are contained in the upper 3 cm of soil.

These soil storages are relatively immune to volatilization during the fire, and thus remain on site after

the burn. Vine (1948, cited by Nye and Greenland 1964) reported that felling and burning a 30-yr-old Nigerian forest had little effect on soil C and N; Nye and Greenland (1964) reported increases in soil C and N (presumably because of admixture of vegetation) after felling an ≈50-yr-old forest in Ghana; and Seubert et al. (1977) found that soil C and N increased after felling and burning of a 17-yr-old forest in Amazonian Peru.

Most of this belowground storage is in organic matter other than roots, which account for only 4% of the belowground C, ≈2% of the belowground N, and 7%

of the belowground S. N incorporated in soil organic matter is not likely to be in forms readily available for plant uptake, but the popular idea that burning results in loss of most N is clearly incorrect.

The soil at our site is relatively nutrient rich, so one might assume that the conservation of N, C, and S during the burn is an artifact of this site characteristic. This is not correct. On the most nutrient-poor tropical sites, such as the sterile sands of Amazonia and Borneo (Andriesse 1969, Herrera et al. 1978, Stark and Jordan 1978), the stature of the aboveground community is low and the soil surface is topped with a deep (up to 30 cm, Stark and Spratt 1977) layer of organic matter and roots (Klinge and Herrera 1977). If this layer is not consumed by fires associated with tropical forest clearing, the fraction of C, N, and S conserved by the surface-soil organic mat is probably even more marked on these extremely infertile soils than on the relatively fertile soils of our site. However, Anderson (*in press*) noted that, on nonhydromorphic white-sand soils of central Amazonia, the root mat is often consumed by fire after the vegetation is felled. On our site the conservation of a substantial fraction of total C, N, and S in the upper portion of the soil reflects both high soil storage (although less than on more nutrient-poor sites) and modest aboveground biomass ($\approx$5.2 kg/m^2).

The distributions of K, C, N, and S in the forest, slash, and after the burn are shown in Fig. 5. The soil accounts for most C, N, and S throughout, whereas most K is accounted for in the wood, fuel, and postburn wood and ash.

The ash is especially rich in K (analyses averaged 2.8%), and accounts for over half of the postburn K on the site. Similar findings have been reported by Nye and Greenland (1960), Brinkmann and Nascimento (1973), and Seubert et al. (1977). The element-rich ash is readily susceptible to wind and water erosion, which may account for the loss of large quantities of nonvolatile elements from burned fields.

Leaves account for only 3–7% of the initial amounts of K, C, N, and S. Leaf decomposition is so complete by 11 wk that most of the nutrients they contain are released to the soil prior to the burn.

Carbon dioxide evolution

Our values of carbon evolution from the soil (Table 3) are higher than most values reported for temperate-zone forests. Schlesinger (1977) reviewed the literature and reported temperate-zone means of 0.3–1.4 kg $C \cdot m^{-2} \cdot yr^{-1}$, assuming a 9-mo season (= 1.1–5.1 g $C \cdot m^{-2} \cdot d^{-1}$). Data (g $C \cdot m^{-2} \cdot d^{-1}$) from tropical areas are higher than those from the temperate zone. Maldague and Hilger (1963, cited by Schlesinger 1977) reported a mean of 3.4 from four equatorial forests; Schulze (1967) reported some of the highest values in the literature (savanna in dry season 2.5, gallery forest 10.4, wet forest 12.1, and young succession 19.5) from

his work in Costa Rica; Yoda and Kira (1969) reported nine measurements from rain forests in Thailand, with a mean of 4.4; Odum et al. (1970) evaluated several methodologies in Puerto Rico and reported values ranging from 1.6 to 10.2; Wanner (1970) measured rates of 0.8–1.5 in Java and 0.9–2.0 in Sarawak; Johnson et al. (1975) reported ranges of 0.5–3.1 and 2.6–7.1 from two sites in Costa Rica; and Ogawa (1978) reported 3.9 from Malaysia. Some of the lowest values in the tropical literature are 0.6 and 1.4, reported by Medina (1969) from two sites in Venezuela. However, we calculate that his weak solution (0.5N KOH), small absorbing volume (10 mL), and long absorption interval (10–12 h) would not have enabled him to detect accurately amounts of evolved CO_2 much larger than those he reported. Some investigators (Schulze 1967, Medina 1969) follow the suggestion of Haber (1958) and multiply the measured amount of absorbed CO_2 by a correction factor of 1.33. Most values in the literature (including ours) do not include this correction factor.

Several workers (Reiners 1968, Schlesinger 1977, Schwartzkopf 1978) have stressed the importance of soil moisture, soil temperature, and/or wind velocity at the soil surface as environmental factors that dramatically affect rates of CO_2 evolution. Wind velocity was eliminated as a variable in our experiments because the absorbing receptacles were enclosed beneath inverted cans.

We anticipated that rates of CO_2 evolution would exhibit diurnal trends, tracking the sinusoidal variation in temperature described as typical of data from temperate-zone forests by Witkamp (1969). Our data showed no diurnal pattern. In fact, three of our four diurnal runs exhibited minima about midday; the fourth showed one just before midnight. Maxima occurred at various times. Under the preburn slash the maximum occurred just prior to dawn, when the convection caused by higher soil than air temperature might explain high rates of CO_2 evolution, as suggested by Witkamp (1969).

Soil moisture probably exerted a great influence over the rates of CO_2 evolution we observed. Before the burn, the slashed field had significantly higher soil moisture content than the surrounding forest (Table 3). The ratio of rate of C evolution from the forest soil to the rate of evolution from the slash (0.69) was almost equal to the ratio of forest soil moisture content to slash soil moisture content (0.72). Prior to the burn, before the rains began, soil moisture may have limited microbial activity.

The postburn CO_2 evolution measurements were made after the first rains. Even though soil moisture was still higher in the burned field than in the forest, the absolute value of soil moisture was greater in both places than it had been prior to the burn. The rains may have increased soil moisture to the point where water was no longer limiting for microbial activity in

CARBON (kg/m²)

FOREST
(5.3)

SLASH
(4 0)

POST - BURN
(2.4)

NITROGEN (g/m²)

FOREST
(219)

SLASH
(214)

POST - BURN
(165)

SULFUR   (g/m²)

FOREST
(27)

SLASH
(23)

POST- BURN
(4)

POTASSIUM (g/m²)

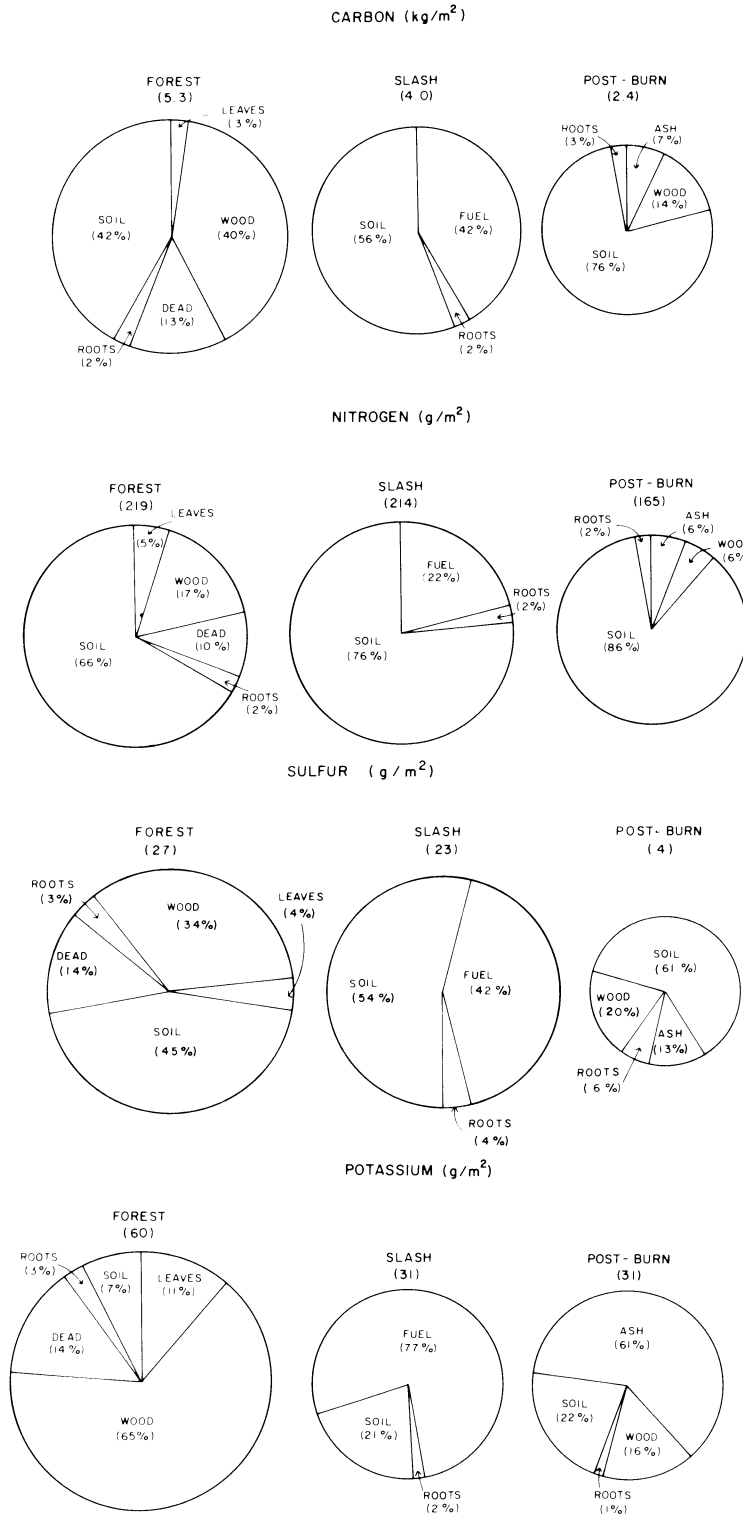FOREST
(60)

SLASH
(31)

POST- BURN
(31)

Fig. 5.   Distributions of the four most mobile elements (C, N, S, and K) in the preburn forest, the 11-wk-old slash, and the postburn field. Values above pie diagram include roots and soil to a depth of 3 cm.

either place, which may account for the similarity in the postburn rates of CO_2 evolution.

Total C (soil organic matter plus roots) in the surface 3 cm after the burn was ≈ 3.4 kg/m². A soil respiration rate of 4.5 g $C \cdot m^{-2} \cdot d^{-1}$ would deplete that soil C in a little over 2 yr if all inputs were eliminated. However, organic matter breakdown slows as the easily decomposed materials are exhausted and more refractory compounds remain, so depletion would occur more slowly. The postburn decomposition of soil organic matter under clean cultivation systems probably results in more drastic site degradation than the burn itself.

Seeds in the soil

The mean number of seeds that germinated from soil sampled from beneath the forest (7786 seeds/m²) was higher than the values reported for other tropical areas. Data (seed number/m²) on soil seed storage in mature forests from other parts of the tropics include: Thailand, 103, 121, and 182 (Cheke et al. 1979); Mexico, 431 and 614 (Guevara and Gómez-Pompa 1972); Sabah, 59 (Liew 1973); and Nigeria, 232 (Keay 1960). Samples from tropical second-growth and agricultural areas are generally higher, but still somewhat lower than ours: Mexico, 1441 and 3125 (Guevara and Gómez-Pompa 1972); and Belize, 6488 (Kellman 1974). All of these values, including those from our Costa Rican study site, are considerably lower than the value reported from 3-yr-old vegetation on abandoned farmlands in the Everglades of South Florida: 30,125 seeds/m² (Ewel and Conde 1979). The seven sites studied by Ewel and Conde (1979) included three mature communities and, excluding the 3-yr-old site, their values ranged from ≈ 500 to 6000 seeds/m².

Comparisons of the number of species recorded at our site with the numbers reported by others are more tenuous because of differences in numbers and sizes of samples, and the duration of the germination period. Our value from the forest (67 species) is higher than others from the tropics (number of species): Thailand, 16, 22, and 27 (Cheke et al. 1979); Mexico, 14, 21, 27, and 28 (Guevara and Gómez-Pompa 1972); Belize, 54 (Kellman 1974); Sabah, 31 (Liew 1973); and Nigeria, 39 (Keay 1960). Former agricultural lands and successional vegetation usually have more species, as well as more individuals, in their soil seed flora.

During the 11 wk that the felled vegetation was decomposing and drying, both the number of individuals and the number of species stored as seeds in the soil dropped to 76% of the values observed beneath the forest. These decreases were probably due to reduced autochthonous seed inputs, coupled with loss of viability of seeds in the soil, and germination.

The burn killed 52% of the seeds and 27% of the species that were present beneath the mulch prior to the fire. Brinkmann and Vieira (1971), working with

seeds of 16 tree species placed in the soil beneath slash in Amazonian Brazil, found that burning reduced germination of seeds in the surface 5 cm of soil to about one-third that of controls. They reported surface temperatures during their burn of $100°-150°C$, which is cooler than most burns associated with tropical land clearing.

The slash and burn decreased soil seed storage by 63%: 24% loss during the mulch period and an additional 39% during the burn. Burning reduces the amount of initial regrowth, which is one reason it is done by most shifting cultivators. Site accessibility, pest control, and nutrient release are other reasons. The mulch and burn reduce the number of competing individuals more than the number of competing species. The species declined only 51%: 24% during mulch period and 27% during the burn.

Conclusions

Wood harvest removed >10% of the total standing crop (to 3-cm soil depth) of each of the seven elements studied, except N (Figs. 3 and 6). Descriptions of shifting agriculture usually indicate that the forest is felled and burned in situ. Today that is still true in remote areas, but the situation is changing quickly. As accessibility increases, forest clearing is more commonly associated with wood harvest, and that trend is sure to continue as wood supplies become more scarce near urban areas. Also, much forest clearing in the tropics today is done by large agricultural and forestry businesses, and wood harvest is often an integral part of their activities. The loss of essential elements via harvested wood will become an increasingly important consideration in tropical ecosystem management, and may lead to rapid degradation of the most nutrient-poor sites.

The drying and mulching period is an important, but often neglected, part of the shifting cultivation cycle. On our site 33% of the K (Fig. 6) and 13% of the P (Fig. 3) were lost during the 11 wk prior to the burn. The concentration of K increased at both the 0–3 and 3–8 cm soil depths during the mulch period, and P increased in the 0–3 cm sample (Table 2), but more K and P were lost than were trapped by the upper 8 cm of soil. Losses of other elements did not exceed 6%. The slash conserved soil moisture better than the surrounding evergreen vegetation, and recolonization began quickly after the burn.

The burn volatilized 31% of the initial amount of C, 22% of the N, and 49% of the S (Fig. 6). C and N supplies might be restored by plant growth and N-fixation during succession, but the loss of S may be more permanent. Formerly S was added to tropical agricultural soils as part of many N fertilizers [e.g., $(NH_4)_2SO_4$], but today, with increasing use of high-N, S-free fertilizers (e.g., urea), S is likely to become in-

CARBON (kg/m²)
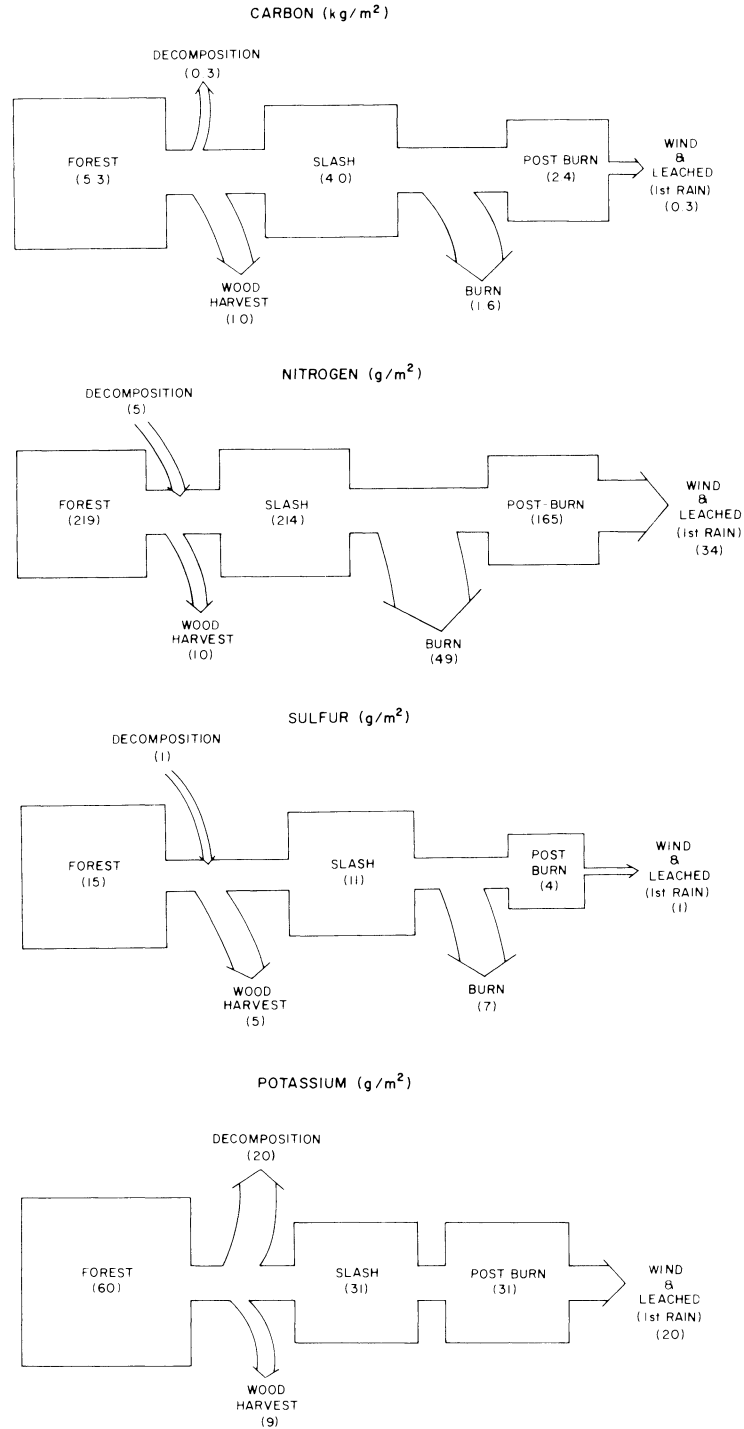
DECOMPOSITION
(0.3)

FOREST
(53)

SLASH
(40)

POST BURN
(24)

WIND
&
LEACHED
(1st RAIN)
(0.3)

WOOD
HARVEST
(10)

BURN
(16)

NITROGEN (g/m²)

DECOMPOSITION
(5)

FOREST
(219)

SLASH
(214)

POST-BURN
(165)

WIND
&
LEACHED
(1st RAIN)
(34)

WOOD
HARVEST
(10)

BURN
(49)

SULFUR (g/m²)

DECOMPOSITION
(1)

FOREST
(15)

SLASH
(11)

POST
BURN
(4)

WIND
&
LEACHED
(1st RAIN)
(1)

WOOD
HARVEST
(5)

BURN
(7)

POTASSIUM (g/m²)

DECOMPOSITION
(20)

FOREST
(60)

SLASH
(31)

POST BURN
(31)

WIND
&
LEACHED
(1st RAIN)
(20)

WOOD
HARVEST
(9)

FIG. 6. Summary storages and losses of the four most mobile elements (C, N, S, and K) during wood harvest, decomposition, burning, and postburn erosion.

creasingly limiting, especially where burning is a routine agricultural practice.

The burn also reduced, by more than half, the number of germinable seeds on our site. Nevertheless, within 3 mo the site was covered by a dense, vigorous regrowth containing >100 species. Burning may reduce initial weed competition by killing on-site seeds, but it did not significantly retard succession on our site.

Burning did not degrade site quality. Substantial

amounts of soil C (essential for cation exchange in many mature tropical soils) and N were conserved, and only S was lost in deleterious quantities. The burn did not consume the root layer and surface soil organic matter, the mycorrhizae survived, and the ability of the site to support vigorous plant life was not impaired. The release of nutrients that had been immobilized in the vegetation significantly increased soil fertility.

After the burn, there was little immediate additional loss of C or S, presumably because they had already been volatilized by the fire. Postburn loss of N (16% of the initial amount) was high (Fig. 6), and may represent the leaching of N as $NO_3^=$ formed by the burn. The losses of nonvolatile elements after the burn and onset of the rains were very high: P (51%); K (33%); Ca (45%); and Mg (40%) (Figs. 3 and 6). Our postburn soil sampling may have missed some of the remaining ash, but we are confident that deficiencies in sampling procedures did not account for the huge losses measured. Some of the P showed up as increased concentrations in the 3–8 cm soil sample (Table 2), but most P, K, Ca, and Mg were either leached deeper into the soil, blown or washed off the site by wind and rain, or converted to unavailable forms. The postburn losses of nonvolatile elements through ash losses were as important as the volatilization of C, N, and S during the burn.

The impact of postburn decomposition on the C balance may be as important as the more dramatic burn. During the burn the site lost an average of 699 g C/m^2. At the mean rate of C evolution from the soil after the burn (4.5 $g \cdot m^{-2} \cdot d^{-1}$), 154 d of decomposition equals one burn; 1 year of clean cultivation could seriously deplete soil organic matter.

LITERATURE CITED

Aguirre, V. 1971. Clasificación de suelos del IICA-CTEI, Turrialba, Costa Rica. Thesis. Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica.

Anderson, A. In press. White-sand vegetation of Brazilian Amazonia. Biotropica.

Andriesse, J. P. 1969. A study of the environment and characteristics of tropical podzols in Sarawak (East Malaysia). Geoderma 2:210–217.

Bolin, B. 1977. Changes of land biota and their importance for the carbon cycle. Science 196:613–615.

Bornemisza, E., M. Constenla, A. Alvarado, E. Ortega, and A. Vásquez. 1979. Organic carbon determination by the Walkley-Black and dry combustion methods in surface soils and Andept profiles from Costa Rica. Soil Science Society of American Journal 43:78–83.

Bower, C. A., R. F. Reitemeier, and M. Fireman. 1952. Exchangeable cation analysis of saline and alkaline soils. Soil Science 73:251–261.

Bremner, J. M. 1965. Total nitrogen. Pages 1149–1178 in C. A. Black et al., editors. Methods of soil analysis. American Society of Agronomy, Madison, Wisconsin, USA.

Brinkmann, W. L. F., and J. C. do Nascimento. 1973. The effect of slash and burn agriculture on plant nutrients in the tertiary region of central Amazonia. Acta Amazonica 3:55–61.

Brinkmann, W. L. F., and A. N. Vieira. 1971. The effect of burning on germination of seeds at different soil depths of various tropical tree species. Turrialba 21:77–82.

Broecker, W. S., T. Takahashi, H. J. Simpson, and T.-H. Peng. 1979. Fate of fossil fuel carbon dioxide and the global carbon budget. Science 206:409–418.

Cheke, A. S., W. Nanakorn, and C. Yankoses. 1979. Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. Biotropica 11:88–95.

Chesnin, L., and C. H. Yien. 1950. Turbidimetric determination of available sulfates. Soil Science Society of America Proceedings 15:149–151.

De las Salas, G., and H. Fölster. 1976. Bioelement loss on clearing a tropical rain forest. Turrialba 26:179–186.

Ewel, J., and L. Conde. 1979. Seeds in soils of former Everglades farmlands. Pages 225–234 in R. M. Linn, editor. Proceedings of the First Conference on Scientific Research in the National Parks. Volume 1. Series 5, National Park Service Transactions and Proceedings, United States Department of the Interior, Washington, District of Columbia, USA.

Fassbender, H. W. 1975. Experimentos de laboratorio para el estudio del efecto del fuego de la quema de restos vegetales sobre las propiedades del suelo. Turrialba 25:249–254.

Fenner, R. L., and J. R. Bentley. 1960. A simple pyrometer for measuring soil temperatures during wildland fires. Miscellaneous Paper 45, United States Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Fox, R. L., R. A. Olson, and H. F. Rhoades. 1964. Evaluating the sulfur status of soils by plant and soil tests. Soil Science Society of America Proceedings 28:243–246.

Greenland, D., and J. Kowal. 1960. Nutrient content of the moist tropical forest of Ghana. Plant and Soil 12:154–174.

Guevara, S. S., and A. Gómez-Pompa. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. Journal of the Arnold Arboretum 53:312–335.

Haber, W. 1958. Ökologische untersuchungen der boden-atmung. Flora 146:109–157.

Harcombe, P. A. 1977a. The influence of fertilization on some aspects of succession in a humid tropical forest. Ecology 58:1375–1383.

———. 1977b. Nutrient accumulation by vegetation during the first year of recovery of a tropical forest ecosystem. Pages 347–378 in J. Cairns, Jr., K. L. Dickson, and E. E. Herricks, editors. Recovery and restoration of damaged ecosystems. University of Virginia Press, Charlottesville, Virginia, USA.

Hardy, F. 1961. The soils of the IAIAS area. Mimeo, Instituto Interamericano de Ciencias Agricolas, (IICA). Available through Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) library, Turrialba, Costa Rica.

Herrera, R. R., C. F. Jordan, H. Klinge, and E. Medina. 1978. Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. Interciencia 3:223–232.

Johnson, C. M., and A. Ulrich. 1959. Analytical methods

for use in plant analysis. Bulletin of the California Agricultural Experiment Station 766:25–78.

Johnson, D., D. Cole, and S. P. Gessel. 1975. Processes of nutrient transfer in a tropical rain forest. Biotropica 7:208–215.

Keay, R. W. J. 1960. Seeds in forest soils. Nigerian Forestry Information Bulletin (New Series) 4:1–4.

Kellman, M. C. 1974. The viable weed seed content of some tropical agricultural soils. Journal of Applied Ecology 11:669–678.

Klinge, H., and R. Herrera. 1977. Composite root mass in tropaquods under Amazon caatinga stands in southern Venezuela. Pages 395–420 in R. Torres de Arauz, editor. Proceedings of the IV International Symposium on Tropical Ecology, Panama. Instituto Nacional de Cultura, in collaboration with other agencies, Panama, Republic of Panama.

Lal, R., and D. J. Cummings. 1979. Clearing a tropical forest. I. Effects on soil and micro-climate. Field Crops Research 2:91–107.

Laudelot, H. 1954. Etude sur l'apport d'éléments minéraux résultant de l'incinération de la jachère forestière. Pages 383–388 in Deuxième Conférence Interafricaine des Sols, Leopoldville, Congo Belge, Document 25.

Levitt, J. 1969. Introduction to plant physiology. C. V. Mosby, St. Louis, Missouri, USA.

Liew, T. C. 1973. Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. Malayan Forester 36:185–193.

Masson, H. 1948. La température du sol au cours d'un feu de brousse au Sénégal. Agronomie Tropicale 3:174–179.

Medina, E. 1969. Respiración edáfica de algunas comunidades tropicales. Boletín de la Sociedad Venezolana de Ciencias Naturales 28:211–230.

Muller, L. 1961. Un aparato micro Kjeldahl simple para análisis rutinarios rápidos de materias vegetales. Turrialba 11:17–25.

Myers, N. 1979. The sinking ark. Pergamon Press, Elmsford, New York, USA.

———. 1980. Conversion of tropical moist forests. National Academy of Sciences, Washington, District of Columbia, USA.

National Research Council. 1980. Research priorities in tropical biology. National Academy of Sciences, Washington, District of Columbia, USA.

Nye, P., and D. Greenland. 1960. The soil under shifting cultivation. Technical Communication 51, Commonwealth Bureau of Soils, Farnham Royal, Bucks, England.

Nye, P., and D. Greenland. 1964. Changes in the soil after clearing tropical forest. Plant and Soil 21:101–112.

Odum, H. T., A. Lugo, G. Cintrón, and C. Jordan. 1970. Metabolism and evapotranspiration of some rain forest plants and soil. Pages I-103–I-164 in H. T. Odum and R. Pigeon, editors. A tropical rain forest. United States Atomic Energy Commission, Washington, District of Columbia, USA.

Ogawa, H. 1978. Litter production and carbon cycling in Pasoh Forest. Malaysian Nature Journal 30:367–373.

Olsen, S. R., and L. A. Dean. 1965. Phosphorus. Pages 1035–1049 in C. A. Black et al., editors. Methods in soil analysis. American Society of Agronomy, Madison, Wisconsin, USA.

Popenoe, H. 1960. Some soil cation relationships in an area of shifting cultivation in the humid tropics. Pages 303–311 in F. A. Van Baren, editor. Transactions of the Seventh International Congress of Soil Science, Volume 2, Madison, Wisconsin, USA. Elsevier, Amsterdam, The Netherlands.

Reiners, W. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecology 49:471–483.

Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. Annual Review of Ecology and Systematics 8:51–81.

Schulze, E. 1967. Soil respiration of tropical vegetation types. Ecology 48:652–653.

Schwartzkopf, S. 1978. An open chamber technique for the measurement of carbon dioxide evolution from soils. Ecology 59:1062–1068.

Sertsu, S. M., and P. A. Sanchez. 1978. Effects of heating upon some changes in soil properties in relation to an Ethiopian land management practice. Soil Science Society of America Journal 42:940–944.

Seubert, C. E., P. A. Sanchez, and C. Valverde. 1977. Effects of land clearing methods on soil properties of an ultisol and crop performance in the Amazon jungle of Peru. Tropical Agriculture (Trinidad) 54:307–321.

Siaz del Rio, J. F., and E. Bornemisza. 1962. Análisis químicos de suelos, métodos de laboratorio para diagnosis de fertilidad. Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica.

Stark, N., and C. Jordan. 1978. Nutrient retention by the root mat of an Amazonian rain forest. Ecology 59:434–437.

Stark, N., and M. Spratt. 1977. Root biomass and nutrient storage in rain forest oxisols near San Carlos de Rio Negro. Tropical Ecology 18:1–9.

Tosi, J. A., Jr. 1969. Republica de Costa Rica, mapa ecológico. Tropical Science Center, San José, Costa Rica.

United States Department of State and United States Agency for International Development. 1978. Proceedings of the United States Strategy Conference on Tropical Deforestation, Washington, District of Columbia, USA.

Uribe, A., F. Suárez de Castro, and A. Rodríguez. 1967. Efectos de las quemas sobre la productividad de los suelos. Cenicafé 18:116–135.

Walkley, A., and I. A. Black. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Science 37:29–38.

Wanner, H. 1970. Soil respiration, litter fall and productivity of tropical rain forest. Journal of Ecology 58:543–547.

Witkamp, M. 1969. Cycles of temperature and carbon dioxide evolution from litter and soil. Ecology 50:922–924.

Wong, C. S. 1978. Atmospheric input of carbon dioxide from burning wood. Science 200:197–200.

———. 1979. Carbon input to the atmosphere from forest fires. Science 204:210.

Woodwell, G. M. 1978. The carbon dioxide question. Scientific American 238:35–44.

Woodwell, G. M., R. H. Whittaker, W. A. Reiners, G. E. Likens, C. C. Delwiche, and D. B. Botkin. 1978. The biota and the world carbon budget. Science 199:141–146.

Yoda, K., and T. Kira. 1969. Comparative ecological studies on three main types of forest vegetation in Thailand. V. Accumulation and turnover of soil organic matter, with notes on the altitudinal soil sequence on Khao (Mt.) Luang, peninsular Thailand. Nature and Life in Southeast Asia 6:83–109.

Zinke, P. J., S. Sabhasri, and P. Kunstadter. 1978. Soil fertility aspects of the Lau' forest fallow system of shifting cultivation. Pages 134–159 in P. Kunstadter, E. C. Chapman, and S. Sabhasri, editors. Farmers in the forest. The University Press of Hawaii, Honolulu, Hawaii, USA.