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Nutrient Dynamics and Early Succession in Fallow Vegetation During the Shifting Cultivation Cycle in Belize, Central America

by

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ABSTRACT

Accumulation of N, P and K in the vegetation of shifting cultivation (milpa) fallow sites aged one, two and three years after abandonment was measured in the semi-evergreen tropical forest region of Belize, Central America. Accumulation of nutrients in the total leaf compartment rapidly reached a plateau level, with 4.9 $g.m^{-2}$ N, 0.26 $g.m^{-2}$ P and 4.7 $g.m^{-2}$ K in the leaves of three year old fallows. Patterns of accumulation of nutrients in the total stem material varied for N, P and K: N increased steadily from a level of 1.9 $g.m^{-2}$ in one year old fallows at a rate of about 2.0 $g.m^{-2}.y^{-1}$; K was accumulated rapidly in one year old fallows, reaching a level of 5.3 $g.m^{-2}$, but further increase in older sites was much slower; levels of P increased slowly from 0.17 $g.m^{-2}$ in one year old sites at a steady rate of about 0.15 $g.m^{-2}.y^{-1}$. In the vegetation of three year old fallow sites total levels of nutrients in leaf and stem were 10.3 $g.m^{-2}$ N, 0.73 $g.m^{-2}$ P and 13.2 $g.m^{-2}$ K. After only three years these levels of N and K were already half of what were estimated in a nearby 45 year old forest site, as reported by Lambert et. al. (1930).

When nutrients in individual species were considered, high concentrations of N, P and K were found in the leaves of Carica papaya, high concentrations of N and P in the leaves of Eupatorium odoratum and high K in leaves of Iresine sp. Nutrient concentrations in stems were much lower than the levels found in leaves. Differences in nutrient concentrations among families of plants were also found: the Compositae had generally high concentrations of all three nutrients, the Leguminosae had high N concentrations and low nutrient concentrations were found in the Sapindaceae and Gramineae. Concentrations of nutrients appeared to be related to the successional status of the plants, with higher concentrations found in opportunistic species than in

later successional species, suggesting different strategies for nutrient utilization.

As early as the end of the first year, woody lifeforms dominated the fallow vegetation, accounting for 80% of the total biomass, while herbaceous species accounted for only 20%. In two year old and three year old fallows the herbaceous component was eliminated, as trees became dominant. This rapid dominance by woody species is vital to good fallow management as these species tend to control population levels of agriculturally noxious herbaceous species and play an important role in the rapid recovery of nutrients from below the rooting zone of crop plants.

RÉSUMÉ

La végétation poussant dans des champs mis en jachère depuis un, deux et trois ans, selon la pratique d'alternance de culture et jachère suivie dans la région, fut examinée afin de déterminer la teneur en N, P et K de ces plantes dans la zone de fôret tropicale dominée par les essences à feuilles semi-persistantes en Bélize, Amérique Centrale. La teneur en éléments nutritifs dans le feuillage atteint rapidement un plateau, avec des niveaux de 4.9 $g.m^{-2}$ N, 0.26 $g.m^{-2}$ P et 4.7 $g.m^{-2}$ K dans les feuilles des plantes dans les jachères de trois ans. L'accumulation de ces éléments dans les tiges fut plus variable: N augmente doucement au taux de 2.0 $g.m^{-2}.an-2$ à partir du niveau de 1.9 $g.m^{-2}$ dans les jachères d'un an; K atteint rapidement le niveau de 5.3 $g.m^{-2}$ dans les jachères d'un an, mais augmente peu dans les sites plus vieux ; la teneur en P augmente lentement au taux de 0.15 $g.m^{-2}.an-1$ à partir du niveau de 0.17 $g.m^{-2}$ dans les jachères d'un an. Dans les jachères de trois ans, les niveaux d'éléments nutritifs dans les feuilles et les tiges étaient 10.3 $g.m^{-2}$ N, 0.73 $g.m^{-2}$ P et 13.2 $g.m^{-2}$ K. Après seulement trois ans, les niveaux de N et K avaient déjà atteint la moitié des niveaux observés par Lambert et al. (1980) dans les forêts avoisinantes agées de 45 ans.

Si l'on considère les éléments nutritifs présents dans diverses espèces de plantes, on retrouve de fortes teneurs en N, P et K dans les feuilles de Carica papaya, de fortes teneurs en N et P dans les feuilles d'Eupatorium odoratum et une forte teneur en K dans les feuilles de Iresine sp. La teneur en éléments nutritifs était beaucoup plus faible dans les tiges que dans les feuilles. Des différences furent aussi notées pour différentes familles de plantes: les Compositae contenaient beaucoup de ces trois éléments et les Leguminosae contenaient beaucoup de N, alors que les

Sapindaceae et Graminae avaient de faibles teneur en N, P et K. La teneur en éléments nutritifs semble associée au stage de succession où l'on retrouve normalement une espèce; une plus forte teneur fut notée dans les espèces colonisatrices que dans les espèces s'installant plus tard dans la succession, indiquant une différence possible dans la stratégie d'utilisation d'éléments nutritifs.

Dés la fin de la première année, les essences ligneuses dominaient la végétation des jachères, représentant 80% de la biomasse totale, contre 20% pour les plantes herbacées. Dans les jachères de deux et trois ans, les arbres étaient devenus dominants et les plantes herbacées étaient éliminées. Cette dominance rapide par les especes ligneuses est importante pour l'aménagement des jachères, puisque ces especes limitent les populations des mauvaises herbes herbacees et récupèrent rapidement les éléments nutritifs qui se trouvent au-delà de la zone des racines des plantes cultivées.

RESUMEN

Se cuantificó la acumulación de N, P y K después de uno, dos y tres años en la vegetación de barbecho en zonas de agricultura de roza y quema (milpa) en la región de bosque tropical semi-perene de Belice. La acumulacion total de nutrientes en el compartimiento foliar del barbechos de 3 anos alcanzó rapidamente un nivel maximo estable de 4.9 $g.m^{-2}$, 0.26 $g.m^{-2}$ y 4.7 $g.m^{-2}$ para N, P y K respectivamente.

El patrón de acumulación de nutrientes para el total de fustes fue variable: el N incrementó constantemente desde un nivel de 1.9 $g.m^{-2}$ en el barbecho de 1 año con una tasa aproximada de 2 $g.m^{-2}.y^{-1}$; el K se acumuló rapidamente en el barbecho de un año de edad, alcanzando un nivel de 5.3 $g.m^{-2}$, sin embargo il incremento posterior en sitios más viejos fue mucho más lento; los niveles de P se incrementaron 0.17 $g.m^{-2}$ en los sitios de un año de edad a razón de 0.15 $h.m-2.y^{-1}$. En la vegetación de 3 años de todas las zonas de barbecho, los niveles totales de nutrientes en hojas y tallos fueron 10.3 $g.m^{-2}$ para el N, 0.73 $g.m^{-2}$ para el P y 13.2 $g.m^{-2}$ para el K. Después de 3 años los niveles de N y K se redujeron hasta la mitad de lo que fue estimado en una zona aledaña hace 45 años, segun lo reprtado por Lambert et al. (1980).

Al considerar los nutrientes por especie, se encontró una alta concentracion de N y P en el follaje de Carica papaya y de K en las hojas de Iresine sp. La concentración de nutrientes en los tallos fue mucho más baja que en las hojas. Por otra parte, se encontraron diferencias en las concentraciones de nutrientes entre familias de plantas: la familia Compositae tuvo en general, altas concentraciones de los 3 nutrientes, la familia Leguminosae tuvo altas concentraciones de N, y bajas

concentraciones de nutrientes fueron encontradas en las familias Sapindaceae y Graminae. Al parecer, las concentraciones de nutrientes estan relacionadas al estado sucesional de la vegetación ya que las concentraciones más altas fueron encontradas en especies oportunistas en comparacion a las halladas en especies sucesionales tardías, sugiriendo esto la presencia de diferentes estrategias en la utilización de nutrientes.

Las formas de vida arbustivas dominaron la vegetación de barbecho prematuramente hacia el final del primer año, representando el 80% de la biomasa total mientras que las herbaceas representaron solamente un 20%. En los barbechos de 2 y 3 anos el componente herbaceo fue eliminado cuando las formas arbustivas fueron dominancia. La dominancia de las especies arbustivas es vital para el buen manejo del barbecho ya que esas especies tienden a controlar los niveles poblacionales de las especies herbaceas nocivas para la agricultura además de que juegan un papel importante en la recuperación espédita de nutrientes de debajo de la zona rizomal de las plantas de cultivo.

ACKNOWLEDGEMENTS

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This work is dedicated to the farmers of Succotz.

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INTRODUCTION

Food production in the developed countries of the north and the less developed countries of the south is fundamentally different. The production of food in much of the industrialized world has become a highly mechanized, energy-intensive endeavor in which high yields may be obtained from the soil with a minimal input of human labour. Much of the world however derives its food supplies from an agricultural system which has been practiced in various forms for hundreds of years: shifting cultivation. In spite of the low yields achieved in shifting cultivation (Watters, 1971) and the high labour requirement per unit of output in this system as compared to mechanized agriculture (Clark and Uhl, 1984), shifting cultivation is the most widespread farming system in the tropics (Okigbo, 1984). The system feeds over 250 million people (Nair and Fernandes, 1984) and occupies 44% of the potentially arable or grazable land in tropical regions (Sanchez, 1976).

In other areas of the tropics and subtropics, shifting cultivation has been an appropriate land use strategy in the past, but is now facing severe socio-economic and ecological pressures. Increased population, government restrictions on the use of forest reserves, increased private land ownership especially for cattle ranches, resettlement due to wars and calamities and the introduction of cash crops have individually or in combination placed restrictions on the shifting cultivator (Nair and Fernandes, 1984). However, the transition to more productive cropping systems, even when appropriate technologies exist, is often hindered by unfavourable economic conditions (Ruthenberg, 1976). Shifting cultivation will, for better or worse, continue to play an important role in feeding many peoples of the tropics well into the future.

It has been widely recognized that shortening of the fallow period in the shifting cultivation cycle, due to decreased land availability, leads to declining soil fertility, increased soil erosion, loss of nutrients from the agroecosystem, increased weed problems and increased crop pests (Nye and Greenland, 1960). An understanding of the details of fallow development, both in terms of nutrient uptake and species composition, would therefore appear to be of major importance to understanding and improving the system (Gomez-Pompa and Vazquez-Yanes, 1974). However, in spite of the importance of the fallow to traditional agricultural systems, very little is known about the ecology of fallow succession, or the consequences of fallow degradation in terms of vegetation dynamics. Furthermore, tropical succession in general has been studied less intensively than temperate succession and is not well understood. It should be evident that a much greater research effort must be devoted to tropical plant ecology than has occurred in the past, if these important ecosystems are to be well managed in the future. There is an immediate need for an understanding of these systems as they are currently undergoing rapid change.

1.1 SHIFTING CULTIVATION DEFINED

Shifting cultivation has been defined as an agricultural system in which temporary clearings are cropped for fewer years than they are left fallow (Sanchez, 1976). The relation between the cropping period and the fallow period has been used to distinguish between different agricultural systems by the calculation of an index of intensification, R, (Ruthenberg, 1976) where:

$$R = \frac{\text{years of cropping}}{\text{years of cropping and years of fallow}} \times 100 \quad \text{Eqn.1.}$$

Thus a system involving two years cropping followed by four years of fallow would

be assigned an R-value of 33. On this basis, four types of land-based cultivation have been defined (Fig. 1), with shifting cultivation encompassing those systems with 'R' less than 33. While these limits are rather arbitrary, they have become generally accepted (Norman, 1979).

Many different names are used to refer to systems of shifting cultivation; 'swidden agriculture', a term favoured by anthropologists (Norman, 1979), 'slash and burn' a descriptive term referring to the method of land preparation, and 'fire agriculture' (Smith, 1972), another descriptive term. Many local names such as 'milpa' (Mexico and Central America), 'jhum' (India), 'hanumo' (Philippines), and chitimene (Zambia, Tanzania) are also used (Okigbo, 1984).

1.2 SHIFTING CULTIVATION IN BELIZE, CENTRAL AMERICA

In Belize and throughout Central America and Mexico, the name 'milpa' is used to describe the method of shifting cultivation that has traditionally been practiced. The term 'milpero' is used to designate a person who farms a milpa field. The milpa cycle begins with the final selection and clearing of a plot of fallow land in December or January (Fig. 2). In Succotz, Cayo District (Fig. 3), land is selected which has been left fallow for a period of 1-15 years, with 7-10 years being most common. In other regions of Central America and in parts of Mexico, the system has degraded to the point where the average fallow length has been reduced to as little as 1-3 years. After clearing, the brush is allowed to dry until just before the beginning of the wet season, towards the end of May, at which time it is burned.

Maize is planted after the first rains, using a heavy pointed stick to make holes in the soil at one meter intervals into which four seeds are planted. Other crops such as squash, climbing beans and various root crops may be intercropped with

Fig.1. Land-based Cultivation Systems

(adapted from Ruthenberg, 1976)

Note: See eqn.1. for definition of R.

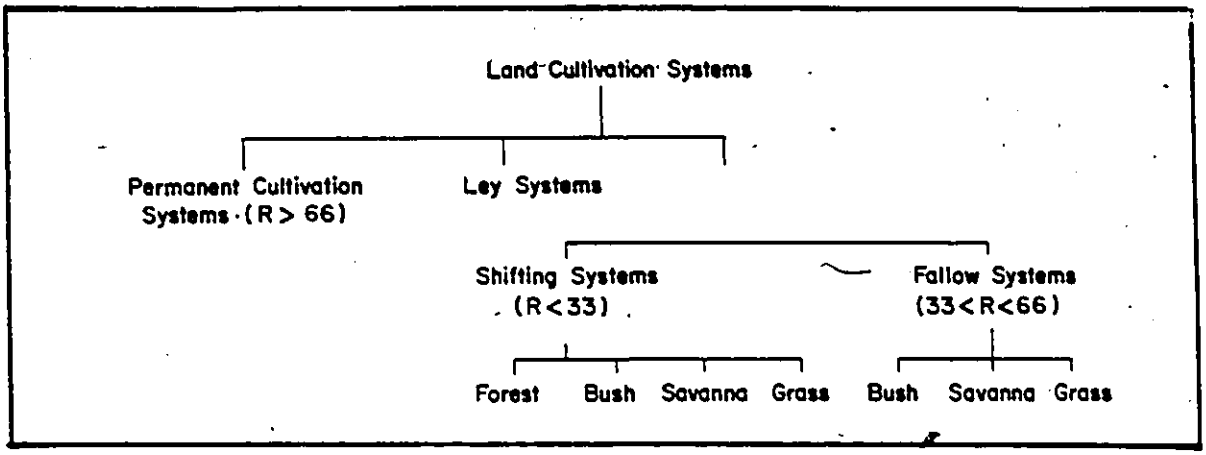

Land Cultivation Systems
Permanent Cultivation Systems (R > 66)
Ley Systems
Shifting Systems (R<33)
Fallow Systems (33<R<66)
Forest
Bush
Savanna
Grass
Bush
Savanna
Grass

Fig.2. The Milpa Cultivation Cycle at Succotz, Belize.

(adapted from Lambert and Arnason, 1986)

Note: The cosecha is a wet season crop, the yaxking a dry season crop.

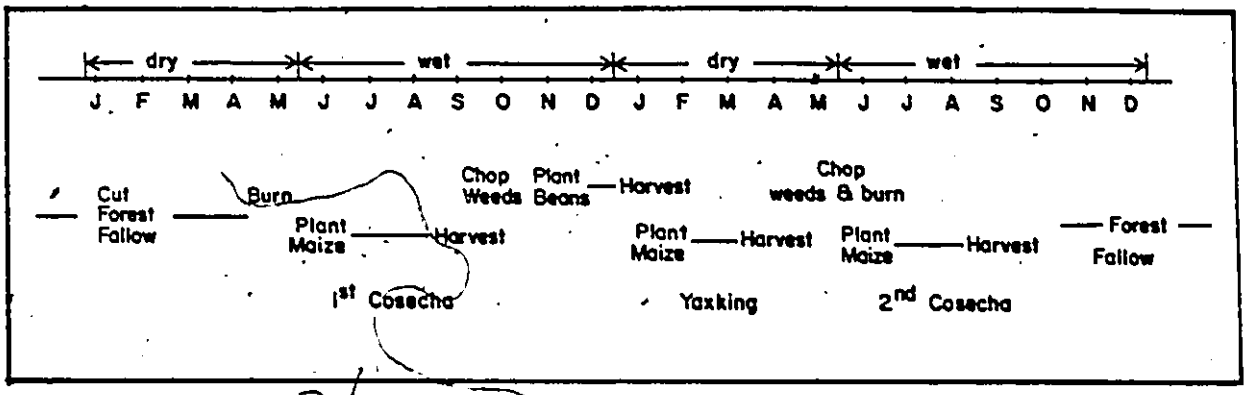
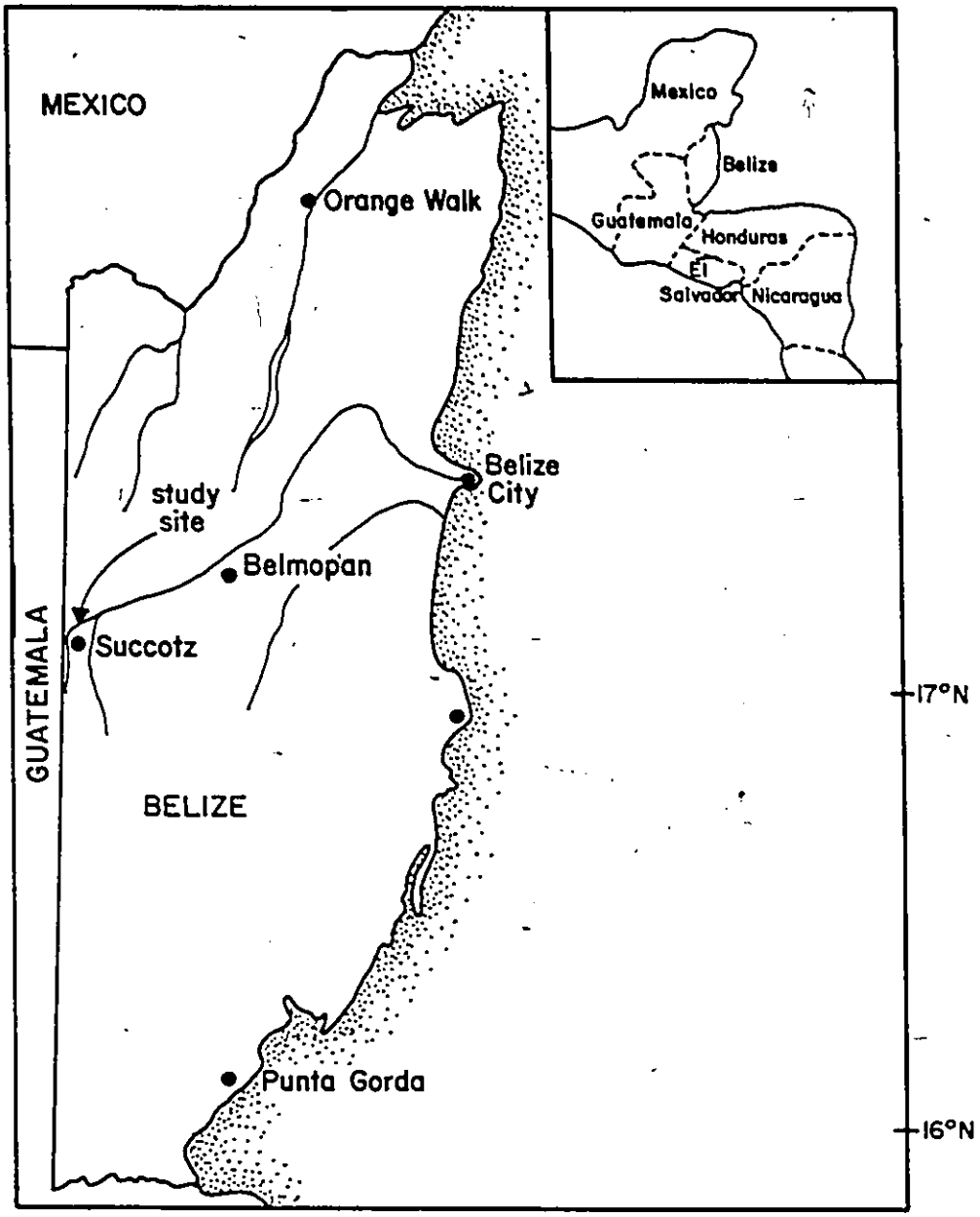

dry
wet
dry
wet
J F M A M J J A S O N D J F M A M J J A S O N D
Cut Forest Fallow
Burn
Plant Maize
Harvest
1st Cosecha
Chop Weeds
Plant Beans
Harvest
Plant Maize
Harvest
Yaxking
Chop weeds & burn
Plant Maize
Harvest
2nd Cosecha
Forest Fallow

Fig.3. Location of Succotz, Belize, Central America.


MEXICO
Orange Walk
Belize City
study site
Belmopan
Succotz
GUATEMALA
BELIZE
Punta Gorda
17°N
16°N
Mexico
Belize
Guatemala
Honduras
El Salvador
Nicaragua

the maize. During the wet season many of the milperos find work as labourers elsewhere in the district and thus may have little time to tend the milpa. The harvest of the rainy season crop, or 'cosecha' as it is called occurs towards the end of August and September. After the ears have dried they are stored with husks intact for better protection from insect damage and are then used as required.

In November a second, though less common and less important crop called the 'yaxking' or dry season crop may be planted. For this crop, consisting of maize and/or beans, vegetation which has grown up after the previous burn is cleared but not burned. The following May the site is cleared and burned once again in preparation for a second cosecha. Generally a second fallow site will also be brought into cultivation so that each season both a first cosecha and a second cosecha crop will be in progress. After the second cosecha the land is left fallow. To some extent a mixing of traditional milpa farming with other activities, such as wage work as labourers, is occurring. The result is a reduction in the sophistication of milpa farming, with less use of intercrop species and less careful weeding activity.

Although some immigration has been occurring in the region around Succotz, this is not extensive and has not yet placed excessive pressure on the land base. The average area of land that a milpero keeps under cultivation in this region has been estimated at 3 to 4 ha (Hartshorn, 1984), although less area will be planted when the farmer finds work elsewhere during the rainy season.

1.3 ECONOMIC CONSIDERATIONS

While an evaluation of the economic considerations relating to systems of shifting cultivation is well beyond the scope of this study, a brief examination of some key points should help to place this work in the broader context of agricultural develop-

ment.

In 1969, only 12% of the fertilizer used in the world was consumed in the tropics, although half of the world's land lies within tropical areas (Norman, 1979). While such inputs could lead to increased yields and in some situations even to permanent agriculture (Sanchez et al, 1982), a lack of reasonably available capital and unfavourable price relations between the cost of inputs and the price of produce has impeded the transition to more capital intensive, higher yielding systems (Ruthenberg, 1976). Poor transportation facilities in many developing countries have further impeded the adoption of economically integrated production systems by driving up the cost of inputs such as fertilizers, as well as reducing outlets for produce and decreasing the proportion of the market price that the farmer receives (Grigg, 1970). Frequent flooding may cut off transportation of produce to markets altogether (Hartshorn, et al, 1984). Because of the need for foreign exchange, agricultural extension services and capital investment has usually focused on larger-scale export crop producers, overlooking the small-scale, semi-subsistence shifting cultivators (Watters, 1971, Robinson and Furly, 1983).

Shifting cultivation is currently in a state of tension from an economic point of view. On the one hand, shifting cultivation has moved more and more from a subsistence economy towards integration with a market economy to which it is not well suited. On the other, major economic blocks exist which make the transition from shifting cultivation to more capital intensive systems difficult at the least.

1.4 THE ROLE OF THE FALLOW

At the same time that economic factors have placed pressure on shifting cultivation systems, ecological factors have forced immediate changes to the system. Increased

pressure on land, for the reasons mentioned earlier, has decreased the period of time that land may remain in fallow. In many cases this has led to a degradation of the systems from a previously balanced form of land use (Ruthenberg, 1976).

Because of the requirement for a long fallow period, shifting cultivation is an extensive form of agriculture which requires large areas of land to support relatively small populations (Watters, 1971). Under conditions where sufficient land is available to the shifting cultivator the traditional system works well, maintaining nutrients in the agroecosystem, preventing soil erosion and controlling weeds (Nye and Greenland, 1960; Rappaport, 1976; Denevan et al, 1984). Under these conditions, shifting cultivation is an ecologically sustainable farming system.

The fallow period in shifting cultivation plays two important roles in preparing a site for the next cropping cycle. It helps to maintain soil fertility and ensures that weed populations do not become unmanageable. In tropical regions where temperatures are suitable for uninterupted growth all year round, fallows may be considered to play a role analogous to that of winter in temperate regions. In the case of the fallow though, weed control is achieved through a successional process, not through extreme climate.

For the farmer, fallows are also of inherent value as they supply firewood, building materials, medicinal plants and a habitat for animals which may be utilized as a food source.

1.4.1 CONTRIBUTION TO SOIL FERTILITY

Soil fertility encompasses a range of both physical and chemical parameters (Brady, 1984; USDA, 1957). The ability of the soil to hold cationic nutrients such as K, referred to as cation exchange capacity (CEC), ensures that these nutrients will not

be leached out of the rooting zone by heavy rains. A reserve supply of these nutrients is thus held in an equilibrium with the soil solution. As cations are removed from the soil solution by plant roots, hydrogen ions are released from the root and these exchange with other cations in the cation exchange complex. As long as sufficient CEC exsists, stocked with adequate amounts of nutrient cations, the supply of these nutrients in the soil solution will be replenished.

The CEC of a soil is determined by both the mineral composition of the soil, and the amount of organic matter (OM) present. Addition of OM to soils thus becomes important since decomposition of OM increases the humus content of the soil and thereby the capacity of the soil to hold nutrients. Organic matter is also very important in developing soil structure, which is important in reducing runoff, compaction and erosion.

The mineralogy of the soil is also an important determinant of CEC. Clay minerals are classified on the basis of the number and arrangement of silica and alumina-magnesia sheets contained in the crystal layers which make up the clay particles (Brady, 1984). Those having two silica layers sandwiching one alumina layer are termed 2:1-type clays and include montmorillonite. Those with one layer of silica alternating with one alumina layer are termed 1:1-type clays, of which kaolinite is most common. In general, montmorillonite may be present in soils which have not undergone extensive weathering processes. As weathering proceeds, montmorillonite gives rise to kaolinite-dominated soils. Under conditions of severe weathering, kaolinite may be weathered further to form oxides of iron and aluminum, such as are found extensively in the Amazon basin. The CEC of 2:1-type clays is higher than that of 1:1-type clays which in turn is higher than in Fe and Al oxides. Therefore, in general, highly weathered soils have lower CEC than soils which have undergone less weathering. Also associated with the weathering process is a decrease in pH so

that highly weathered soils are also very acidic.

The base status of a soil refers to the proportion of the CEC occupied by cations other than hydrogen or aluminum. Acid soils such as Oxisols and Ultisols are dominated by these two ions and are said to have a low base saturation (Sanchez, 1976). Because the CEC is saturated by hydrogen and aluminum, these soils have little capacity to retain other cations, referred to as bases, such as K, and therefore these nutrients are readily leached out of the upper soil horizons. Alkaline soils such as those developed over limestone parent material may have a high base saturation and are less susceptible to loss of nutrients by leaching. Furthermore, since these soils have not advanced as far along the weathering series they have higher CEC as well.

Based upon these fertility properties of soils, Jordan and Herrera (1981) have proposed two nutrient cycling strategies. An oligotrophic strategy is adopted by ecosystems that are based on highly weathered, highly acidic and very infertile soils such as the Oxisols of the Amazon basin. A eutrophic strategy may be found on nutrient-rich soils having high base saturation and high CEC. While nutrient leaching in eutrophic systems may not be great enough to affect vegetative development (Harcombe, 1977), in oligotrophic systems, many adaptations have been made by the vegetation to facilitate very efficient nutrient cycling. When the vegetation of oligotrophic systems is removed, leaching of nutrients, most of which were stored in the vegetative biomass, can be very severe (Jordan and Herrera, 1981). While these two categories are extremes on a continuum, it is important to keep them in mind when considering the role of nutrients in tropical ecosystems.

Fallow vegetation contributes to soil fertility in several ways. Throughout the fallow period, leaves and stem material fall as litter. Decomposition of this material restores OM levels in the soil thereby increasing CEC (Nye and Greenland, 1960). Root

growth and root exudates improve soil structure, loosening and stabilizing it (Sanchez, 1976), as well as providing an environment for soil organisms. The activity of soil organisms is important in decomposition processes and in improving soil structure (Brady, 1984).

Growth of fallow vegetation conserves nutrients in the agroecosystem by storing them in the biomass, thereby reducing potential loss by leaching. In this respect deep-rooted fallow species are able to recover nutrients which have been leached out of the rooting zone of crop species and thus play an important role in maintaining these nutrients in the system (Norman, 1979).

1.4.2 WEED MANAGEMENT

The term 'weed' will be used to designate any plant growing in an agricultural field which was not intentionally planted there. 'Weed control' refers to a reduction in the yield-reducing effects of weeds on crop plants. Weed control may be accomplished by the elimination of weeds, but it may also involve a reduction in the net yield-reducing effects of weeds by replacing more noxious weeds (those that have a large negative effect on yield) by species which are less problematic from an agricultural perspective.

Burning of fallow vegetation leaves the soil relatively free of weeds during the first year of cultivation (Ruthenberg, 1976; Uhl and Jordan, 1984; Lambert and Arnason, 1986). With subsequent use of the land however, weeds become more abundant, to the point where they may become the primary factor leading to the abandonment of the plot (Nye and Greenland, 1960; Ruthenberg, 1976). Sanchez (1976) suggested that while declining soil fertility may be the cause for abandonment of low base status soils, weeds are likely to be important on the more fertile high

base status soils.

Not all non-crop plants are equally detrimental to crop production. Rappaport (1971) noted that in New Guinea, shifting cultivators weeded out only herbaceous species; tree seedlings were protected as it was recognized that they played important roles in the eventual regeneration of the fallow. In Mexico, shifting cultivators utilize a terminology which recognizes both 'good' and 'bad' weed species, and selective weeding is carried out accordingly (Chacon and Gliessman, 1982).

Weeds may be beneficial to the traditional tropical agroecosystem in several ways. They provide a cover for the soil, thus reducing soil erosion (Moody, 1975), they retain nutrients in the agroecosystem (Lambert and Arnason, 1986) and deep-rooted species recover nutrients from depths beyond the rooting zone of the crop (Rappaport, 1971). Species of weeds may also alter the proportions of harmful and beneficial insects, and may offer potential in the management of more harmful weed species by less harmful ones (Chacon and Gliessman, 1982).

In spite of the contributions of weeds to the agroecosystem, weeds reduce crop yields and must be controlled (Moody, 1978). In systems of shifting cultivation, weeding is a very labour-intensive process, the only tools being the hoe or machete. Furthermore, the absence of a severely curtailed growing season such as winter as in temperate regions means that weed growth may continue all year. When the effort required to control weeds becomes greater than that required to shift to a new plot, the site is abandoned and a new site will be cleared (Sanchez, 1976). During the resulting fallow period weed control will proceed through a successional process in which herbaceous weeds and grasses are replaced by bush regrowth (Nye and Greenland, 1960).

1.4.3 CONSEQUENCES OF SHORTENED FALLOWS

Shortening the fallow and lengthening the cultivation period leads to increased weed problems. This is due to a shift in the weed population from successional forest tree species to rapidly reproducing herbs and grasses. If grasses take over, they may become very difficult to control. Burning does not destroy the underground rhizomes by which many grasses undergo extensive vegetative reproduction. Other plants such as bracken fern may similarly establish and inhibit the normal course of succession to secondary forest.

In Nigeria for example, bush fallow species gave way to herbs and grasses as cultivation periods were extended (Moody, 1975). If the land was abandonded at this point, the bush fallow re-established and control of weeds proceeded. However if cultivation continued, the succession of weed species proceeded through arable weeds and smaller grasses to bracken fern, which is very difficult to control. Saxena and Ramakrishnan (1984) found that short fallow cycles in N.E. India led to higher weed growth, as the succession was 'arrested' at a stage dominated by herbaceous species having high reproductive capabilities and produced seeds which remained viable in the seed bank until the next cropping period. In longer cycles, herbaceous species were replaced by bamboos and trees. Not only was the viable weed seed bank reduced, but the higher intensity of the burn due to the greater amount of fuel in these fallows was more effective in killing weeds at the start of the next cropping cycle. In Belize, Cayo District, Kellman and Adams (1970) found that the weed flora of fields under permanent agriculture consisted primarily of herbaceous species, many of which were of widespread geographical distribution (pan-tropical or pan-american). Fields under shifting cultivation contained weeds of more local distribution, many of which were woody species of the surrounding successional forest.

More intensive land use may lead to increased yields per unit area, however the consequence is that the regrowth of fallow vegetation will take longer, and the fallow period itself will be shorter (Ruthenberg, 1976). Thus the benefits of the fallow, both in terms of weed control and in soil conditioning will be reduced. The system then changes from a condition of 'balanced exploitation' to one of 'soil mining', and the labour required to maintain yields increases (Ruthenberg, 1976).

In order to gain a fuller understanding of the consequences of shortened fallows, a general understanding of the processes involved in vegetative succession in the tropics must be achieved.

1.5 TROPICAL SUCCESSION

Vegetation succession may be defined as the sequence of change following a disturbance (McIntosh, 1980). It is generally differentiated from fluctuation by qualifying that the change is directed, leading to a different 'type' of vegetation community (Miles, 1979). The wide range of tropical environments, from the humid lowland tropics through tropical and subtropical seasonally dry regions to tropical alpine ecosystems has led to a large variety of successional communities (Ewel, 1980), equally as diverse as the models of succession proposed to describe succession in temperate regions (see McIntosh, 1980 for review of these models).

Connell and Slatyer (1977) proposed three models to describe different processes that might occur during the revegetation of an area: the 'facilitation' model, the 'tolerance' model and the 'inhibition' model. In each case 'opportunist' species initially colonize the available space but are unable to reproduce in the presence of other individuals. Hence they are restricted to recently disturbed areas. The way in which these species are replaced is where the models differ. In facilitation, later

species can only grow after the early species have modified the environment in some way. The tolerance model suggests that later species can invade and grow to maturity in the presence of early species due to their ability to tolerate lower resource levels. The inhibition model suggests that the first species to arrive will resist invasions by later species and that these later species will only be able to reach maturity after the earlier species release resources upon their death or damage. These models shall be used as a loose framework within which to focus a brief description of several factors involved in secondary succession in the tropics.

Pomeroy (1970) has suggested that from the viewpiont of nutrient cycling, succession is a process through which early plant populations accumulate sufficient nutrients to allow the establishment of subsequent populations. Harcombe (1977) noted that the growth rates of the early successional species in the area he was investigating were relatively constant, rather than highly variable when varying levels of nutrients were available. While highly variable growth would be expected in plants that were adapted for the exploitation of sudden increases in the supply of available nutrients following forest removal, Harcombe (1977) suggested that a constant rate of growth is an adaptaion for the utilization of the slow but relatively reliable inputs of nutrients from soil weathering or from the atmosphere. Hence the rate and course of succession may be determined by the ability of plants to accumulate nutrients. As previously mentioned, Jordan and Herrera (1981) have emphasized that not all tropical forests are the same in their nutrient cycling characteristics and have differentiated oligotrophic systems based on very infertile soils from eutrophic systems based on soils richer in nutrients. The volcanic soils of the system that Harcombe (1977) studied would fall into this second group, so it is not surprising that he did not obtain a great response to nutrient additions in his study (Jordan and Herrera, 1981).

The consequence of the highly evolved adaptations of vegetation in oligotrophic systems to low soil fertility, as discussed earlier, is that while the amounts of biomass are similar in both oligotrophic and eutrophic systems, in oligotrophic systems practically all the nutrients are held in the biomass. Hence disturbance of an oligotrophic system would have a more severe effect on nutrient cycling than would a disturbance of a eutrophic system. In terms of the models of Connell and Slatyer (1977), we might consider that in an oligotrophic system opportunist species may facilitate growth of later species by preventing loss of nutrients from the system.

A second major factor influencing tropical succession is the means of reproduction. In the humid tropics, where there is abundant moisture and warm temperatures throughout the year, revegetation following disturbance arises predominantly from viable seeds already present in the soil prior to disturbance, or from seeds which have dispersed into the area following disturbance (Ewel, 1980). Provided that nutrients are sufficient, growth will be rapid due to favourable climatic conditions. Thus the 'window' for colonization will be narrow and the species composition of the resulting successional community will be determined to a large extent by the species which are able to contribute seed at the time of disturbance (Webb et al., 1972). In regions having a dry season the probability of successful regeneration from seed is lower and vegetative reproduction through coppicing becomes important (Ewel, 1980).

Succession in the humid tropics tends to proceed through a number of identifiable phases or 'seres', beginning with herbs and vines which commonly have seeds which can remain dormant in the soil for long periods of time, followed by light-loving shrubs and longer-lived herbs, then fast-growing pioneer trees and finally slow-growing, shade tolerant trees. Succession in the seasonally dry tropics is floristically simpler however, having fewer seral stages due to the rapid regrowth of

typically later successional species from shoots (Ewel, 1980).

Uhl and Jordan (1984), after a five year study of succession in an oligotrophic site in the Amazon basin, concluded that the tolerance model best described the process, in which late successional tree species were found to grow beneath the pioneer-dominated overstory, and continued to grow as the pioneer species senesced. In a study in Ghana, Swaine and Hall (1983) concluded that after five years of succession following the clearing of a forest, the only reason why forest species did not form a conspicuous part of the regrowth was due to their slow height growth, rather than to an inability to establish in the presence of earlier successional species. Again the tolerance model tends to fit this successional process better than the facilitation model does.

A third factor which may play an interesting role in tropical succession is the role of mycorrhizae. Janos (1983) suggested that changes in soil fertility and in the probability of mycorrhizal infection can influence succession. St. John and Coleman (1983) suggested that dependance on mycorrhizae will be greater in seedlings, which have not established extensive root systems nor nutrient reserves in tissues, than in mature individuals. Association with mycorrhizal fungi however does not come cheaply, and support of the fungus could require as high as 50% of the net photosynthate in some host plants (St. John and Coleman, 1983). It is clear that the relative competitive abilities of mycorrhizal vs. non-mycorrhizal plants will change as demand for and availability of nutrients varies. Janos (1980) distinguished three types of mycorrhizal associations. Obligate mycotrophs refer to those plants which commonly lack root hairs and hence rely on the fungus for mineral uptake. They are adapted to situations in which mineral availability, especially P availability is low. Because P diffuses poorly in soils, and is easily rendered unavailable, P depletion zones soon overlap around root hairs lowering their efficiency. In situations of low P

availability therefore, obligate mycotrophs should be generally most efficient. Non-mycorrhizal species should be favoured in situations where the probability of finding a mycorrhizal associate is low, since they have root hairs and can therefore out-compete mycotrophic species which lack their mycosymbiont. Areas which have undergone disturbance may have such a reduced availability of mycorrhizal fungi. Janos (1983) suggested that non-mycotrophs might be expected to have the demographic characteristics of fugitive species, able to exploit newly disturbed areas before mycotrophic species are able to establish their symbiotic association. The third group consists of facultative mycotrophs, species which retain root hairs but which may establish mycorrhizal associations in infertile soils. Their ability to grow in the absence of mycorrhizae allows them to establish in early successional stages, but due to the cost of maintaining root hairs, they will be less efficient than obligate mycotrophs in situations of low fertility. Janos (1983) suggests therefore that the condition of obligate mycotrophy will predominate in mature forest canopy and sub-canopy tree species while the facultative and non-mycorrhizal condition should be most common in earlier successional stages. The impact of cutting and burning on mycorrhizal fungi may therefore have a considerable effect on the following succession (Toky and Ramakrishnan, 1983b).

1.6 OBJECTIVES

This study was initiated within the context of a long-term study beginning in 1976 and carried out by the Ottawa-Carleton research group, documenting the nature and problems of small farm agriculture in Belize, Central America. Studies on mineral cycling in tropical hardwood forests (Lambert et al., 1980; Arnason and Lambert, 1982a) and tropical palm forests (Arnason and Lambert, 1982a; Arnason et al., 1984) used for shifting agriculture, indicated that substantial nutrient reserves were

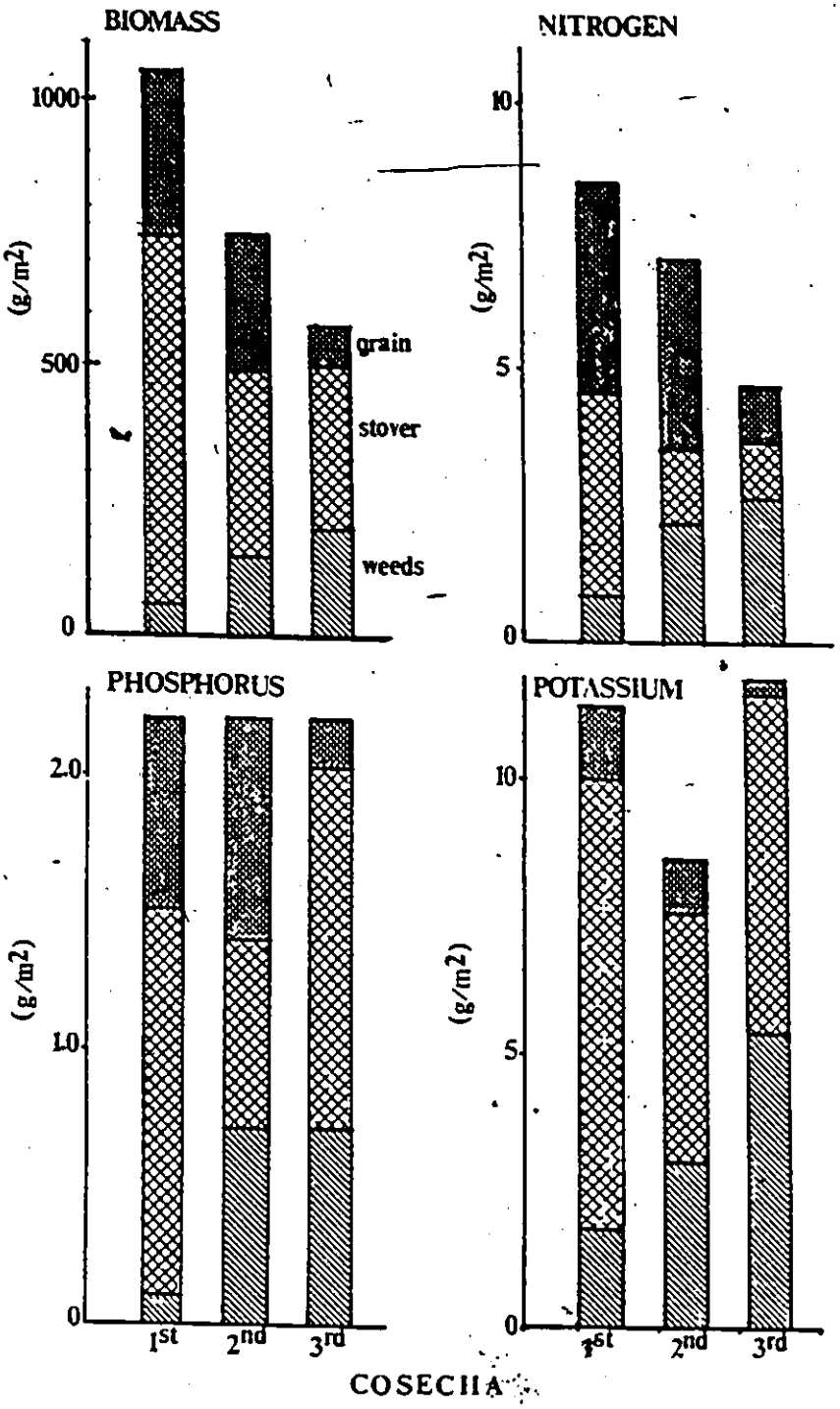
accumulated in the biomass of these forests before they were cleared and burned for milpa production. Although both forest associations developed over soils having similar nutrient status, the palm forest accumulated greater biomass and more nutrients than the hardwood forest. Phosphorus and Na concentration were higher in palm forest biomass while K concentrations were lower than in the hardwood forest. The high nutrient reserves of the palm forest explained why this association was preferred by local milpa farmers.

During a three year period of milpa cultivation initiated at Indian Church, a region that had not been cultivated intensively for 30–40 years, no decline in available nutrients was detected (Lambert and Arnason, 1986). Nitrogen and OM in the milpa soils rapidly reached equilibrium at lower levels than in the soils of the surrounding forest, but these levels were maintained throughout the three years. In spite of maintained soil fertility, yields of maize declined by 70% between the second and third cropping seasons. At the same time, weed biomass and nutrients, especially N, contained in the weeds increased each year (Fig. 4). Reduction in crop yield was therefore considered to be due to increased competition against weeds for nutrients. While N was considered to be the most critical nutrient in the short term, P was found to be more critical in areas which had undergone prolonged periods of milpa cultivation. Comparison of nutrients in crop plants and soils from Succotz, where milpa farming had been carried out since the Mayan period, with those from Indian Church indicated that available P was depleted in soils from Succotz (Arnason et al., 1982b). Yields at Succotz were less than half those obtained at Indian Church (800 $kgha^{-1}$ and 1700 $kgha^{-1}$ respectively).

The composition of the weed population at Indian Church was also examined and was found to shift from herbaceous species to woody species during the three year cropping period (Lambert and Arnason, 1986).

Fig.4. Allocation of Biomass and Nutrients During Cropping at Indian Church, Belize.

(data from Lambert and Arnason, 1986)


BIOMASS
NITROGEN
PHOSPHORUS
POTASSIUM
(g/m2)
1000
500
0
10
5
2.0
1.0
grain
stover
weeds
1st
2nd
3rd
COSECHA

As a continuation of this earlier work, the objective of the present study was to provide an insight into the role of the natural bush fallow in the shifting cultivation system as practiced at Succotz. Details of the early stages of secondary succession were also studied in order to increase our understanding of the basic ecology of the fallow, as well as contributing toward a general understanding of tropical succession.

Specifically, the rate of accumulation of nutrients by fallow vegetation was to be estimated, plant species that were most important during the early stages of fallow succession identified, and changes in plant lifeform groups during the succession measured. The identification of individual species able to accumulate high concentrations of nutrients was also carried out. This information was to be used in determining and evaluating appropriate fallow management strategies. A knowledge of the total nutrient accumulation by natural fallow vegetation after a defined period of time provides a baseline against which alternative fallow management strategies can be compared in the future.

METHODS

2.1 FIELD WORK

2.1.1 STUDY SITE

The study site was located at the village of San Jose Succotz, Belize in the semi-evergreen seasonally dry forest zone of Central America, located at 17°05' N, 89°08' W (Fig. 3). Average annual rainfall is 1300 mm with a dry season from January to the end of May, and a period of reduced rainfall in August. The landscape is hilly and undulating with a maximum elevation of 200 m. Soils are Rendolls of the Mollisol order and have been classified by Wright et al, (1959) as belonging to the Cuxu suite, developed over Cretaceous limestone. Field work was carried out from May to August, 1985 with the aid of three men from the village; Feliz Uck, Lelo Uck and Mirto Uck.

2.1.2 SELECTION OF FALLOW SITES

A total of fifteen sites which had previously been used for milpa farming and then left fallow for one, two or three years were located within walking distance of the village. The ages of these fallow sites, or 'guamiles' as they are locally called, were determined with the assistance of Feliz Uck, a local milpa farmer, and through conversations with the owners who had previously cultivated the sites. Because there

is a uniformity in the agricultural cycle practiced by the milperos of Succotz it was possible to establish with a high degree of confidence the age and general land use history of the sites. Those sites which had been used for a second cosecha crop during the wet season of 1982 and abandoned in September of that year contained weed growth which had begun to grow the previous May, following the last burn. These sites made up the 3 year old sites. Similarly 2 year old sites had been abandoned in 1983 and one year sites were those which had been abandoned in September of 1984. As the 1985 wet season was unusually dry, growth during this season was slow and therefore variation due to different sampling dates was not expected to be very important.

Sites of different ages belonging to one milpa farmer were sampled first, before beginning those of a different milpero. An attempt was made to select only those sites which had similar cropping histories. To this end sites which had been cropped for two consecutive years, thus having two cosechas were selected when possible. Although sites having only one cosecha were used if insufficient two-cosecha sites were available, in no case was a site that had a yaxking (dry season) crop used. No attempt was made to select only lowland sites or only those on hillsides since there were not enough sites close to the village to allow such selectivity.

2.1.3 SAMPLING OF SOILS

At each site three soil samples were taken at 0-15 cm and 15-30 cm depth using a soil auger. The samples for each depth were pooled and sent to Dr. Marla Holden at the Belize Central Agricultrual Farm where they were analyzed for N, K, pH, organic carbon (OC) and cation exchange capacity (CEC).

2.1.4 SAMPLING OF FALLOW VEGETATION

At each site a machete was used to cut a straight 40 m path from one side of the fallow toward the centre. Three plots were located 3 m in from this access path on alternating sides, at 10 m, 25 m, and 40 m. This systematic sampling approach was chosen over a random method due to the difficulty of movement through the densely tangled vegetation of the fallows. A systematic approach ensured that experimenter bias was not a factor influencing the location of plots and thereby the results obtained.

At each plot vegetation less than 3 m in height was sampled by establishing a 4 m^2 quadrat. A rectangular quadrat with dimensions 1.3 m X 3.0 m was chosen to reduce between-plot variability due to clumping of vegetation sprouting from stumps. Vegetation greater than 3 m in height was sampled by expanding the initial quadrat to 2.0 m X 6.0 m, forming a 12 m^2 quadrat. In this larger quadrat both trees and their associated lianas were sampled.

In each quadrat vegetation was removed at ground level and separated according to species. Feliz Uck's considerable knowledge of the local flora was very useful at this point. Leaves were removed from stems and both components weighed, either in the field with a spring balance or back in the village using a triple beam balance when quantities were less than 350 g (the lowest weight for which the spring balance was reliable). Subsamples were then taken for later determination of dry weight and nutrient content. Species occurring in only small amounts were pooled according to lifeform. Voucher specimens were collected to allow the identification of species.

2.2 ANALYSIS OF PLANT MATERIAL

2.2.1 DRY WEIGHT DETERMINATION

Samples from the field were stored in open paper bags. Once a week these were taken to the Belize Central Agricultural Farm where they were dried in a forced air oven at 60°C for 48–72 hr. After drying, the samples were kept in large air–tight plastic bags and transported back to Succotz where dry weight was measured with a triple–beam balance. All samples were sent by air to Carleton University (Ottawa, Canada) for nutrient analysis.

2.2.2 IDENTIFICATION OF SPECIES

Plant specimens were identified using the 'Flora of Guatemala' (e.g. Standley and Steyermark, 1946), and herbarium collections at Central Farm and at the University of Ottawa as references. Collection numbers were assigned and these specimens were deposited with the Ottawa–Carleton herbarium collections. While family names are used as in the Flora of Guatemala, it should be noted that in more recent classifications, 'Compositae' is covered by the family Asteraceae, 'Gramineae' by the family Poaceae and the family 'Leguminosae' is often treated as three families: Caesalpiniaceae, Mimosaceae, and Papilionaceae or Fabaceae.

All species were assigned to one of seven lifeform categories: grass/sedge, herb, herbaceous vine, woody vine, shrub, tree, or 'other'. In the following text the term 'weak shrub' will occasionally be used to designate shrub species having only partly lignified stems.

2.2.3 NUTRIENT ANALYSIS

2.2.3.1 Preparation of Plant Material

The dried plant samples were ground in a Wiley mill at the grain quality lab at Agriculture Canada in Ottawa during the fall of 1985 and stored in plastic vials. For K and P determinations 0.500 ± 0.005 g quantities of each sample were ashed at 500°C for 12 hr in a muffle furnace. The ash was digested with 5 ml of 6 N HCl for 2 hr. This digest was then poured into labelled nalgene bottles, the crucibles rinsed twice with 5 ml and once with 10 ml of distilled water, and finally the solution was diluted to 50 ml by adding an additional 25 ml of distilled water. These solutions were subsequently used for P and K determinations.

2.2.3.2 Nitrogen Determination

Nitrogen analysis was performed at the grain quality lab at Agriculture Canada using an automated kjehldahl N analyser manufactured by 'Kjeltec'. 0.500 ± 0.005 g samples were weighed out onto 'Kjelfoss' N-free paper, digested in boiling sulphuric acid with two selenium 'Kjeltabs' as a catalyst for 55 min. Total N was then determined and expressed as a percentage of the dry material.

2.2.3.3 Phosphorus Determination

Phosphorus was determined using a colorimetric method after Olsen and Dean (1965). In this method 0.25 ml of sample was added to 5.0 ml of 0.5 M sodium bicarbonate (pH=8.5), 2.3 ml of 1.0 N HCl and 13.45 ml distilled water. To this was added 4.0 ml of a solution containing 1.056 g ascorbic acid dissolved in 200 ml of a previously prepared reagent consisting of 8.0 g ammonium molybdate in 250 ml distilled water, 0.2908 g antimony K tartrate dissolved in 100 ml distilled water, both added to a solution containing 431 ml concentrated HCl and made to 1000 ml final solution. Phosphorus standards were similarly prepared. After 10 min. a light blue

colour developed and absorbance was measured at 820 nm, and phosphorus determined from a standard curve.

2.2.3.4 Potassium Determination

Potassium was measured using a Perkin-Elmer 703 atomic absorption spectrophotometer. The digests from 2.2.3.1 were appropriately diluted and read against a standard of 2.00 and 7.00 ppm K. This resulted in an expression for K as a percentage of dry plant weight.

2.2.4 MEASURMENT OF ERROR

In the field the spring balance had an error of ± 50 g associated with its readings. While this resulted in a large error when weighing quantities as low as 350 g (14% error), generally quantities wieghed were in the range of 550 to 1200 g, so that the average weighing error in the field would be ± 5%. The precision of the triple beam balance as used for obtaining wet weights was ± 0.5-2% depending on the quantity weighed. Greater care was taken when weighing dried material so the the precision was ±0.05 g or about 0.5%.

Replication of N analysis was 10% and indicated an error term associated with this analysis of 0.02 ± 0.006%. For P and K analysis 2.5% replication was done. The error terms associated with these analyses were 0.0015 ± 0.0007% and 0.032 ± 0.016% for P and K respectively.

2.3 DATA ANALYSIS

Values obtained for dry weight, N, P and K contents, the part of the plant analysed (leaf or stem or combined leaf and stem), the lifeform category of the species and

the site and plot within the site from which the sample was taken, along with the species name, were entered in a data file to be sorted and analyzed by the Statistical Analysis Systems package of programs (SAS, 1982). The NPAR1WAY procedure was used to provide a non-parametric test (Kruskal-Wallis) for differences in biomass and nutrient content between fallows of different ages. The UNIVARIATE procedure was used to provide descriptive statistics for total biomass and nutrients as well as for the allocation of biomass and nutrients by plant lifeform type. These statistics were used to produce 'box-and-whisker' plots of the quantiles and extreme values after Tukey (1977), and provided a convenient illustration of the variability among the various fallow sites. The GLM procedure, using a nested ANOVA model with the MEANS option was used to test for pair-wise differences between ages and between lifeforms within ages. This procedure was also used to analyse nutrient concentrations of individual species.

RESULTS

3.1 PHYSICAL DESCRIPTION OF STUDY SITES

All fifteen sites examined in this study were located within three kilometers of the village of Succotz. Locations of each site are indicated in Fig. 5. Due to the undulating landscape, sites varied considerably in slope, aspect and elevation. These factors are listed for each site in Table 1, along with the number of years since the last harvest and the number of rainy season harvests ('cosechas') in the previous cropping cyle. All sites had undergone two consecutive cosechas except sites 'F' and 'O', which had only one.

Results of soil analysis are presented in Table 2. No significant differences in any measured parameter were found by an ANOVA at the 95% level, with respect to the age of the sites from which the samples were taken. Important trends are however evident from the data, even though variation among sites was large. In particular, OC appears to increase with fallow age. K and N also appear to increase with fallow age.

3.2 ACCUMULATION OF BIOMASS AND NUTRIENTS BY FALLOW VEGETATION

Total above-ground biomass averaged over the fifteen plots of the five one year old sites was 630 $g \cdot m^{-2}$ (dry weight). Two year old sites averaged 1200 $g \cdot m^{-2}$, and three year sites averaged 2070 $g \cdot m^{-2}$ (Table 3). Nitrogen accumulation was 5.8 $g \cdot m^{-2}$, 7.3 $g \cdot m^{-2}$ and 10.3 $g \cdot m^{-2}$ for one, two and three year old sites

Fig.5. Location of Fallow Sites

Note: Letters refer to sites as described in Table 1.

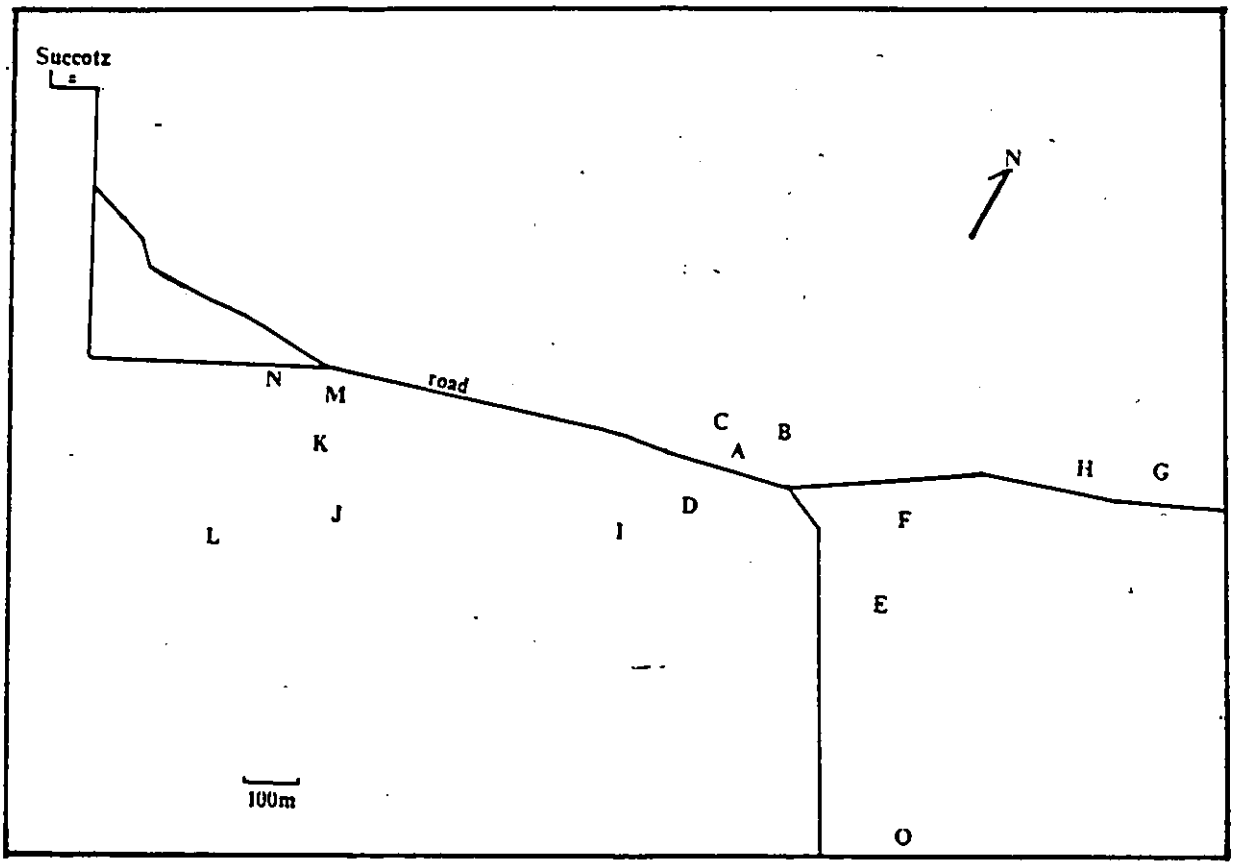

Succotz
N
road
N
M
K
J
L
C
A
B
D
I
F
H
G
E
O
100m

Table 1. Physical Aspects of Study Sites

Age (years)	Site	Site Location	Slope	Aspect	Harvest History
1	A	midslope	level	——	two cosechas
	E	hilltop	steep	SW	two cosechas
	H	hilltop	moderate	S	two cosechas
	K	lowland	level	——	two cosechas
	O	hilltop	moderate	N	one cosecha
2	B	hilltop	moderate	S	two cosechas
	D	lowland	level	——	two cosechas
	F	hilltop	steep	NW	one cosecha
	M	lowland	level	——	two cosechas
	N	lowland	level	——	two cosechas
3	C	midslope	level	——	two cosechas
	G	hilltop	slight	SW	two cosechas
	I	midslope	level	——	two cosechas
	J	lowland	level	——	two cosechas
	L	midslope	slight	E	two cosechas

Table 2. Soil Physical Properties

Age (years)	Depth (cm)	pH	Nitrogen (%)	Potassium (ppm)	O.C. (%)	C.E.C. (meq/100g)
1	0-15	7.4 (0.69)	0.31 (0.10)	327 (72)	3.30 (1.06)	54.2 (16.3)
	15-30	7.3 (0.87)	0.20 (0.08)	299 (105)	2.14 (0.82)	47.1 (23.5)
2	0-15	7.6 (0.46)	0.29 (0.10)	335 (54)	3.58 (1.07)	59.3 (11.9)
	15-30	7.2 (0.93)	0.22 (0.12)	285 (110)	2.36 (1.22)	50.4 (18.8)
3	0-15	7.7 (0.30)	0.47 (0.14)	367 (55)	4.86 (1.43)	55.6 (7.9)
	15-30	7.6 (0.68)	0.32 (0.15)	342 (81)	3.52 (1.47)	50.7 (10.5)

Note: Values are the mean of 4 samples with standard deviation indicated in brackets.

Table 3. Biomass and Nutrient Content in Above-ground Fallow Vegetation

Age (years)	Part	Biomass (g/m^2)	Nitrogen (g/m^2)	Phosphorus (g/m^2)	Potassium (g/m^2)
1	L	230^{x}	3.9^{x}	$0.22^{x,y}$	4.0^{x}
	S	400a	1.9a	0.17a	5.3a
	Total	630_1	5.8_1	0.39_1	9.3_1
2	L	240^{x}	$3.9^{x,y}$	0.20^{x}	3.4^{x}
	S	960b	3.4b	0.28b	7.7b
	Total	1200_2	7.3_1	0.48_1	$11.1_{1,2}$
3	L	350^{y}	4.9^{y}	0.26^{y}	4.7^{y}
	S	1720c	5.4c	0.47c	8.5b
	Total	2070_3	10.3_2	0.73_2	13.2_2

Note: L=leaf S=stem

Figures represent mean values for fifteen plots, three in each of five different sites. Results of Duncan's test are indicated using the suffixes x,y,z for leaf, a,b,c for stem and 1,2,3 for totals. Means within these categories having different suffixes are significantly different ($p=0.05$).

respectively, while P accumulation was 0.39 $g \cdot m^{-2}$, 0.48 $g \cdot m^{-2}$, and 0.73 $g \cdot m^{-2}$, and K accumulation was 9.3 $g \cdot m^{-2}$, 11.1 $g \cdot m^{-2}$ and 13.2 $g \cdot m^{-2}$. The Kruskal–Wallis test was used to test for significant differences due to site age. The effect of age on biomass, N, P and K was significant at the p=0.05 level.

Considering leaf and stem components of the vegetation separately, allocation of biomass and nutrients to stem material increased in two and three year old sites as compared to one year sites, while allocation to the leaves did not increase significantly after the first year (Fig 6). Analysis of the leaf data by the Kruskal–Wallis test failed to reject the null hypothesis of no difference between ages for biomass, N, P or K at the p=0.05 level of significance. Stem biomass on the other hand underwent exponential increase as described by the equation:

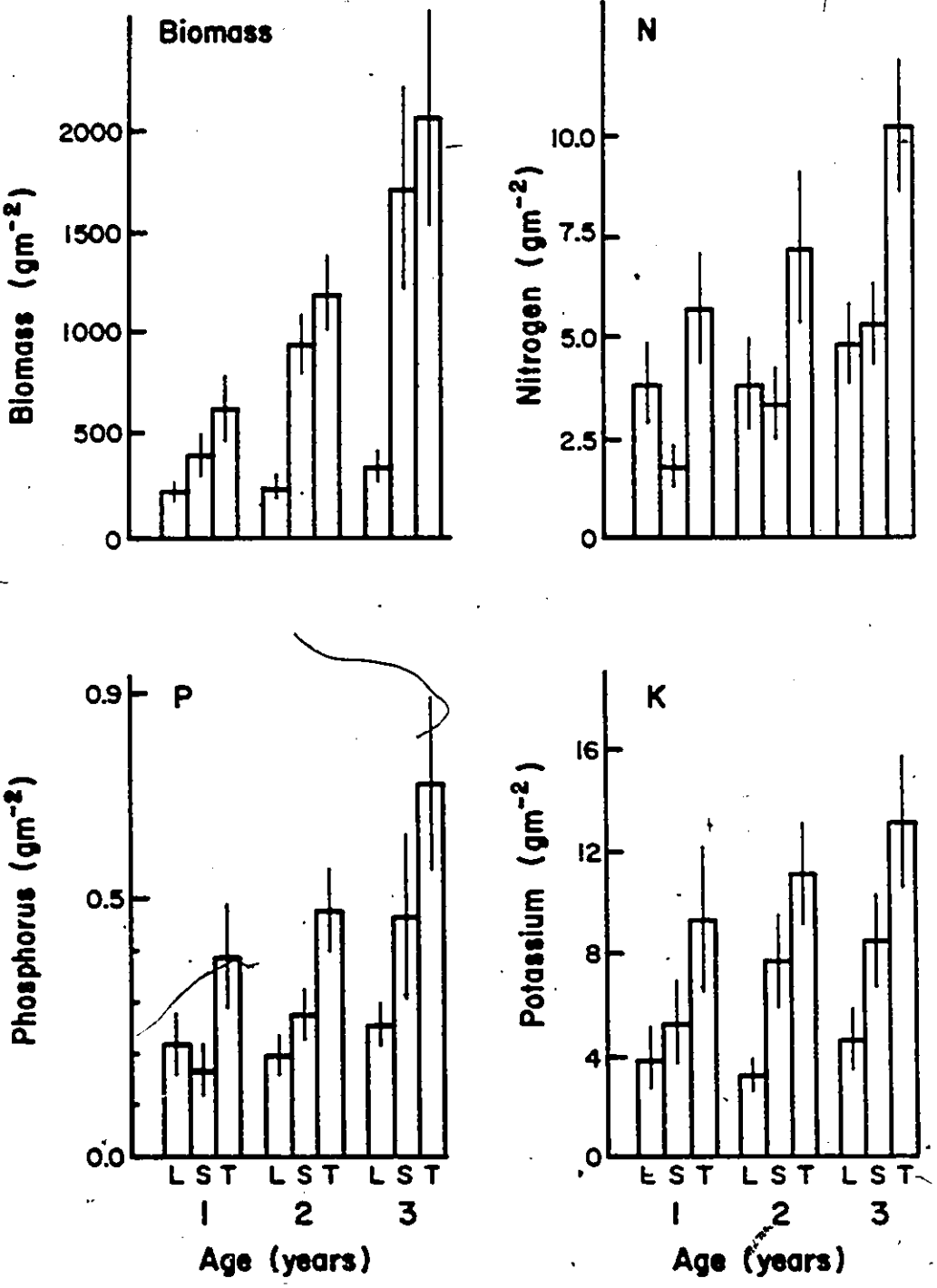
$$y = e^{(kt+c)} \quad r=0.83. \qquad \text{Eqn.2.}$$

where y is stem biomass, k is a rate constant equal to 0.77 $g \cdot m^{-2} yr^{-1}$ and c is a constant equal to 5.13 $g \cdot m^{-2}$. Accumulation of nutrients in stem material did not fit this exponential equation. There was a significant increase in N and P at the p=0.05 level (Kruskal–Wallis test), however K did not increase significantly. In Table 3 means for leaf, stem and combined leaf and stem data ('Total') can be compared between ages. Within a category, means having different letters are significantly different at the p=0.05 level on the basis of Duncan's Multiple Range test. It should be noted that this test is a somewhat liberal test.

As illustrated in Fig. 6, leaves accounted for a larger proportion of total nutrient stocks, especially N and P, than they did for biomass. With reference to the data in Table 3, leaves in one year old sites accounted for 37% of total biomass, while they contributed 68% of the N, 57% of the P and 44% of the K.

Fig.6. Accumulation of Biomass and Nutrients in Leaves and Stems During Fallow Development

Note: Bars indicate 95% confidence intervals for the mean of the values from 15 plots of each age. N=nitrogen, P=phosphorus K=potassium, L=leaf, S=stem and T=total.


Biomass
Biomass (gm⁻²)
2000
1500
1000
500
0
N
Nitrogen (gm⁻²)
10.0
7.5
5.0
2.5
0
P
Phosphorus (gm⁻²)
0.9
0.5
0.0
K
Potassium (gm⁻²)
16
12
8
4
0
L S T L S T L S T
1 2 3
Age (years)

The range of values found in the 15 plots for each age may best be illustrated by the use of 'box-and-whisker' plots (Tukey, 1977) as found in Fig. 7. In such figures the median value falls on the line running through the box. The upper limit of the box represents the seventy-fifth percentile, the lower limit represents the twenty-fifth percentile and the lines extending from the box show the extreme plot values. These are labelled by the site in which they occurred. It is evident from these figures that site 'J' had considerably higher biomass and nutrient levels in two plots than was usual for three year old sites. Actual values for each plot are presented in Appendix 1.

An analysis of variance, nesting the effects of the three plots within the five sites in each age group indicated that differences in the age of fallows accounted for the largest portion of the total variation in biomass, but that variation between sites and between plots within a site accounted for more variation in nutrient levels (Table 4). This was especially the case for K, in which only 5.3% of the total variation could be accounted for by age.

Annual rates of increase for biomass and nutrients between the final burning of the milpa before abandonment and the first year of fallow, between the first and second years of fallow, and between the second and third year of fallow succession may be estimated if it is accepted that biomass and nutrient levels immediately after the burn are zero and that the rate of accumulation of biomass and nutrients for a one year old site were the same in 1982, the year the three year old sites were burned and left to fallow, as they were in 1983 (beginning of two year sites) and in 1984 (the beginning of one year sites). These are summarized in Table 5. Although these assumptions are likely to be only approximately true, it becomes evident that accumulation of biomass and nutrients in the leaf component occurred to the greatest extent during the first year following abandonment. Stem biomass,

Fig.7. Box-and-Whisker Plots for Accumulation of Biomass and Nutrients in Vegetation with Increasing Fallow Age

Note: Figures represent data from fifteen plots of each age. Letters indicate the sites from which extreme values occurred. The '+' indicates the mean values while the box delineates the quartiles as explained in the text (Sec. 3.2).

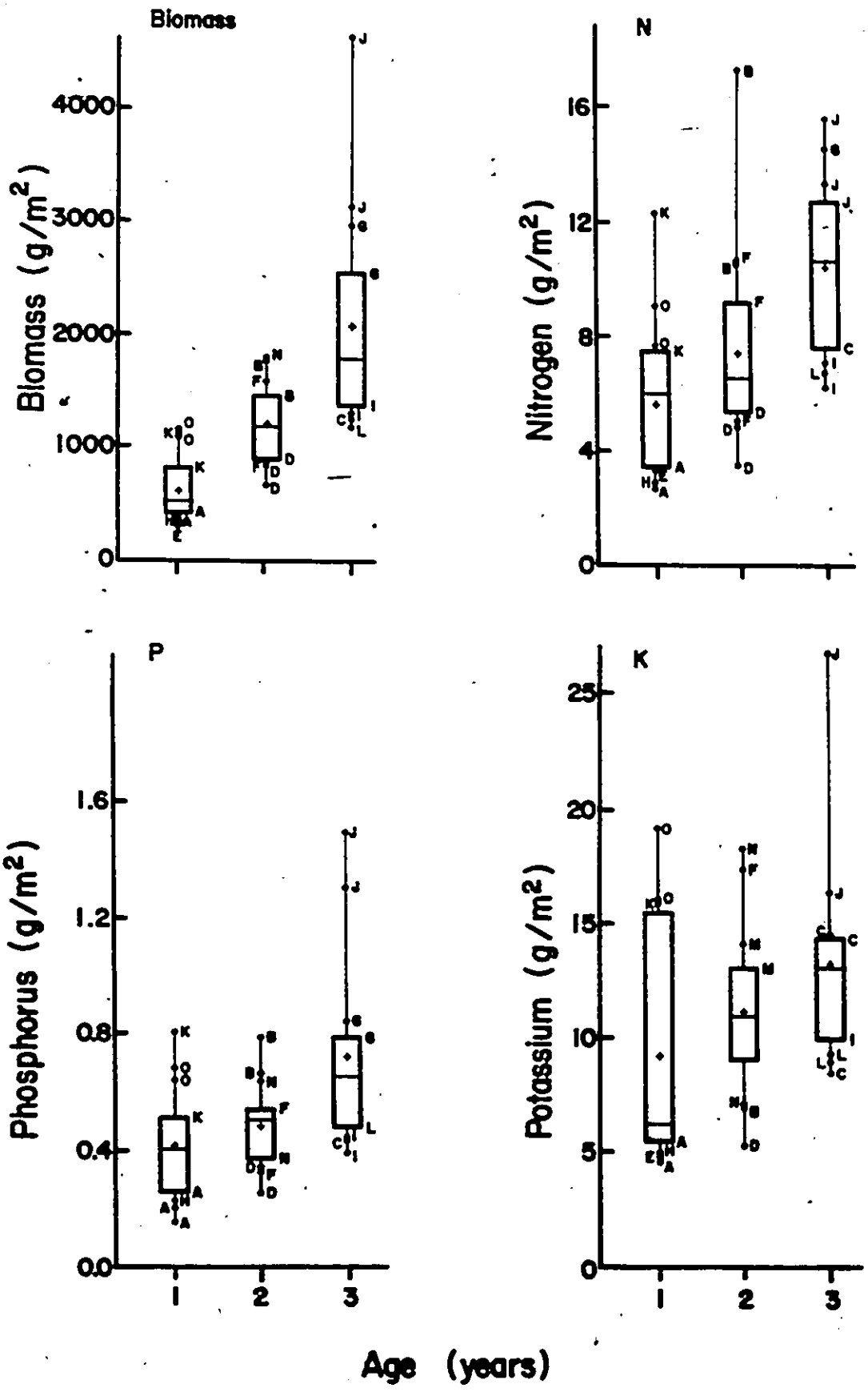

Biomass
Biomass (g/m²)
4000
3000
2000
1000
0
N
Nitrogen (g/m²)
16
12
8
4
0
P
Phosphorus (g/m²)
1.6
1.2
0.8
0.4
0.0
K
Potassium (g/m²)
25
20
15
10
5
0
1
2
3
Age (years)

Table 4. Sources of Variation for Total Biomass and Nutrient Accumulation

Source of Variation	Percent of Total Variation			
	Biomass	Nitrogen	Phosphorus	Potassium
Age	55.0	29.6	24.7	5.3
Site within age	26.1	32.8	49.0	42.3
Plot within site	18.9	37.6	26.3	52.4

Variation as determined by ANOVA.

Table 5. Rates of Accumulation for Biomass and Nutrients During the First Three Years of Fallow Succession

Part	Interval (years)	Biomass ($g/m^2/y$)	Nitrogen ($g/m^2/y$)	Phosphorus ($g/m^2/y$)	Potassium ($g/m^2/y$)
Leaf	0-1	230	3.9	0.22	4.0
	1-2	10	0	-0.02	-0.6
	2-3	110	1.0	0.06	1.3
Stem	0-1	400	1.9	0.17	5.3
	1-2	560	1.5	0.11	2.4
	2-3	760	2.0	0.19	0.8
Total	0-1	630	5.8	0.39	9.3
	1-2	570	1.5	0.09	1.8
	2-3	870	3.0	0.25	2.1

Note: Total nutrients in the leaves of two year old fallows were equal to or less than in one year old sites, hence zero and negative values were obtained for the rate estimates.

accumulated at an increasing rate during the first three years of succession. Nitrogen and P accumulation in stem material remained approximately constant during this period while the rate of K accumulation decreased considerably with time.

3.3 SUCCESSIONAL TRENDS IN FALLOW VEGETATION

3.3.1 TRENDS IN LIFEFORM COMPOSITION

Within the first year after a burn, the most important contributors to biomass and nutrient stocks in the vegetation were already shrubs and trees. In one year old sites each of these components accounted for approximately 33% of the total biomass, N, P and K (Tables 6a–d). Shrubs accounted for somewhat more K (40%) and trees accounted for slightly more N (38%) and P (37%) than indicated by their biomass. Woody vines accounted for 14% of the biomass in one year old sites. Thus in only one year, 80% of the biomass and a corresponding proportion of N, P and K was accumulated by woody perennials. Among first year sites, much of the woody regrowth was observed to arise from roots which had survived the burn. Although the relative importance of shoot regeneration compared with establishment from seed sources was not quantified, shoot regeneration was very common and appeared to be an important means by which post-burn colonization occurred. Herbs, herbaceous vines, grasses and sedges accounted for only 16% of the total biomass as a group, in one year old sites. Other lifeforms, ferns and palms, accounted for the remaining 4% of the biomass.

By the second year of fallow growth, trees began to dominate, accounting for nearly 70% of the total biomass. The herbaceous lifeforms decreased significantly

Table 6a. Allocation of Biomass by Lifeform in g/m^2

Lifeform	Age (years) 1	2	3
Grass/Sedge	12^{1}_{a}	$7^{1,2}_{a}$	1^{2}_{a}
Herbs	54^{1}_{ab}	24^{2}_{a}	2^{2}_{a}
Herbaceous vines	$32^{1}_{a,b}$	5^{2}_{a}	5^{2}_{a}
Woody vines	90^{1}_{b}	160^{2}_{b}	250^{3}_{b}
Shrubs	210^{1}_{c}	220^{1}_{b}	200^{1}_{b}
Trees	210^{1}_{c}	780^{2}_{c}	$1{,}600^{3}_{c}$
Total	630	1,200	2,070

Note: Values are means from fifteen plots in each age category. Means within a row with different superscript show significant differences between ages (Duncan's multiple range test, $p=0.05$). Means within a column having different subscripts show significant differences between lifeforms within an age group.

Table 6b. Allocation of Nitrogen by Lifeform in mg/m^2

Lifeform	Age (years) 1	2	3
Grass/Sedge	90^{1}_{a}	$40^{1,2}_{a}$	10^{2}_{a}
Herbs	420^{1}_{ab}	150^{2}_{a}	10^{2}_{a}
Herbaceous vines	$390^{1}_{a,b}$	50^{2}_{a}	40^{2}_{a}
Woody vines	840^{1}_{b}	$1,200^{2}_{b}$	$1,700^{2}_{c}$
Shrubs	$1,700^{1}_{c}$	$1,000^{2}_{b}$	870^{2}_{b}
Trees	$2,200^{1}_{c}$	$4,800^{2}_{c}$	$7,600^{3}_{d}$
Total	5,800	7,300	10,300

Note: Explanation as in Table 6a.

Table 6c. Allocation of Phosphorus by Lifeform in mg/m^2

Lifeform	Age (years)		
	1	2	3
Grass/Sedge	8^{1}_{a}	$4^{1,2}_{a}$	1^{2}_{a}
Herbs	32^{1}_{a}	9^{2}_{a}	1^{2}_{a}
Herbaceous vines	26^{1}_{a}	3^{2}_{a}	3^{2}_{a}
Woody vines	59^{1}_{a}	$72^{1,2}_{b}$	97^{2}_{b}
Shrubs	120^{1}_{b}	84^{1}_{b}	77^{1}_{b}
Trees	150^{1}_{b}	310^{2}_{c}	540^{3}_{c}
Total	390	480	730

Note: Explanation as in Table 6a.

Table 6d. Allocation of Potassium by Lifeform in mg/m^2

Lifeform	Age (years) 1	2	3
Grass/Sedge	160^{1}_{a}	40^{2}_{a}	2^{2}_{a}
Herbs	860^{1}_{a}	$450^{2}_{a,b}$	4^{3}_{a}
Herbaceous vines	510^{1}_{a}	5^{2}_{a}	4^{2}_{a}
Woody vines	$1{,}200^{1}_{a}$	$1{,}200^{1}_{b}$	$1{,}800^{1}_{b}$
Shrubs	$3{,}700^{1}_{c}$	$2{,}400^{2}_{c}$	$2{,}000^{2}_{b}$
Trees	$2{,}600^{1}_{b}$	$6{,}800^{2}_{d}$	$9{,}300^{3}_{c}$
Total	9,300	11,100	13,200

Note: Explanation as in Table 6a.

between first and second year fallows, while shrubs maintained their biomass at the same level as in first year sites and woody vines increased. In three year old sites trees were clearly the dominant lifeform, accounting for nearly 80% of the total biomass. Herbaceous lifeforms were almost completely eliminated while woody vines had again increased. Shrubs continued to maintain their biomass in three year sites although the nutrients allocated to this lifeform decreased. Comparisons between means of the various lifeforms within age categories and between ages within life-form categories are indicated in Tables 6a-d using Duncan's Multiple Range Test to test for significant differences. Trends and variation for biomass, N, P and K for each lifeform are illustrated using box-and-whisker plots in Figs 8a-d. These plots have been described previously in section 3.2. It should be noted that the vertical scale is not the same for each component.

3.3.2 TRENDS IN SPECIES

Species which were identified at least to genus are listed in Appendix 2. Because species diversity in all sites was high, it was difficult to determine species of major importance. However some species were clearly more important than others on the basis of their biomass and frequency. Consequently importance values were assigned to species by summing their relative biomass and relative frequency. The top 20 species for each age group are listed by lifeform in Table 7. Using this method of ranking, a species which exhibited complete dominance in all sites of a particular age would have a score of 200. If two species were each found in all sites with equal biomass, each would have an importance value of 100.

In one year old sites, a weak shrub (Coll. no.215), a herb Eupatorium odoratum and the herbaceous vine Bidens squarrosa were found to be the most important. The trees Trema micrantha, Psychotria grandis and Thevetia ahoui and Coll. no. 215

Figs. 8a–d. Box-and-Whisker Plots for Allocation of Biomass and Nutrients by Plant Lifeforms with Increasing Fallow Age

Note: Figures as explained for Fig. 7.

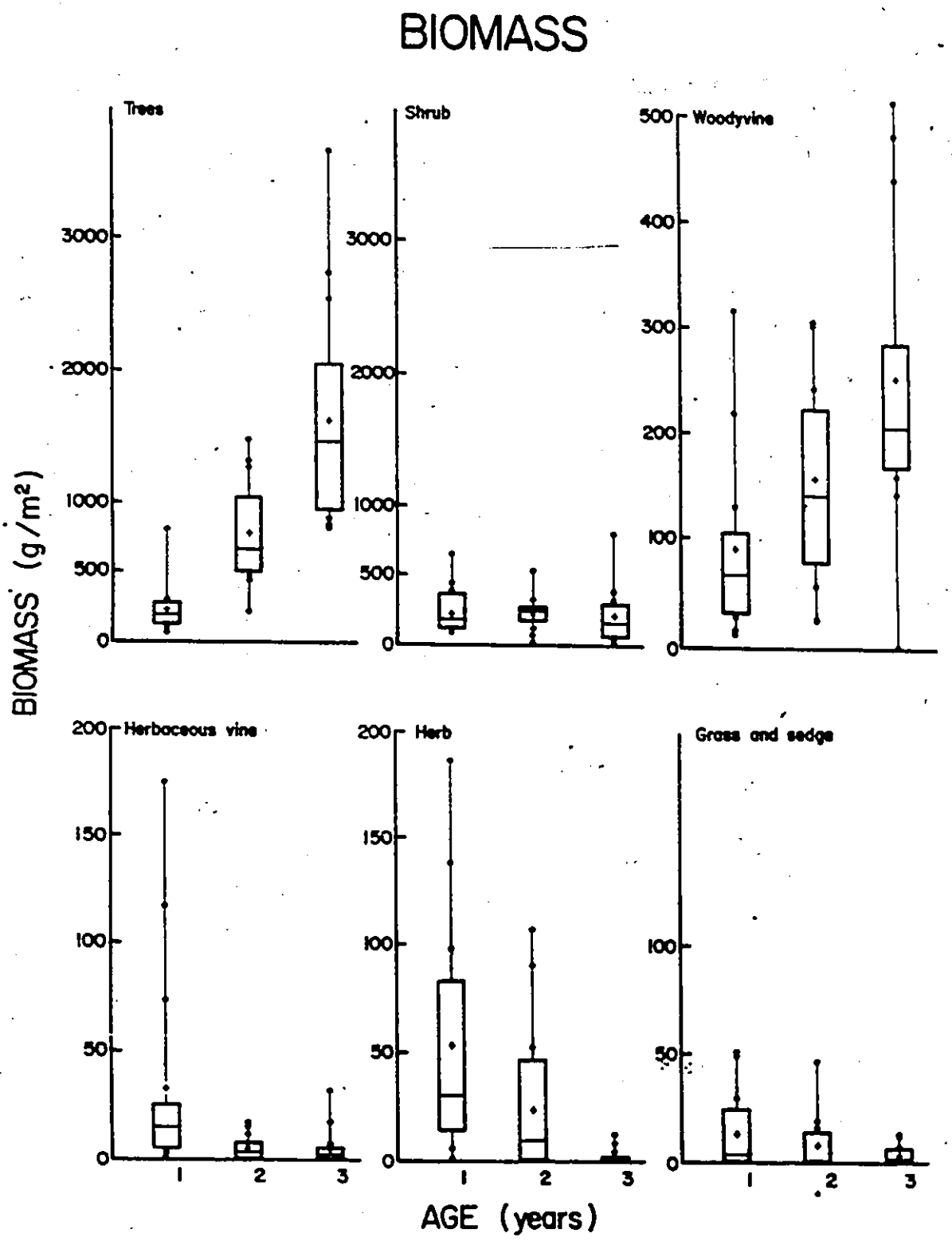

BIOMASS
Trees
Shrub
Woodyvine
Herbaceous vine
Herb
Grass and sedge
BIOMASS (g/m²)
AGE (years)
0
500
1000
2000
3000
100
200
300
400
50
150
1
2
3

Fig. 8a

NITROGEN

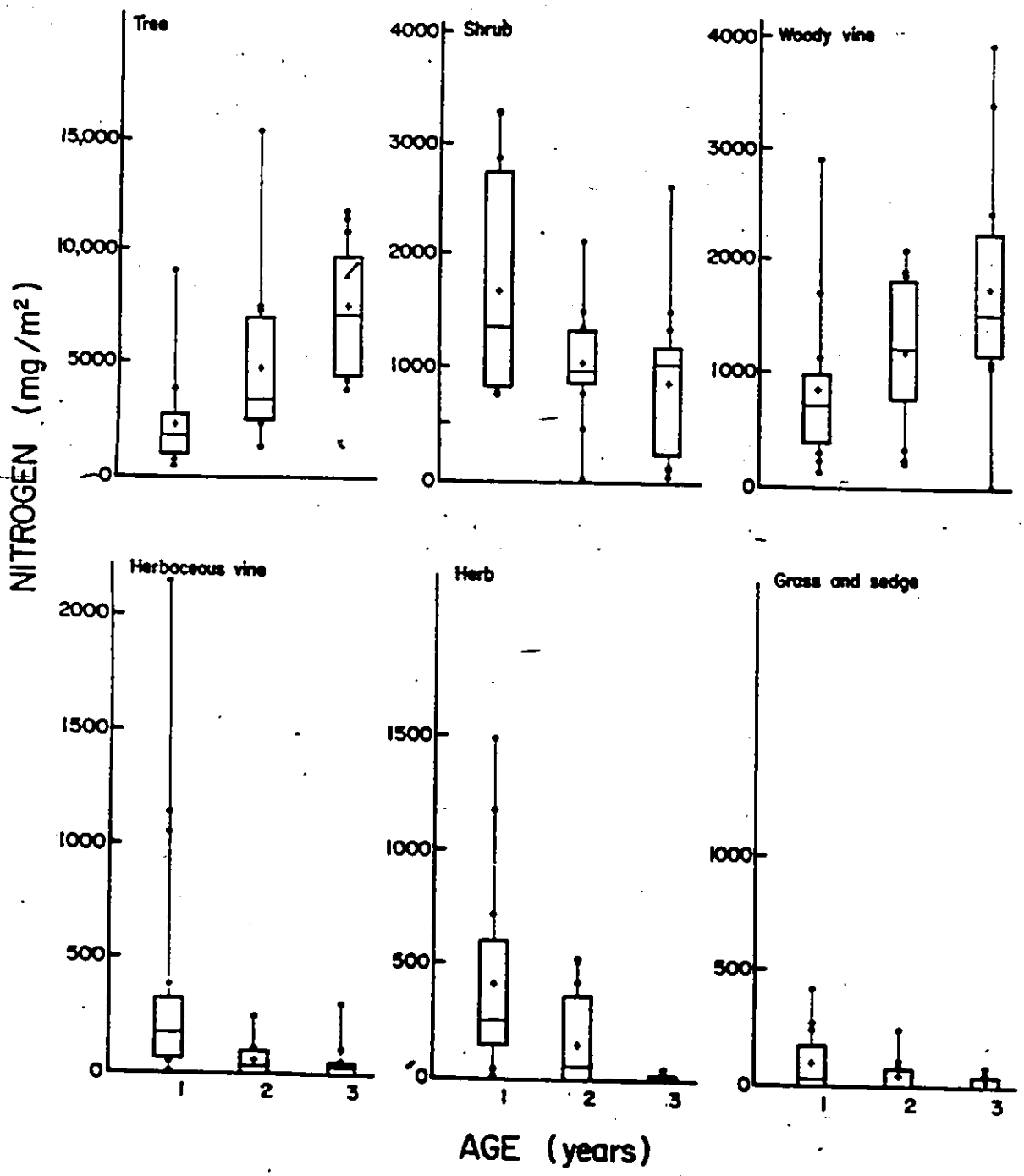


Fig. 8b

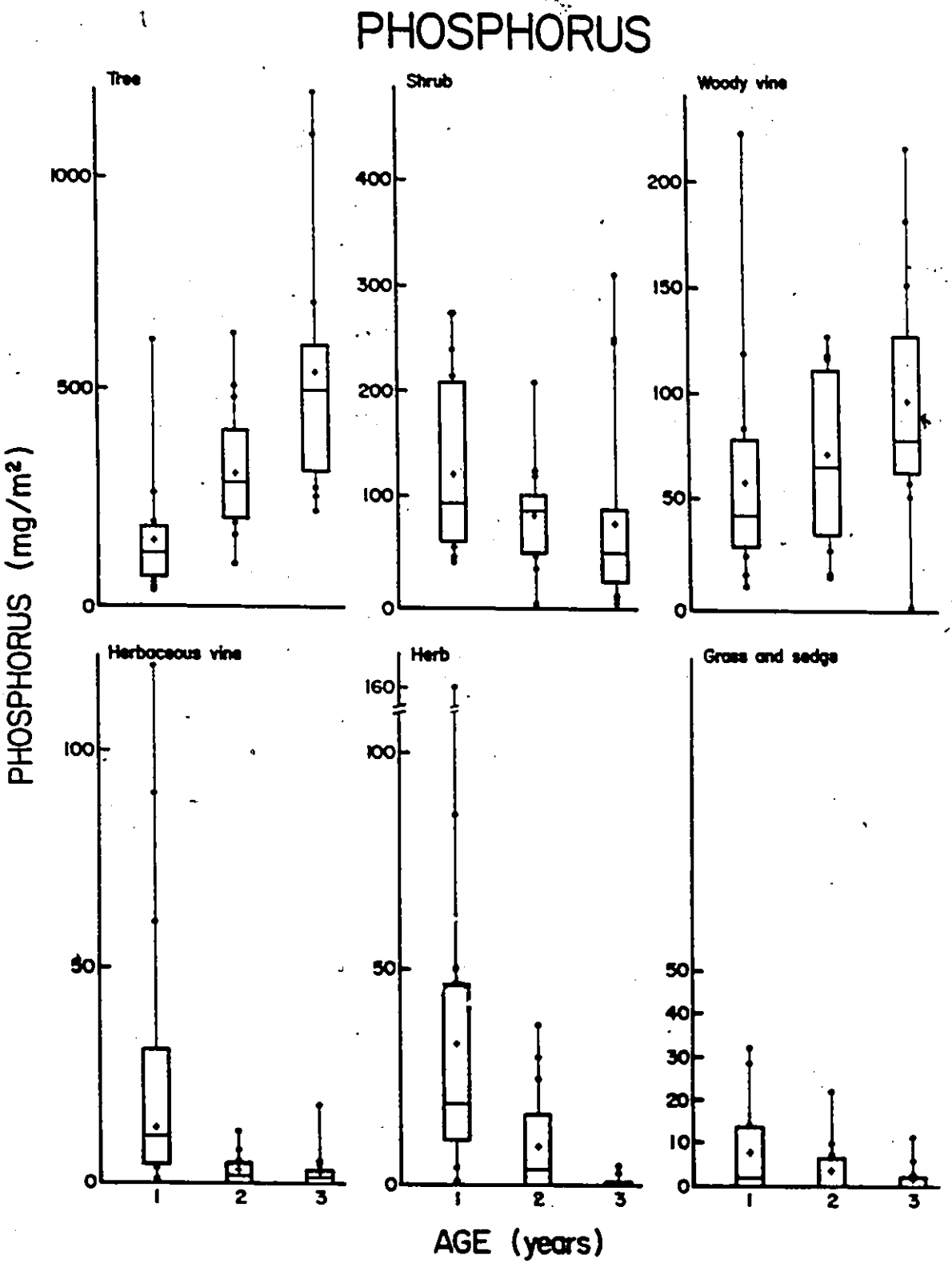

PHOSPHORUS
Tree
Shrub
Woody vine
Herbaceous vine
Herb
Grass and sedge
PHOSPHORUS (mg/m²)
AGE (years)
1000
500
0
400
300
200
100
150
50
160
40
30
20
10
1
2
3

Fig. 8c

POTASSIUM

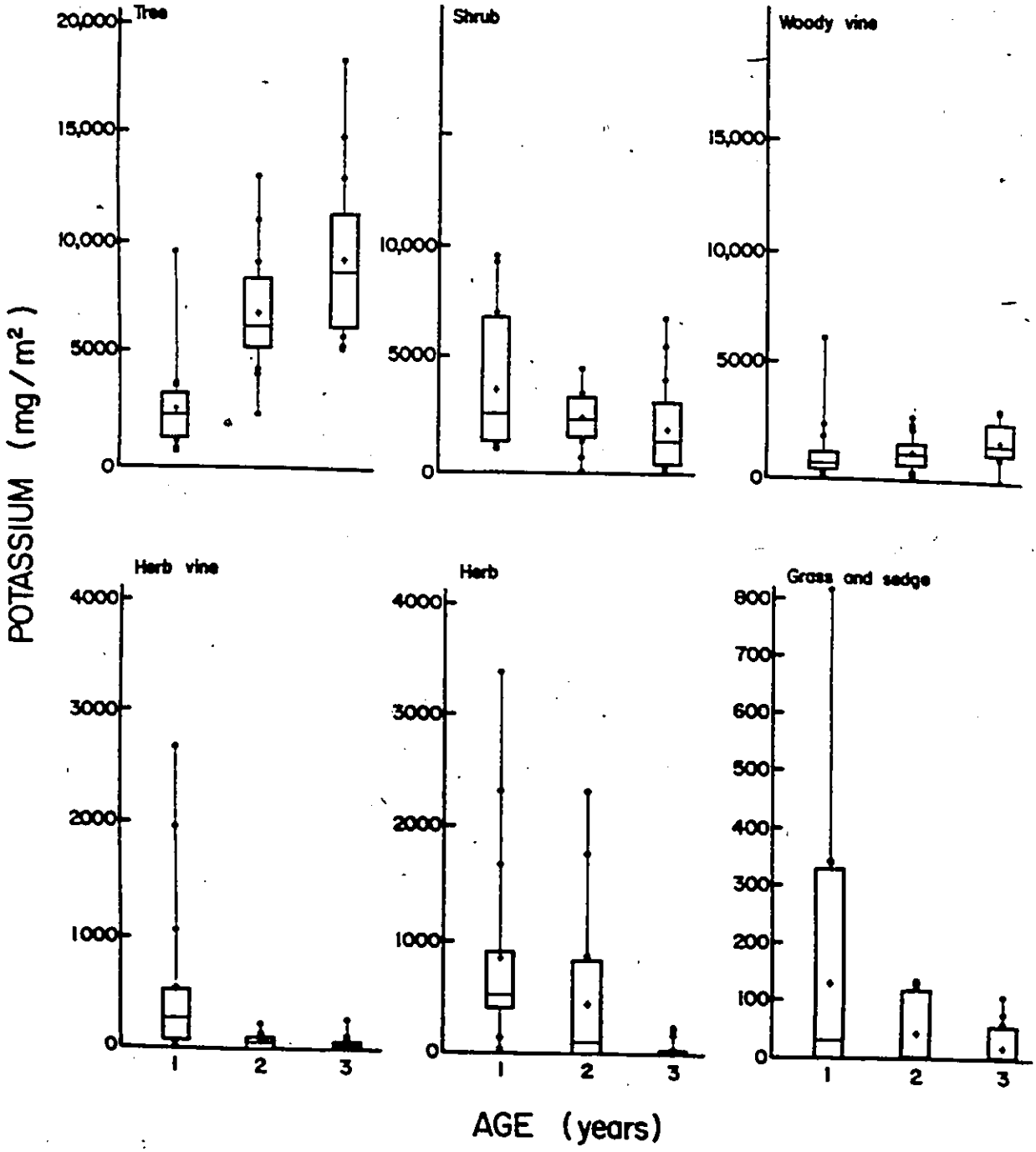


Fig. 8d

Table 7. Important Species in Milpa Fallow Sites

Age (years) 1			2			3		
Species	Form	I.V.	Species	Form	I.V.	Species	Form	I.V.
Eupatorium pycnocephalum	H	5.2	Neurolaena lobata	H	3.2	Thevetia ahoui	S	5.0
Neurolaena lobata	H	3.1	Thevetia ahoui	S	8.7	Lasianthaea sp.	S	4.6
Iresine sp.	H	2.7	Compositae (coll.215)	S	8.3	Randia aculeata	S	3.5
Bidens squarrosa	HV	7.5	Lasianthaea sp.	S	6.4	Bidens squarrosa	HV	3.8
Compositae (coll.215)	S	18.4	Aegiphila monstrosa	S	5.1	'Kibix' (coll.280)	WV	5.0
Eupatorium odoratum	S	9.4	Psychotria fruticetorum	S	4.0	Morinda yucatanensis	WV	4.4
Lasianthaea sp.	S	5.4	Piper nitidulifolium	S	3.1	Coll.335	WV	3.8
Thevetia ahoui	S	5.3	Smilax sp.	WV	4.3	Mimosa hondurensis	WV	3.7
Psychotria tennuifolia	S	5.1	Morinda yucatanensis	WV	3.5	Croton glabellus	T	16.7
Piper nitidulifolium	S	3.2	Coll.335	WV	2.8	Ternstroemia sp.	T	10.7
Morinda yucatanensis	WV	4.6	Trema micrantha	T	11.8	Acacia sp.	T	9.5
Smilax sp.	WV	3.3	Psychotria grandis	T	10.5	Guettarda combsii	T	9.3
Paullinia pinnata	WV	2.8	Bursera simaruba	T	5.4	'Soecha' (coll.565)	T	7.8
Psychotria grandis	T	5.9	'Soecha' (coll.565)	T	4.6	Psychotria grandis	T	7.6
Ternstroemia sp.	T	4.0	Reneonia salvadorica	T	4.2	Chrysophyllum mexicanum	T	6.5
Chrysophyllum mexicanum	T	3.8	Guettarda combsii	T	3.3	Eugenia sp.	T	5.9
Lonchocarpus castilloi	T	3.6	'Holol' (coll.240)	T	3.3	Swartzia sp.	T	5.5
Trema micrantha	T	3.4	Cupania sp.	T	3.1	Bursera simaruba	T	4.5
Bursera simaruba	T	3.4	Cordia diversifolia	T	3.1	Cordia diversifolia	T	4.1
Carica papaya	T	3.3	Spondius mombin	T	2.9	Lonchocarpus castilloi	T	3.7

Note: I.V. = Importance Value = Relative Frequency + Relative Biomass.
Quotations indicate locally used name.
Form = Lifeform grouping as follows: H = herb, S = shrub, T = tree, WV = woody vine

were most important in two year old sites. In three year sites, Croton glabellus, Ternstroemia sp., Acacia sp. and Guettarda combsii, all trees, were the most important species. In each age class, over one hundred different species were encountered among the fifteen plots that were sampled, thus accounting for the low scores obtained.

While Table 7 may be of use in identifying trends in the relative importance of individual species, it does not allow the determination of whether a species found in a one year old fallow site is eliminated in older sites or if it is capable of sustained growth. To determine the potential of a species for sustained growth, the mean biomass obtained in the different age groups is of less interest than the extreme values, which demonstrate the growth a species is capable of. While mean biomass is to a large extent influenced by the length of time a plant has been established at a site, as opposed to site age, the extreme biomass values will more often represent the biomass obtained by plants which have been established for a period approaching the age of the site in which they were found. The potential of a species for growth may thus be estimated by plotting the biomass of each species occurrence against the age of the plot in which it occurred, and examining the extreme values. Such plots are presented for twelve frequently occurring species in Fig. 9a,b,c. As shown in Fig. 9a, Eupatorium odoratum, E. pycnocephalum, Coll. no.215 and Neurolaena lobata all had the highest biomass occurrences in one year plots. Maximum biomass in two year old plots was lower than in one year old plots, and, with the exception of one high occurrence of Eupatorium odoratum, the maximum occurrence of biomass in three year plots was less than in second year plots. These species therefore appeared to decrease with age. In contrast, many tree species such as Swartzia sp., Psychotria grandis, Chrysophyllum mexicanum and Guettarda combsii increased with age, as in Fig. 9b. The woody vine Smilax sp. and the herbaceous vine Bidens squarrosa were found with similar ranges of biomass

Figs. 9a–c. Biomass potential of Individual Species During Fallow Succession

Note: Points indicate the biomass of each occurrence of a species in the 15 study plots according to age of site. Zero values (no occurrence) not plotted. Further explanation as in text (Sec. 3.3.2).

Fig. 9a

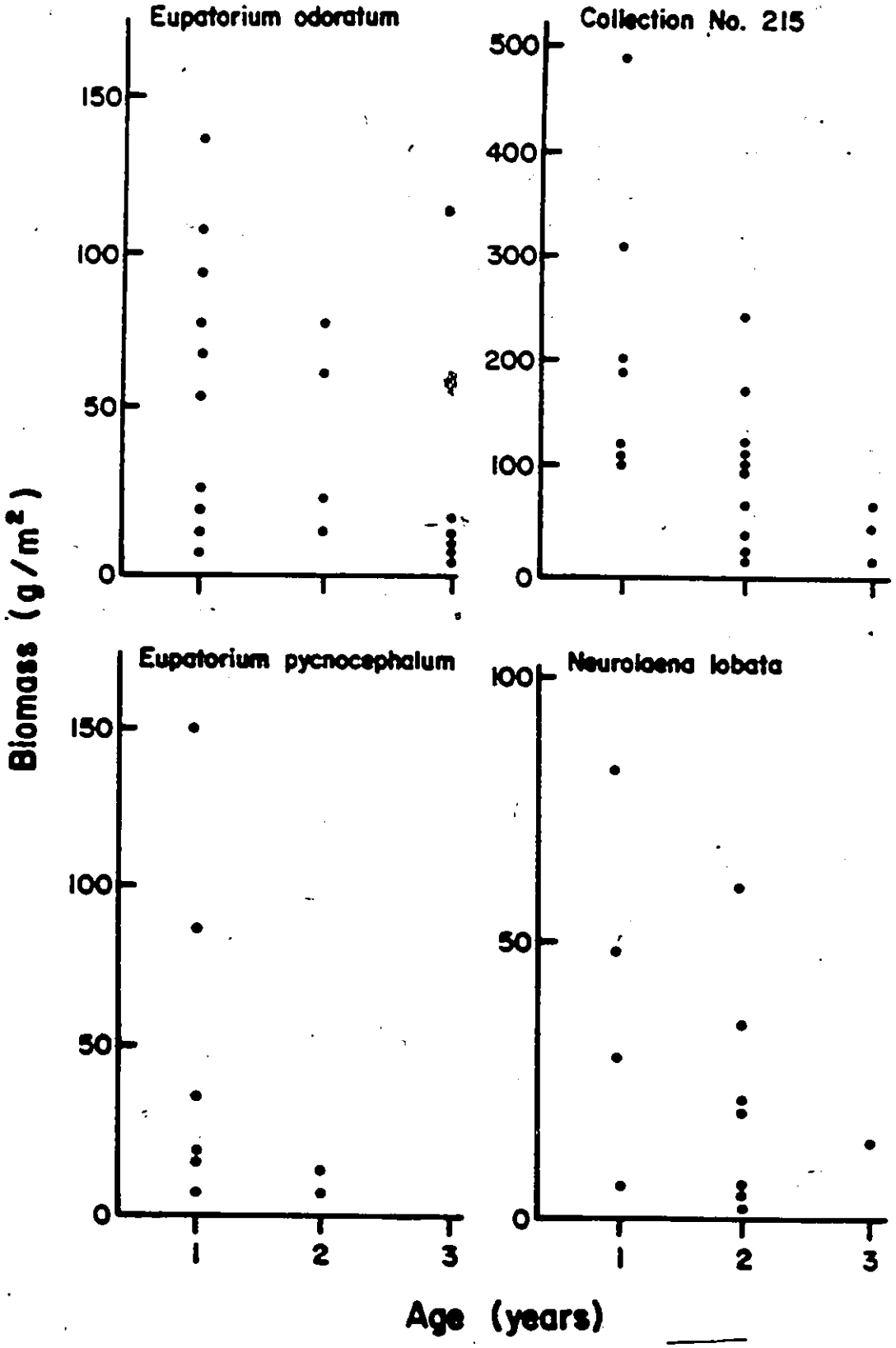

Eupatorium odoratum
Collection No. 215
Eupatorium pycnocephalum
Neurolaena lobata
Biomass (g/m²)
Age (years)
0
50
100
150
200
300
400
500
1
2
3

Fig. 9b

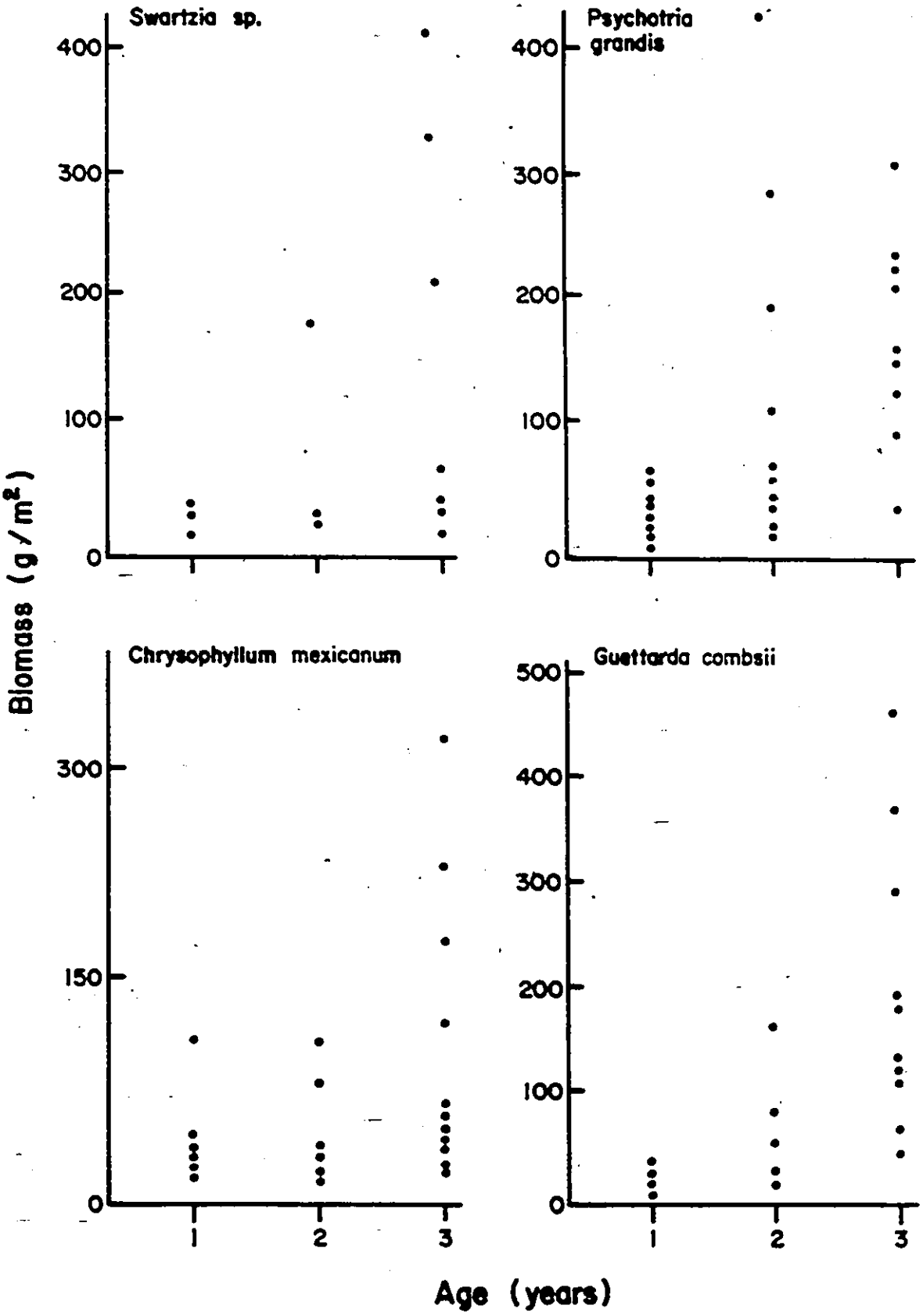
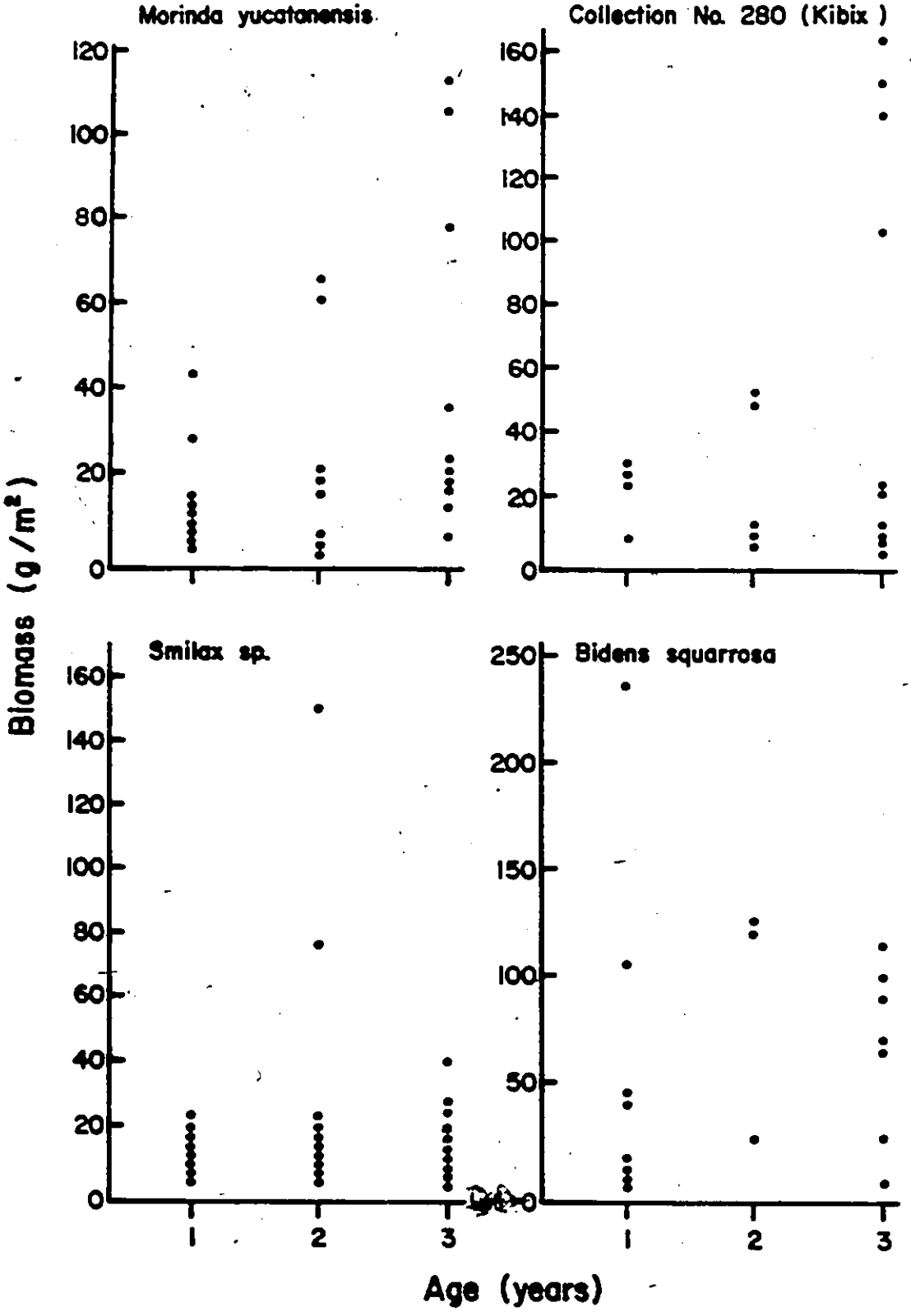

Swartzia sp.
Psychotria grandis
Chrysophyllum mexicanum
Guettarda combsii
Biomass (g/m²)
Age (years)
0
100
200
300
400
150
500
1
2
3

Fig. 9c


Morinda yucatanensis
Collection No. 280 (Kibix)
Smilax sp.
Bidens squarrosa
Biomass (g/m²)
Age (years)
0
20
40
60
80
100
120
140
150
160
200
250
50
1
2
3

regardless of plot age, suggesting that these species maintained their position through this period of early succession. Other woody vines such as Morinda yucatanensis and Coll. no. 280 ('Kibix') tended to increase with age (Fig. 9c).

Using these plots, frequently occurring species have been tabulated on the basis of whether they increased, decreased or maintained their biomass with increasing successional time (Table 8). All the tree species which occurred frequently enough to be plotted in this way increased their biomass as succession progressed. Herbs decreased as did three of the four shrub species and one of two herbaceous vines. Among the species which decreased, all but two belonged to the Compositae. The shrub species which decreased were weak shrubs, having only partially lignified stems.

3.4 NUTRIENT CONCENTRATION IN SUCCESSIONAL SPECIES

An analysis of variance indicated that classification by species accounted for 61% of the total variation in N concentrations of leaf matter, while the age of the site accounted for only 7% of the variation (Table 9). Ten percent of the variation was due to differences between individuals of a species within an age category and 22% to sampling error. For stem material, more variation was accounted for by age (22%) than was the case for leaves, and somewhat less due to species (45%). For P and K, sources of variation in leaves were similar to those of N, with only a small proportion due to age. In stem material, only 17.5% of the variation in P was due to differences between species, so that a larger proportion was accounted for by the site and error components. Total variation was less for stem P values than for either N or K, hence the absolute variation due to age was not necessarily greater for P than for the other two nutrients. Variation due to species differences was greatest for K; only 2.8% was due to age in leaves and 8.2% in stem material.

Table 8. Successional Trends in Species Biomass.

Decrease		Maintain		Increase	
Species	Form	Species	Form	Species	Form
Eupatorium pycnocephalum	H	Bidens squarrosa	HV	Lasianthaea sp.	S
Neurolaena lobata	H	Smilax sp.	WV	'Kibix' (coll.280)	WV
Iresine sp.	H	Petria volubilis	WV	Morinda yucatanensis	WV
Centrosema plumerii	HV			Swartzia sp.	T
Eupatorium odoratum	S			Psychotria grandis	T
Compositae (coll.215)	S			Chrysophyllum sp.	T
Psychotria tennuifolia	S			Guettarda combsii	T
				'Soscha' (coll.565)	T
				Cupania sp.	T
				Ternstroemia sp.	T
				Acacia sp.	T

Note: Based on data as in Fig. 7-9. See text for explanation.
Form = Lifeform grouping as follows: H = herb, HV = herbaceous vine, WV = woody vine, S = shrub, and T = tree.

Table 9. Sources of Variation for Species Nutrient Concentrations

Source of Variation	Part	Nitrogen	Phosphorus	Potassium
Species	L	61.3	50.6	57.0
	S	44.9	17.5	65.5
Age	L	6.8	5.1	2.8
	S	22.1	21.9	8.2
Site	L	9.7	18.6	20.6
	S	10.1	23.4	10.7
Error	L	22.2	25.7	19.0
	S	22.9	37.2	15.6

Note: Variation due to 'Error' includes natural variability among different individuals of the same species as well as variation due to sampling error.

An analysis of variance which included the part of the plant tested (leaf or stem) as a source of variation found that this division accounted for 82% of variation in N concentrations, 64% of P and only 33% of variation in K, reflecting that K concentrations between leaf and stem material were more similar than either N or P.

Nitrogen, P and K concentrations in leaf and stem material for the same species listed in Table 7 and Table 8 are presented with 95% confidence intervals in Table 10. Phosphorus concentrations were generally an order of magnitude lower than N or K for both leaf and stem material. Concentrations of N and P in leaf material was consistantly higher than that in stem material: leaf N concentrations averaged 1.68% while stem concentrations averaged 0.44%. Phosphorus averages were 0.093% and 0.036% for leaf and stem concentrations, while averages for K were 1.70% for leaves and 0.95% for stem material. Several species such as Psychotria grandis, P. tennuifolia and Bursera simaruba had K concentrations in stem material equal to those in their leaves. This was never the case for either P or N.

Species which had particularly high concentrations of one or more nutrient in either leaf or stem material are of interest as they may play an important role in reducing loss of nutrients due to leaching by rapidly accumulating nutrients in their biomass. Those species which had nutrient concentrations in the top 25% are shown in Table 11. Carica papaya had very high N, P and K concentrations in leaves and high P and K concentrations in stem material. Leguminosae spp; Centosema, Swartzia and Coll. no. 280 ('Kibix'), had high N concentrations in leaf and stem. Although P concentrations had a relatively small range of values (0.024 – 0.089%), several soft-wood trees, Spondius mombin, Rensonia salvadorica, and Coll. no. 240 ('Holol') had high P concentrations in their leaves, along with the herbaceous species Eupatorium odoratum and Iresine sp. Iresine sp. also had very high K concentrations while Eupatorium odoratum had high N concentrations in its leaves. Species with nutrient

Table 10. Nutrient Concentrations of Important Species

Species	No.	Part	%N	95% CI	%P	95% CI	%K	95% CI
Acacia sp.	7	L	2.2	0.62	0.09	0.013	0.9	0.19
		S	0.50	0.26	0.03	0.020	0.3	0.23
Aegiphila monstrosa	11	L	2.0	0.3	0.12	0.02	1.1	0.17
		S	0.3	0.1	0.03	0.005	0.6	0.25
Bidens squarrosa	17	L	1.7	0.1	0.10	0.009	2.4	0.28
		S	0.43	0.06	0.05	0.018	1.2	0.25
Bursera simaruba	20	L	1.5	0.10	0.11	0.018	1.5	0.20
		S	0.35	0.09	0.04	0.012	1.4	0.19
Carica papaya	6	L	3.3	0.75	0.24	0.020	3.8	0.91
		S	0.60	0.21	0.06	0.026	3.7	1.3
Centrosema plumieri	5	L	3.0	0.19	0.13	0.019	1.5	0.10
		S	1.2	0.28	0.06	0.015	1.2	0.15
Chrysophyllum mexicanum	27	L	1.2	0.04	0.14	0.006	0.9	0.08
		S	0.37	0.05	0.03	0.003	0.50	0.08
Cordia diversifolia	14	L	1.3	0.12	0.06	0.009	1.6	0.15
		S	0.30	0.05	0.03	0.003	0.68	0.09
Croton glabellus	9	L	1.7	0.09	0.09	0.012	3.4	0.44
		S	0.42	0.15	0.03	0.012	0.48	0.21
Cupania sp.	14	L	1.2	0.10	0.07	0.013	1.1	0.16
		S	0.30	0.06	0.03	0.008	0.55	0.14
Eugenia sp.	17	L	1.2	0.09	0.06	0.017	1.6	0.77
		S	0.38	0.06	0.03	0.007	0.47	0.10
Eupatorium odoratum	15	L	2.6	0.17	0.16	0.011	2.5	0.26
		S	0.38	0.04	0.04	0.007	1.2	0.19
Eupatorium pycnocephalum	7	L	2.0	0.66	0.13	0.051	2.4	0.64
		S	0.44	0.09	0.04	0.010	1.2	0.22
Guettarda combsii	22	L	1.5	0.12	0.09	0.013	2.2	0.29
		S	0.36	0.05	0.03	0.004	0.63	0.10
Lasianthaea sp.	15	L	1.7	0.15	0.09	0.013	2.6	0.29
		S	0.39	0.08	0.05	0.009	1.4	0.27
Lonchocarpus castilloi	7	L	2.0	0.17	0.08	0.011	0.85	0.16
		S	0.63	0.17	0.03	0.010	0.25	0.13
Mimosa hondurensis	8	L	1.8	0.14	0.10	0.026	1.1	0.32
		S	0.73	0.12	0.03	0.004	0.45	0.11
Morinda yucatanensis	24	L	1.6	0.12	0.07	0.008	1.3	0.16
		S	0.64	0.07	0.03	0.004	0.92	0.14
Neurolaena lobata	7	L	1.9	0.22	0.11	0.017	1.7	0.47
		S	0.27	0.09	0.02	0.005	1.6	0.50
Paullinia pinnata	11	L	1.3	0.12	0.08	0.012	1.1	0.11
		S	0.46	0.06	0.05	0.012	0.49	0.09
Least Significant Difference		L	0.30		0.022		0.44	
		S	0.14		0.016		0.36	

—continued on next page —

Table 10. (Continued)

Species	No.	Part	%N	95% CI	%P	95% CI	%K	95% CI
Petria sp.	9	L	1.2	0.17	0.07	0.012	1.3	0.12
		S	0.50	0.08	0.05	0.013	0.68	0.16
Piper nitidulifolium	14	L	1.8	0.20	0.10	0.013	2.3	0.29
		S	0.60	0.08	0.05	0.009	2.0	0.22
Psychotria fruticetorum	12	L	1.5	0.37	0.08	0.019	1.5	0.18
		S	0.39	0.03	0.03	0.004	0.60	0.07
Psychotria grandis	28	L	1.5	0.12	0.08	0.009	1.2	0.02
		S	0.36	0.04	0.03	0.004	1.0	0.19
Psychotria tennuifolia	13	L	1.7	0.07	0.10	0.008	1.4	0.24
		S	0.49	0.05	0.04	0.005	1.3	0.22
Randia aculeata	16	L	1.3	0.10	0.06	0.015	1.9	0.25
		S	0.50	0.14	0.03	0.012	0.40	0.26
Rensonia salvadorica	9	L	2.1	0.35	0.13	0.03	3.1	0.72
		S	0.33	0.11	0.04	0.011	1.1	0.50
Smilax sp.	25	L	1.7	0.11	0.08	0.006	1.5	0.13
		S	0.50	0.04	0.04	0.008	0.71	0.10
Spondius mombin	9	L	1.5	0.35	0.14	0.021	1.3	0.25
		S	0.31	0.11	0.04	0.014	1.3	0.29
Swartzia sp.	13	L	2.8	0.33	0.10	0.178	0.8	0.11
		S	0.67	0.11	0.03	0.004	0.04	0.06
Thevetia ahoui	31	L	1.6	0.10	0.10	0.007	2.6	0.26
		S	0.37	0.04	0.04	0.005	1.2	0.11
Trema micrantha	20	L	1.8	0.14	0.10	0.010	1.3	0.10
		S	0.26	0.06	0.02	0.040	0.51	0.15
'Holol' coll.240	5	L	2.2	0.24	0.14	0.02	2.1	0.35
		S	0.24	0.11	0.03	0.008	1.6	0.60
'Kibix' coll.280	17	L	2.5	0.13	0.10	0.015	1.7	0.16
		S	0.74	0.10	0.03	0.004	0.66	0.11
'Soscha' coll.565	12	L	1.8	0.11	0.11	0.008	1.9	0.22
		S	0.28	0.04	0.03	0.034	0.56	0.12
Compositae coll.215	20	L	1.7	0.12	0.11	0.012	2.7	0.22
		S	0.28	0.05	0.03	0.034	1.5	0.22
woody vine coll.335	7	L	1.1	0.20	0.06	0.014	1.0	0.31
		S	0.50	0.14	0.03	0.012	0.40	0.26
Least Significant Difference*		L	0.30		0.022		0.44	
		S	0.14		0.016		0.36	

* Due to differences in the numbers of each species these L.S.D. values may lead to liberal estimates of significance.

Note: L = leaf, S = stem. The 95% confidence range is indicated in parentheses after the mean. The number of samples upon which these mean values are based is indicated in 'No.' collumn. Scientific names are used where they are known, otherwise local names and/or collection numbers are given.

Table 11. Species With High Nutrient Concentrations*

Nitrogen		Phosphorus		Potassium	
Species	%N	Species	%P	Species	%K
LEAF					
Carica papaya	3.28	Carica papaya	0.24	Iresine sp.	5.8
Centrosema plumieri	2.96	Eupatorium odoratum	0.16	Carica papaya	3.8
Swartzia sp.	2.79	Iresine sp.	0.16	Croton glabellus	3.4
Eupatorium odoratum	2.57	'Holol' coll. 240	0.14	Rensonia salvadorica	3.1
'Kibix' coll. 280	2.52	Spondius mombin	0.14	'Shelil' coll. 550	3.1
		Vitis tilifolia	0.13		
STEM					
Centrosema plumieri	1.20	Cissus sp.	0.09	Carica papaya	3.7
Justica brevifolia	0.79	Carica papaya	0.06	Iresine sp.	2.6
'Kibix' coll. 280	0.74			Justica brevifolia	2.0
Mimosa hondurensis	0.70			Piper nitidulifolium	2.0
Swartzia sp.	0.67			Neurolaena lobata	1.6
				'Holol' coll. 240	1.6

* Nutrient concentrations in the top 25% of values found in frequently occurring species.

Table 12. Species With Low Nutrient Concentrations*

Nitrogen		Phosphorus		Potassium	
Species	%N	Species	%P	Species	%K
LEAF					
Ternstroemia sp.	0.79	Ternstroemia sp.	0.040	Coll. 535	0.60
Cupania sp.	1.15	Coll. 335	0.057	Swartzia sp.	0.82
Coll. 335	1.14	Justica brevifolia	0.057	Loncocarpus sp.	0.85
Eugenia sp.	1.16	Eugenia sp.	0.061	Chrysophyllum sp.	0.87
Chrysophyllum sp.	1.20	Cordia sp.	0.063	Acacia sp.	0.90
Stem					
Ternstroemia sp.	0.23	Neurolaena lobata	0.024	Lonchocarpus castilloi	0.25
'Holol' Coll. 240	0.24	Trema micrantha	0.024	Coll. 535	0.26
Trema micrantha	0.26	Aegiphila monstrosa	0.025	Acacia sp.	0.30
Neurolaena lobata	0.27	Ternstroemia sp.	0.025	Swartzia sp.	0.35
Coll. 215	0.28	Coll. 215	0.026	Coll. 335	0.40

* Nutrient concentrations in the bottom 25% of values found in in frequently occurring species.

concentrations in the low 25% are shown in Table 12.

Plants belonging to thirty-one families were found within the sample plots. Of these, seven families were represented by three or more species which occurred at least three times each, allowing a comparison of average nutrient concentrations between these families. Mean N, P and K concentrations for leaf and stem material for these seven families are presented in Table 13. Legumes were found to have high concentrations of N in both leaf and stem material. Potassium concentrations in species in this family were low while P was moderate. Species of the Compositae, which were mostly herbs or weak shrubs, accumulated high concentrations of all three nutrients in both leaf and stem material, except for P which was not significantly different in stem material. Members of the Sapindaceae, which included trees and woody vines, had low nutrient concentrations as did the grasses.

3.5 SUCCESSIONAL TRENDS AND NUTRIENT CONCENTRATION

Nutrient concentrations found in species which had their greatest biomass in recently abandoned sites were compared with those that increased in biomass in older sites (Table 14). Mean nutrient concentrations for species in each group are given, along with the results of t-tests to test the hypothesis that the means of the 'decreasing' group are equal to those of the species which were able to grow as sites became older. Nutrient concentrations, especially for P, were higher in leaves of those species which were most successful in young sites but which were apparently unable to maintain their growth through successional time. In stem material, K was higher in this group, while N and P concentrations were not significantly different between the two categories.

Table 13. Nutrient Concentrations in Families of Plants

Family	LEAF %N	LEAF %P	LEAF %K	STEM %N	STEM %P	STEM %K
Leguminosae	2.2^{a}	$0.09^{b,c}$	1.1^{a}	0.74^{a}	0.03^{a}	0.57^{b}
Compositae	$1.9^{a,b}$	0.12^{a}	2.4^{a}	0.34^{b}	0.03^{a}	1.22^{a}
Verbenaceae	$1.6^{b,c}$	$0.10^{a,b}$	$1.4^{b,c}$	0.41^{b}	0.04^{a}	0.74^{b}
Rubiaceae	$1.6^{b,c}$	$0.09^{b,c}$	1.6^{b}	0.48^{b}	0.03^{a}	$0.88^{a,b}$
Bignoneaceae	1.5^{c}	$0.10^{b,c}$	1.6^{b}	0.52^{b}	0.04^{a}	0.62^{b}
Sapindaceae	1.4^{c}	0.08^{c}	$1.2^{b,c}$	0.42^{b}	0.04^{a}	0.55^{b}
Gramineae*	0.6^{d}	0.05^{d}	1.0^{c}	—	—	—

Note: Means within a column having different superscripts are significantly different on the basis of paired t-tests ($p=0.05$).

* Grasses were not differentiated into leaf and stem parts.

Table 14. Relationship Between Successional Trend and Nutrient Concentration

Trend	%N	%P	%K
	LEAF		
Decreasing	2.17	0.13	2.56
Increasing	1.65	0.08	1.38
t-test	*	**	*
	STEM		
Decreasing	0.35	0.04	1.50
Increasing	0.34	0.03	0.71
t-test	n.s.	n.s.	**

Note: ** indicates significance at 0.01 level, * at 0.1 level and n.s. indicates that there was no significant difference between the average nutrient concentrations of the two groups.

The nutrient concentration values are the means of the species of each category as grouped in Table 9:'Successional Trends in Species Biomass'.

DISCUSSION

The results of this study fell into two distinct but related categories: plant succession and nutrient dynamics. These categories are related in that nutrient dynamics may be influenced by the characteristics of the species involved, and succession may be related to nutrient dynamics.

Establishment of woody species during the earliest stages of fallow succession quickly eliminated herbs and grasses and thus was important in allowing the fallow to rapidly return to a tree-dominated community. It is probable that a rapid return to forest vegetation prevents widespread establishment of the more opportunistic herbs and grasses and thus keeps the populations of these species at relatively low levels. The predominance of woody species during early succession may be considered to be an indication of relatively mild disturbance and minimal land use intensity, so that the recovery potential of the land has remained high. It is expected that shortening of fallows would lead to greater establishment of these more opportunistic species. Because grasses are difficult to control by burning, they can inhibit the re-establishment of successional forest species and thereby prolong the recovery phase.

Rapid increase of nutrients in the vegetative biomass is typical of tropical forest regeneration. Storage of nutrients in the biomass ensures their conservation in the agroecosystem. The lower rate of P accumulation and low P concentrations in the vegetation reflects the limited availability of this nutrient in the soils of this region.

4.1 PLANT SUCCESSION

4.1.1 METHODOLOGY

There are two general approaches to studying plant succession. The first involves the establishment of permanent plots which can be sampled as the succession progresses. This may be referred to as a temporal series. The second method involves a spatial series; sampling of plots which are at different points in a successional series at one time. This method is based on independent knowledge of the past history of the plots in order to place them accurately on a temporal scale. Knowledge of past history is also useful in order to determine that a particular plot belongs to the successional pattern which is being elucidated. Eliminating plots with unusual histories will decrease statistical noise, thus reducing the number of spatial replicates required to detect trends. At the same time the generality of the results will be reduced. For either method to be generalizeable in both time and space for a particular region, replication must be carried out. In the first method, replication in space will be essential to ensure that aberrant plots can be detected. Replication in time will also be needed in order to avoid unique results such as might occur if the first year or two were unusually wet or dry. In the second case sufficient replication in space will be required to allow trends based on age to be separated from the noise resulting from spatial variation, as well as variations in past history (Austin, 1981). Again, replication in time will be required to avoid systematic errors such as would result in the case of an unusually wet or dry season. In this study the second approach was adopted. Maximum replication in space, as allowed by the available sampling time was carried out. Elimination of sites which had undergone the dry season harvest (yaxking) increased the efficiency of sampling. As a consequence the

results reported here are not necessarily applicable to these sites. Because sampling was not replicated in time, the procedure is susceptable to differences in past history which could systematically affect all sites of one age group. Systematic spatial sampling errors were avoided by adopting a method of site selection which effectively interspersed fallows of the various ages. Since the milpas of one farmer tended to be grouped together year after year, fallows of differing years were together, rather than being grouped together on the basis of age.

4.1.2 LIFEFORM COMPOSITION OF EARLY FALLOWS

In the seasonally dry tropics, dominance by woody species is generally reported to occur following a period of extensive herbaceous growth during the cropping period. Snedaker and Gamble (1969) indicated that in the Lake Izabal region of lowland Guatemala, herbaceous species which were present at abandonment were replaced by woody species during the first or second year of succession. These woody species may regenerate by coppice growth from previously established root systems, or by seed. In Belize, Lambert and Arnason (1986) found that during a three year cropping period herbaceous species dominated the non-crop component of the vegetation during the first two years. By the third year, woody species, which had been increasing annually, came to dominate. In some situations however, herbaceous species do not dominate the early vegetation: Tergas and Popenoe (1971), in Guatemala, reported that one year after abandonment, woody vegetation predominated in eight of ten fields which were studied. While lifeform composition in sites that were currently under cultivation was not quantified in the present study, much of the regrowth was of woody species, many of which were seen to be regenerating by sprouting. The summer during which this study was carried out was unusually dry,

so establishment and growth of herbaceous species may have been reduced. The appearance of many small seedlings of herbaceous species indicated that seeds of these species were available, however plants that already had a developed root system would have greater access to water deeper in the soil and thus be capable of more vigorous growth. Kellman (1984) noted that coppice growth is common on the limestone soils of Belize.

While herbaceous vines were relatively unimportant in terms of biomass or nutrient stocks, they may play a role in early succession by covering the soil thus reducing moisture loss. Many of the herbaceous vines tended to creep over the soil surface and thus would cover the soil efficiently. Coverage of the soil surface in this way will also result in seedlings of annual species being shaded out, since these species require high light intensities (Bazzaz, 1979). Kellman and Adams (1970) suggested that the abundant vine growth they found in recently abandoned milpas near Succotz played an important role in suppressing noxious weeds.

4.1.3 SUCCESSIONAL STRATEGY

In considering above ground biomass of species, three groups of plants could be roughly identified. Herbaceous species and weak shrubs such as Eupatorium odoratum, Neurolaena lobata and Coll. no. 215 were most successful in first year sites but rapidly declined during the following two years. These species were considered to be decreasing with time. Another group, which included mainly tree species and woody vines, was found with increasing biomass as site age increased. The third group was composed of woody and herbaceous vines, and maintained its biomass throughout the first three years of succession.

In terms of the models of Connell and Slatyer (1977), the trees and woody vines, many of which were present from the beginning, tolerated the more rapidly growing herbs and weak shrubs. As the trees increased in height, competition for light increased and the opportunist herbaceous species were shaded out. Vines have a rather unique strategy for excelling in competition for light. In the initial stages of succession the vines were sprawled out on the ground, with a maximum surface-area exposed to the sun. As the vegetative density increased and competition for light at ground level became more intense, the vines moved upward, growing among the branches of the trees. In this way vines are able to maximize their exposure to light in a vegetative environment with a rapidly changing structure.

On the basis of observations that some of the woody species were establishing from already existing root stocks, a somewhat modified view of the dynamics involved in fallow succession in this region may be developed. In this view, a different grouping of plants is considered. The first group includes those woody individuals which regenerate from root stocks established before the previous cropping cycle. Such root systems may have existed over many cropping cycles. For these species, shifting cultivation is only a temporary perturbation of their above-ground parts. A second group involves those species which require a disturbed environment for establishment and growth but which are unable to survive in the low light conditions of later secondary growth. While these species have no pre-existing root systems, they may have efficiently dispersed seeds, or maintain a viable seed bank in the soil between burn cycles. The extent of such a seed bank will depend on the length and frequency of the cropping period in the milpa cycle. The third group involves those individuals which are capable of surviving in the forest but which cannot establish from an already present root system. This group includes both those species which are not capable of sprout regeneration following a burn as well as individuals of species which could regenerate from an existing viable root system if

it were present, but which had not been established previous to the burn. Saxina and Ramakrishnan (1983) suggested that both sprouting and nonsprouting strategies can be successful as means of capitalizing upon the transient resource supplies that become available upon burning in regions of shifting cultivation. Those species which allocate maximum resources to reproduction and high growth rate, such as Eupatorium odoratum are considered by these authors to be adapted to disturbed environments, while sprouting species, which allocate more of their resources to roots, have a lower growth rate, and are adapted to the more competitive environment of later successional stages.

Development of fallow vegetation following a cycle of milpa cultivation will therefore involve the establishment of new individuals as well as the recovery of individuals which have been present throughout the cycle. The importance of this latter process will depend not only on the previous abundance and physiological state of species which are capable of sprout regrowth, but also on the nature of the succeeding milpa cycle. Miyanishi and Kellman (1986) studied regeneration from roots of two shrub species, Miconia albicans and Clidemia sericea of the Mountain Pine Ridge in Belize. It was found that depleted starch reserves brought about by frequent removal of sprouts was responsible for a loss of regeneration capability. Annual burning also led to decreased starch reserves and hence would eventually lead to root death. The shrubs were able to replenish their starch reserves between burns when burns were two or more years apart. In regions such as Belize where the forest is semi-deciduous, cutting and burning of the vegetation during the dry season occurs at a time when trees are in the best physiological state to withstand it. Many trees in this region drop their leaves during the dry season. Nutrients previously contained in the leaves will be remobilized to the roots and trunk prior to leaf fall (Bidwell, 1979). Thus it is during this time that starch and nutrient reserves in the roots will be at a maximum.

While Miyanishi and Kellman (1986) found that burning cycles of greater than two years would not control the shrubs they studied, Uhl et al. (1981) found that few new shoots had sprouted within 4 months after mature forest on an Oxisol soil in the humid tropics of Venezuela had been cut and burned. Maximum temperatures at 1 cm soil depth ranged from 48–199°C. Presumably burn intensity and duration, as well as adaptations of individual species to regeneration following burning will influence the degree of sprouting from surviving root systems. Lambert and Arnason (1986) reported that sprouting from roots accounted for about 25% of tree replacement after one year of cropping in Belize, but that after the third burn of a three year cropping cycle trees established from seed.

In Succotz weeding involves chopping the vegetation at ground level with a machete. No attempt is made to pull plants out by the roots. Hence weeding will not be as traumatic for the plant as it was in the study by Uhl et al. (1982). Frequency and thoroughness of weeding is variable among farmers at Succotz. In some milpa sites no weeding activity was evident during the duration of this study while at other sites plants were chopped at least once during the summer. Thorough weeding is often not possible, as many milperos leave the village for much of the summer to work as hired labourers elsewhere.

While many of the plants found in the fallows regenerated by coppice growth from established root systems, such growth tended to be patchy, as it was derived from an older fallow community in which considerable thinning had taken place. Thus a large surface area was left bare in which regeneration from seed could occur.

When the soil surface becomes exposed, unfiltered light; wide temperature fluctuations and nutrient release act as triggers for the germination of seeds which have lain dormant in the soil (Bazzaz and Pickett, 1980). Seeds having long dormancy are generally limited to early successional species such as Cecropia and Trema, and

many opportunistic herbs (Kellman, 1980). Lambert et al. (1980) found abundant germination of Canna edulis arising from buried seeds which had lain dormant for at least 45 years in their study at Indian Church. While some seeds may be added to the seed bank during the fallow period, many will originate during the cropping cycle. During this time the composition of the seed bank changes, reflecting the change in the weed vegetation from the fallow to the crop communities. Uhl et al. (1982) found that although seeds of woody successional plants initially dominated the soil seed bank, seeds of herbs and grasses increased in abundance due to their ability to germinate in exposed soil and to their short life cycle which allowed them to mature and set seed between weeding periods of the cropping cycle. As cultivation periods increase, the numbers of herbaceous seeds in the seed bank will therefore be expected to increase.

Species which were not present at the site prior to cultivation either as viable roots or as viable seeds may establish through seed dispersal. Regeneration from newly dispersed seeds requires that a nearby seed source has fruited recently (Webb et al., 1972). Thus the species available for seed dispersal will depend both upon the species present in the immediate vicinity, and hence on land use patterns in the region, and on the timing of seed production. Webb et al. (1972) have noted that the fleshy seeds of many tropical tree species may be carried by animals over distances in the range of 100 m. As land use intensity increases, and rapidly dispersing pan-tropical weeds become more plentiful, seeds of these species may be expected to become more important, both in terms of new seed dispersal and in the composition of the seed bank. Kellman and Adams (1970) reported that weed composition of permanent fields near Succotz contained a much higher representation of pan-tropical species than did milpa fields, which were dominated by woody species having more limited geographical ranges. They noted that the greatest potential weed problems were found in permanent fields which became dominated by prolific

species of wide geographical distribution. The woody species common to milpas on the other hand were considered to assist in the regeneration of the bush fallow.

It is to be expected that in a region such as Succotz, where farming has been practiced for many generations by Mayan farmers, those species which are capable of sprout regeneration will have a competitive advantage over those which depend on dispersal and germination by seed. Thus the forests in this area are likely to be enriched in those species which are adapted to rapid recovery after disturbance by the capacity to regenerate from a permanent root system.

4.2 NUTRIENT DYNAMICS

The soils in this study were relatively fertile due to their high cation exchange capacity resulting from the limestone parent material from which they were derived, and a considerable portion of montmorillonite in the clay fraction (Arnason et al, 1982). Using the terminology of Jordan and Herrera (1981), these soils would be classified as eutrophic, in contrast to the highly infertile oligotrophic soils of regions such as the Amazon basin. While changes in soil properties with fallow age were not significant at the 95% level, there was an indication of increasing trends for some of the parameters. Particularly N and OM, and to a lesser extent K, did appear to increase with age. It is clear that more intensive sampling would be required to overcome the large between-site variability in order to understand the influence of the fallow period on the fertility characteristics of these soils. While soil fertility is recognized to improve with fallow length, the rate of increase in nutrients and OM, and the improvement of soil structure varies with the type of fallow vegetation, the properties of the soil, and the degree to which fertility has been depleted

during the previous cropping cycles (Nye and Greenland, 1960).

Total accumulation of nutrients in the above ground vegetation was comparable to values reported for one year old sites in Guatemala (Tergas and Popenoe, 1971) and in Mexico (Williams-Linera, 1983), although the Belize values obtained in this study were somewhat lower (Table 15). Accumulation of biomass and nutrients by fallow vegetation as reported in other studies are also presented in Table 15. While N and K levels in the first year are higher at Succotz than reported by Toky and Ramakrishnan (1983a) for sites in N.E. India, P is lower. Arnason et al. (1982) have previously reported indications of P deficiency at Succotz, as discussed earlier in section 1.5.

Although root biomass and nutrients stored in the roots were not measured in this study, roots are an important component of the fallow vegetation. Uhl et al. (1982) estimated that roots of successional trees generally account for 15-20% of total biomass. In the Congo, Bartholomew et al. (1953) estimated roots in a 5 year old bush fallow to account for 2500 $g \cdot m^{-2}$ or 23% of the total biomass (Table 15). Concentrations of N, P and K in these roots was calculated by these authors to be 0.7%, 0.03% and 0.4% respectively. These concentrations were somewhat higher than those reported for woody material from these fallows. Thus roots accounted for 36% of the N in these fallows, 27% P and 26% K. It is clear that along with leaves and stems, roots play a very important role in the accumulation of nutrients by fallow vegetation.

Although soil fertility will be reduced over time due to removal of nutrients contained in crops, rapid uptake of nutrients by fallow regrowth during the initial stages of fallow development plays an important role in reducing losses of nutrients from the agroecosystem. Both N and K are generally susceptible to leaching and would tend to be lost from the rooting zone of the soil if they were not constantly

Table 15. Biomass and Nutrient Accumulation in Forest Fallows

Reference	Location	Age (years)	Part	Biomass (g/m^2)	N (g/m^2)	P (g/m^2)	K (g/m^2)
Bartholomew et al., 1953	Congo	2	Leaf*	556	8.0	1.1	8.0
			Stem	536	1.8	0.6	3.7
		5	Leaf	563	12.5	0.7	7.9
			Stem	7,107	18.1	1.4	24.3
			Root	2542	17.6	0.8	11.1
		8	Leaf	538	12.0	0.7	7.9
			Stem	11,631	20.6	1.5	57.9
		18	Leaf	644	14.3	0.8	8.0
			Stem	11,464	30.1	6.2	30.5
			Root	3094	13.9	3.4	18.7
Toky and Ramakrishnan, 1983a.	N.E. India	1	Total	N.A.	3.1	0.5	3.5
		5	Total	N.A.	14.3	2.0	18.9
		10	Total	N.A.	19.3	2.5	54.3
		15	Total	N.A.	33.9	4.4	97.7
Williams-Linera, 1983.	Veracruz, Mexico	1	Leaf	71	2.8	0.16	4.0
			Stem	337	2.9	0.23	13.7
		7	Total	5,268	31.1	3.5	42.1
Tergas and Popenoe, 1971	Lake Izabal, Guatemala	1	Total	971	13.0	1.0	11.2
Uhl and Jordan, 1984	Amazon, Venezuela	1	Leaf	32	n.a.	n.a.	n.a.
			Stem	24	n.a.	n.a.	n.a.
		2	Leaf	270	n.a.	n.a.	n.a.
			Stem	694	n.a.	n.a.	n.a.
		3	Leaf	324	n.a.	n.a.	n.a.
			Stem	1,391	n.a.	n.a.	n.a.
		4	Leaf	435	n.a.	n.a.	n.a.
			Stem	2,453	n.a.	n.a.	n.a.
		5	Leaf	486	n.a.	n.a.	n.a.
			Stem	3,517	n.a.	n.a.	n.a.

* Annual herbs were included with the leaves in the second year sample in this study.

recycled by the vegetation. Rapid uptake is less important as a means of preservation of P since it is rapidly immobilized by calcium in the soil (Brady, 1984). Rapid uptake of P is important however since P becomes increasingly unavailable the longer it remains in the soil, as it penetrates deeper into calcium carbonate particles, thus reducing the surface area accessible to plants (Brady, 1984). Herrera et al. (1978) have described an efficient mechanism for P uptake by vegetation of infertile soils in the Amazon, in which roots obtain P directly from decomposing litter by way of mycorrhizal fungi. By holding it in a more rapidly cycling compartment, uptake by fallow plants ensures that P will be more readily available for subsequent crop use. Rapid cycling by fallow vegetation also tends to concentrate P in the upper horizons of the soil where it will be more available to crop plants (Zinke et al., 1978).

Nutrients in woody stem material and nutrients in leaves undergo different paths back to the soil. Nutrients in the leaf component will continually cycle between the plant and the soil as leaves fall and decompose, while those in woody stem material are essentially immobilized until they are released by burning at the beginning of the next cropping cycle. It is therefore convenient to consider the immobilized and the cycling components of the nutrients accumulated by fallow vegetaion separately.

4.2.1 NUTRIENTS IMMOBILIZED IN STEM MATERIAL

Nutrients held in woody stem material contribute to soil fertility when fallow vegetation is burned. At this time nutrients which were stored in above ground biomass will be released as ash. Although nutrient concentrations were higher in leaves, in older sites stem material accounted for most of the biomass. Thus most of the standing nutrient stocks at the time of burning will be contained in the stem material. Singh et al. (1985) noted that nutrient concentrations in the wood of tropical forest trees are generally higher than in temperate trees. They suggested that increased storage

of nutrients in wood is a strategy for nutrient conservation and may explain the more rapid accumulation of nutrients by tropical forests as compared to temperate forests.

Nitrogen is subject to some volatilization during the burn, as is carbon and sulfur. The extent of this loss has generally been considered to be great. Nye and Greenland (1960) suggested that all N stored in the fallow will be lost in the burn. However, Ewel et al. (1981) reported that only 22% of the N stored in standing vegetation in a study in the Amazon was lost during burning. Similarly Seubert et al. (1977) found that a 17 year old forest in the Peruvian Amazon yielded 67 $kg \cdot ha^{-1}$ N in the ash upon burning. In Thailand, however, Zinke et al. (1978) measured only 10 $kg \cdot ha^{-1}$ N in the ash of a burned 9 year old fallow, while 193 $kg \cdot ha^{-1}$ N was stored in the vegetation and litter of a seven year old fallow nearby. It is evident that N stocks in fallow biomass should not be disregarded, though estimates of N held in standing vegetation will not indicate the actual amounts of N which will be made available for crop growth.

The rates of accumulation of nutrients during fallow development are of interest as a means of assessing the benefit in terms of additional nutrient stocks in relation to the cost of maintaining potential crop land in fallow. An understanding of the trends begun during the early fallow period will be of value in understanding the system. As fallow periods throughout the region become shorter such data will become increasingly important.

Accumulation of P in stem material continued at a constant rate throughout the first three years of fallow development. Such a linear pattern of accumulation is reasonable considering that P is fixed as various forms of calcium phosphate which are only slightly soluble, and thus not readily available to plants. Since the amount of P available at any time is very low relative to the total P reserves in the soil,

continued accumulation would be expected to occur over a long period of time, with a relatively insignificant reduction in the soil P reserves. Hence the benefit obtained in terms of increased P stocks in a recycleable form may be expected to continue to increase with time as the fallow matures. Bartholomew et al. (1953) found a similar pattern for P accumulation in fallows in Zaire (Table 15). In their study, P continued to accumulate in the vegetation throughout an eighteen year period of fallow growth, while N and K increased rapidly during the first five years and then leveled out. An alternative pattern of nutrient uptake is possible however. Zinke et al. (1978) observed that while nutrient accumulation was slow between the third and seventh years of fallow succession, it increased at a later stage. They suggested that changes in the type of vegetation comprising the fallow might explain such a pattern. Toky and Ramakrishnan (1983b) found a similar pattern in N.E. India where bamboo, which did not begin to establish until after 10 years of fallow, was important in accumulating K (see Table 15).

The pattern of accumulation of K in stem and wood was very different from that of P, with the rate of accumulation falling rapidly after the first year. As was seen in Table 4, little of the variation in K was accounted for by the age of the fallows. This is probably because K is rapidly taken up by the vegetation. The presence of deep roots may allow an initial rapid recovery of K cations which have been leached from the upper soil horizons. The K which is not rapidly accumulated may be leached from the rooting zone so that further accumulation will proceed slowly from atmospheric inputs and inputs from weathering.

After only three years, K levels reached 132 $kg \cdot ha^{-1}$. Lambert et al. (1980) estimated that K levels in a 45 year old hardwood forest in a nearby region were 234 $kg \cdot ha^{-1}$ Considering this value to be a good estimate for K levels that would be obtained by the similar hardwood forests around Succotz it can be seen that

after only 3 years, K levels in the vegetation are already half of what is found in a forest fifteen times as old. A similarly rapid recovery was observed for N. Lambert et al. (1980) estimated levels of 203 $kg \cdot ha^{-1}$ in their 45 year old forest while in the present study, 3 year old fallows accumulated 103 $kg \cdot ha^{-1}$ N on average. The pattern of N accumulation however differed from that of K. Unlike K, the increase in N held in stems of increasingly older fallows remained constant at about 2.0 $gm^{-2}yr^{-1}$ (Table 5). This is probably related to important additions of N to the system by N-fixing bacteria, either free-living or in association with legumes.

While nutrient levels in the biomass may increase rapidly, improvement of soil physical properties such as its bulk density (degree of compaction) may proceed more slowly. Shortened fallow periods may thus lead to a decline in soil structure before losses of nutrients from the agroecosystem become critical.

Total nutrient stocks in vegetation at the time of slash and burn however may not be a good indication of the contribution the fallow will make to soil fertility, even considering those nutrients which are not susceptible to volatilization. This is because the peak in nutrient availability following the burn is probably not synchronous with the demand for nutrients by the crop. Although the maize seeds may germinate and begin growing before the rains start, the maximum nutrient demand of the maize will not occur until after the rains have come. Because nutrients in the ash are very susceptible to leaching or fixation, the peak availability of nutrients accumulated by fallow vegetation will occur before the peak in nutrient demand of developing maize. Losses of nutrients may therefore be expected to be high. In N.E. Thailand, Tulaphilak et al. (1985) estimated that 80% of the loss of K and P from soil during a two year cropping cycle occurred in the initial period between burning and the establishment of a vegetation cover.

Losses of nutrients contained in the ash may be high even before the rains begin, due to relocation of the ash from the field to the surrounding areas by wind. Ewel et al. (1981) found that 16% of N and 33% of K that had been stored in fallow vegetation was lost due to removal of ash by wind and to leaching by the time of the first rain. They report that a further 33% of K and 13% of P had been lost during the period between felling the vegetation and burning it, presumably due to high rainfall in the humid region of Costa Rica where their study was located. As previously mentioned 22% of the N in this study was lost during the burn.

In considering the importance of leaching however, the distinction between eutrophic and oligotrophic soils as described in section 1.4.1 must be kept in mind. The soils of Succotz fit closer to the eutrophic end of this continuum and thus may not be as susceptible to leaching. In a series of nutrient retention studies on Ultisols of the Mountain Pine Ridge in Belize (Kellman and Sanmugadas, 1985; Kellman et al, 1985; Kellman, 1985) it was determined that leaching of nutrients in ecosystems of this region was relatively mild. The soils involved in the study by Ewel et al. (1981) were of volcanic origin, located in Costa Rica. It may be that heavier rainfall in this region contributed to the degree of leaching that was observed, as well as different soil properties.

Not all of the nutrients stored in fallow vegetation will be released upon burning during the first year. Especially when older fallows are burned, much of the wood is not burned completely, and may become an important source of nutrients for second year crops (Lambert and Arnason, 1986).

Due to the transient nature of the increase in fertility after the burn, particularly with respect to K, and loss of N by volatilization, input of organic matter in the form of fallen leaves during the fallow period, and subsequent release of stored nutrients to the soil by decomposition is probably as important as the pulse of

nutrients following the burn. Zinke et al. (1978) considered that while P and K may be mostly returned to the soil in the ash from burned fallows, N additions arise mainly during the period of fallow growth.

4.2.2 NUTRIENTS IN LEAVES

Leaf biomass and the nutrients stored in leaves increased rapidly during the first year. Subsequent accumulation proceeded more slowly, with an apparent drop in nutrient stocks between first and second year fallows followed by a slight increase between second and third year sites (Table 5). While the decline in leaf nutrients during the second year may have been related to the replacement of annual species of Compositae, having high nutrient concentrations, by perennial species, it may also have been a sampling artifact related to the lack of replication in time as discussed in section 4.1.1.

Maximum levels of nutrients were quickly reached in the leaves so that subsequent accumulation is expected to be slow. Bartholomew et al. (1953) found that levels of N, P and K stored in leaves of an 18 year old fallow in the Congo were essentially the same as those of a 5 year fallow (Table 15). Unlike nutrients stored in woody stem material however, nutrients stored in leaves undergo rapid recycling and are therefore of considerably greater importance than their levels in the biomass at any one time may suggest. Litter production by leaf fall and its subsequent decomposition will not only return nutrients to the soil in an organic form, but will enhance soil physical properties through the addition of humus. Although litter dynamics were not measured during this study, it is probable that nutrient input from leaves may be as important as inputs from the immobilized nutrient pool in the wood. Ewel (1968) found that annual returns of N, P and K for a 3 year site at Lake Izabal in Guatemala were 97, 3.7 and 16.6 kg/ha respectively. As a fallow

increases in age, continued inputs of litter will increase the importance of this aspect of the fallow's contribution to soil fertility.

4.2.3 NUTRIENT CONCENTRATIONS IN INDIVIDUAL SPECIES

It is within the context of nutrient additions by litter fall that nutrient concentrations in leaves of particular species becomes interesting. A species which is capable of accumulating high concentrations of one or several important nutrients in its leaves may play an important role in making those nutrients more readily available to the rooting zone of the soil. Thus Spondius mombin, Rensonia - salvadorica and Coll. no. 240 may aid in more rapid accumulation of P in the soils where they occur. In Guatemala, pure stands of Heliconia sp. and Gynerium sp. accumulated more P than mixed vegetation (Tergas and Popenoe, 1971). The possibility for utilizing these and other such species in a fallow system specifically managed to increase nutrient recovery warrants examination. There is indeed some evidence that indigenous farmers practice selective weeding in order to allow species they view as being good for the soil to remain (Chacon and Gleissman, 1982). Managed fallow systems have been developed which employ fast-growing legumes such as kudzu (Pueraria lobata) to improve N fertility, retain nutrients in the agroecosystem and control weed populations (Sanchez, 1976).

The question arises as to the origin of nutrients which are accumulated and how some species manage to concentrate greater quantities than others. As Bartholomew et al. (1953) noted, fallow vegetation does not create nutrients or accelerate weathering of primary soil minerals to any great extent, although addition of N by N-fixing bacteria in symbiotic relation with fallow species is an exception. Rather they suggested that the main role of fallow vegetation in terms of nutrient cycling was to immobilize nutrients in organic forms which would become available to

crops upon decomposition.

Atmospheric influx of nutrients through precipitation is a source of new nutrients which may be of considerable importance over time. Kellman and Carty (1986) measured annual influxes of 3.40 $kg \cdot ha^{-1}$ K and 0.12 $kg \cdot ha^{-1}$ P in Belize. Further additions to nutrient stocks will come from weathering of primary soil minerals. Plants having deep root systems may play an important role in pumping nutrients to the upper soil horizons, thereby replenishing these horizons. This may be particularly important with respect to nutrients which are readily leached.

Individual species may vary in their ability to utilize relatively unavailable forms of nutrients. In the case of P, which is very immobile in the soil, zones of depletion form around root hairs. Species having mycorrhizal associations develop a more extensive 'virtual' root system and thus have access to greater amounts of P. Olsen and Fried (1957) have noted that some crops such as alfalfa and Ladino clover are able to extract more P from phosphate rock than can grasses. They suggested that differences in a plant's ability to absorb calcium could influence P uptake; a plant which decreased the calcium content of the soil solution surrounding its roots would reduce fixation of P by calcium thereby increasing its availability. A second mechanism they suggested was that release of CO_2 by the roots would decrease pH, thus increasing the solubility of calcium phosphate. Plants which gave off more CO_2 at the roots would thus have access to greater amounts of P in soils which where high in calcium.

Differences in nutrient concentrations of leaves may reflect different ratios of cytoplasm to cell wall. Since most of the nutrients are contained in the cytoplasm, highly scleritized leaves, which are common in many tropical tree species, will have lower concentrations. High N concentrations in Eupatorium odoratum have previously been noted by Saxena and Ramakrishnan (1983). They suggested that a correlation

between leaf N concentration and photosynthetic rate could explain the high growth rate of this species.

The relationship between successional trends and nutrient concentration as indicated in Table 14 is interesting in this context. High nutrient concentrations were generally found among the species which were successful only in the young fallow sites, while species which continued to grow in the more competitive environment of older fallows (the 'increasing' group) tended to have lower concentrations. High nutrient concentrations in leaves seem to be associated with opportunistic species, probably being a factor in their high growth and reproductive rates. Such a strategy is successful when nutrients are sufficiently abundant to support the high growth rates of which these species are capable and when light levels are high enough for the high photosynthetic capability of these plants to be efficiently exploited. As below-ground competition for nutrients and above-ground competition for light increases, a strategy which emphasizes maximum height growth at a minimal nutrient cost will be favoured. This is achieved by an increased allocation of biomass and nutrients to woody stem material by which the plant can achieve great height at a relatively low nutrient cost. Because the emphasis is not on rapid growth rates, leaves can be more highly scleritized which leads to greater permanency and reduced nutrient losses due to leaching by rain water (Jordan and Herrera, 1981).

The differences in nutrient concentration of leaves among plant families, as presented in Table 13 is of interest. High concentrations of N, P and K in the Compositae may be related to the apparent success of this family in the early stages of fallow development: of the seven common species which were found with their highest biomasses in the one year old fallows ('decreasing' species of Table 8), five belonged to this family. The high N concentrations in the Leguminosae may reflect the ability of these species to associate with N-fixing bacteria.

The ability of plants to obtain nutrients, especially P is greatly affected by the presence or absence of associations between the roots and mycorrhizal fungi. In the tropics, associations with endomycorrhizal fungi (VAM) are extremely widespread. Barea and Azcon-Aguilar (1984) estimated that four fifths of all land plants may form VA mycorrhizal associations. Although mycorrhizal associations are widespread, the extent to which plants are dependent upon the fungus is known to vary among families of plants. Legumes for example form more extensive associations than grasses (Barea and Azcon-Aguilar, 1984). It is probable that the availability or lack of availability of mycorrhizal associations and differing dependencies upon mycorrhizae will play an important role in nutrient dynamics during fallow succession. Not only will burning and other agricultural practices affect the availability of propagules for plants to regenerate, but it will also influence the availability of mycorrhizal fungi. Variable degrees of association could be a factor in explaining the high nutrient concentrations in some families and lower accumulation in others, such as the Gramineae and Sapindaceae.

4.3 WEED MANAGEMENT BY FALLOW-VEGETATION

The principle involved in the use of fallow vegetation to manage weed populations is to prevent or eliminate growth of aggressive and prolific weed species by species less harmful to crop production. Specifically this means controlling noxious pan-tropical herbs and grasses by local woody species. Although species belonging to the woody lifeforms gained importance from the beginning of the successional period they do not represent as serious a potential weed problem as herbaceous species and grasses do. First, survival strategy in trees and shrubs tends towards the allocation of resources to assure permanency, not proliferation. Large expenditures of resources are invested in the woody material of above ground stem and branches

and the below ground root system. The deep root systems of trees allow them to obtain part of their nutrient requirement from depths not accessible to crop plants. Short-lived herbaceous species such as Eupatorium odoratum and Iresine sp. on the other hand focus resource allocation towards rapid growth and seed production (Saxena and Ramakrishnan, 1984). These species are therefore capable of extensive proliferation and may become very serious competitors with crop plants. Kellman and Adams (1970) considered that these pan-tropical weeds are a greater problem than slower growing woody species. Secondly, Eupatorium odoratum and Iresine sp. were found to have high nutrient concentrations in their tissues, suggesting that these species could be very aggressive competitors for nutrients. Early regrowth of woody species during the cropping period may compete with crop plants both for light and for nutrients, and therefore may be considered as a weed problem. However this regrowth may play an important role in suppressing more aggressive herbaceous weed species, such as Eupatorium odoratum or rhizomatous grasses, which were not abundant in any of the plots studied. In light of such a role, competitive effects on crops due to woody material may be a small price to pay for protection against more severe weed problems. In the case of one young farmer at Succotz who had insufficient land to allow a fallow period, yearly cultivation had led to complete infestation by an aggressive rhizomatous grass. In India, Toky and Ramakrishnan (1983a) reported that herbaceous species dominated for five years following abandonment. When the agricultural cycle (cropping and fallowing) was five years, as is usually the case, they noted that the fallow succession was arrested at a herbaceous stage, and found that Eupatorium odoratum or Imperata cylindrica, a noxious rhizomatous grass, dominated. In Mindanao (the Philippines), Kellman (1969) found that repeated weedings of fields under shifting cultivation resulted in severe infestations by this grass, leading to their abandonment.

The importance of the woody lifeforms in the very early stages of fallow succession at Succotz would seem to indicate that the level of disturbance at these sites is low. In spite of the burn and whatever weeding may have been done during the two years of cropping, root stocks of many of the woody individuals which had been growing in the previous fallow appear to have survived and have led to the abundant shoot growth that was observed in early sites. Thus the first plants to regenerate after the burn, as observed in plots which were currently under cultivation, tended to be those arising from shoots. Subsequent growth presumably arose either from buried seeds or from seeds which were able to disperse to the site during and after the last cropping season. The early importance of woody species is of major significance to the vegetational development of the fallow and hence to control of aggressive weed populations. It could also play an important role in the accumulation of nutrients. By having a developed root system already in place at the time of peak nutrient availability after burning, these plants are able to get a head start on potential competitors which must begin establishment from seed. Deep root systems may be very important at this point in recycling K, which would otherwise be leached out of the rooting zone. In the absence of already established deep roots, it is to be expected that K recovery would require considerably more time.

The traditional method of weed control practiced by the milperos at Succotz involves simply chopping regrowth several times during the cropping season. This method is well suited to the situation as described above as it will control competition for light while maintaining viable root stocks. This ensures that the woody component rapidly dominates the early succession at the expense of aggressive herbaceous species. If more aggressive weed management techniques, such as the use of herbicides were adopted and woody species were eliminated from the crop cycle, early fallow succession would be considerably altered. Specifically, elimination of sprouting potential of species from cultivated sites with established root systems

would result in a delay in the successional progression back to forest species. This would have two consequences. First, since the site would be open for colonization for a longer period of time, species having a large viable seed bank or those able to disperse rapidly into the area would be favoured. Herbaceous pan-tropical species such as Eupatorium odoratum have such characteristics. Thus the elimination of sprouting potential would favour colonization of more aggressive weed species. Secondly, recovery of nutrients, in particular those which are susceptible to leaching, would be delayed, as considerable time would be required for the re-establishment of deep root systems. Competition with herbaceous species would further delay the establishment of woody species.

4.4 FUTURE WORK

This study has indicated the importance of woody species in the earliest stages of fallow succession and has suggested that vegetative regeneration from roots which survived the burn and cultivation period of the shifting cultivation cycle is in part responsible for this importance. Further studies are required to quantify the role of sprouting and the effect of various cultivation practices on this form of regeneration. It is believed that as land use intensifies and fallows become shorter, woody growth will be replaced by herbaceous growth and that fallow succession will proceed more slowly. It is important that this process be understood in detail, in order to determine management strategies for shortened fallows, both with a view toward controlling weed problems and in order to ensure the retention of nutrients in the agroecosystem. The measurement of nutrients accumulated by the natural bush fallow in this study will serve as base-line data against which to compare degraded fallows and fallows which may be specifically managed to achieve the results of the bush fallow in a shorter time period.

More intensive examination of soil properties is also required to determine what the long term effects of shortened fallows will be on not only soil nutrient levels but also on structural properties of the soil. The current method of planting maize seeds directly into the soil using only a stick requires that the soil be relatively loose. If soils become compacted with more intensive use, other cultural practices will have to be implemented in order to prepare the soil.

As our understanding of the ecology of traditional fallow systems increases, alternative fallow systems may be developed which can provide the same benefits under shorter fallow periods. Such experimental systems must be feasible not only from an ecological point of view, but they must also be acceptible to the population which is expected to utilize them.

APPENDICES

Appendix 1.
Biomass and Nutrient Totals for Individual Plots

Age (years)	Site	Plot	Biomass (g/m^2)	N (mg/m^2)	P (mg/m^2)	K (mg/m^2)
1	A	1	321.70	2522.1	148.29	4595.7
		2	479.35	4380.1	248.40	6865.5
		3	399.12	3708.5	203.38	5434.5
	E	1	510.57	6617.7	444.84	6196.3
		2	291.92	3171.2	260.52	4856.8
		3	582.15	6393.2	445.76	6208.3
	H	1	344.85	2766.0	228.68	4938.7
		2	473.82	3901.7	276.26	6211.8
		3	463.17	4239.3	268.45	5667.6
	K	1	1107.25	12171.9	803.48	15531.6
		2	815.25	7359.5	511.91	12129.8
		3	733.99	6661.1	500.26	16014.5
	O	1	1142.22	8891.4	685.49	19228.8
		2	630.46	5852.5	400.77	9161.6
		3	1083.08	7738.3	642.62	16092.4
2	B	1	1765.96	17170.2	788.90	11842.7
		2	1440.75	10426.3	660.32	10915.3
		3	1360.04	5667.5	540.30	6958.7
	D	1	851.05	5186.7	380.30	8970.4
		2	860.17	4728.1	337.07	9307.8
		3	643.86	3325.4	250.84	5203.3
	F	1	854.58	4826.6	327.77	10629.5
		2	1561.53	9066.4	527.69	17420.7
		3	1315.08	10440.6	540.83	10217.6
	M	1	1170.80	7725.8	503.08	14114.7
		2	1040.97	6374.9	441.82	11143.8
		3	1103.22	5778.7	454.89	13075.5
	N	1	1291.80	6729.2	500.13	11821.9
		2	1022.90	5430.6	360.10	6967.8
		3	1769.84	6869.7	635.97	18288.8
3	C	1	1776.14	10482.5	654.57	14388.7
		2	1240.87	7379.7	438.08	8357.6
		3	750.81	11175.9	733.92	14349.1
	G	1	1911.16	11067.1	795.92	12384.2
		2	2548.43	10670.3	744.39	11389.3
		3	2973.91	14402.1	842.26	11199.5
	I	1	1695.65	8076.5	572.72	13398.1
		2	1294.75	6108.1	440.83	14067.4
		3	1347.26	6927.8	395.40	9839.7
	J	1	2291.43	13189.6	779.59	13108.2
		2	4634.60	15432.9	1498.16	26826.1
		3	3121.06	12549.4	1306.86	16342.2
	L	1	1174.80	6559.8	476.67	9169.2
		2	1851.06	10154.5	633.11	13911.2
		3	1467.47	9937.8	537.91	8847.5

Appendix 2. Species Found in Fallows

Species	Collection Number
Acacia sp.	585
Aegiphila monstrosa	385
Allophylus sp.	70
Annona sp.	15
Bauhinia sp.	905
Bidens squarrosa	95
Brysonima crassifolia	370
Bunchosia sp.	65
Bursera simaruba	105
Carica papaya	855
Cecropia mexicana	865
Centrosema plumieri	655
Chrysophyllum mexicanum	645
Cissus sicyoides	810
Corchorus siliquosus	135
Cordia diversifolia	165
Croton glabellus	415
Cupania sp.	110
Cyperus sp.	530
Dendropanax arboreus	510
Desmodium canum	180
Desmoncus sp.	60
Eugenia sp.	125

Eupatorium albicaule	410
Eupatorium odoratum	225
Eupatorium pycnocephalum	205
Guarea sp.	910
Hamelia patens	625
Heliconia sp.	920
Heliotropium sp.	230
Iresine celosia	260
Justica breviflora	275
Lantana camara	290
Lasianthaea sp.	545
Lonchocarpus castilloi	325
Lonchocarpus sp.	330
Metopium brownei	130
Mimosa hondurensis	860
Morinda yucatanensis	365
Neurolaena lobata	340
Orbignya cohune	870
Ouratea lucens	405
Pachyrrhizus erosus	270
Passiflora coriacea	350
Passiflora foetida	450
Passiflora macrostemma	440
Paullinia pinnata	425
Petria volubilis	300
Piper nitidulifolium	170
Porophyllum punctatum	465

Pouteria sp.	520
Psychotria fruticetorum	475
Psychotria grandis	470
Psychotria nervosa	480
Psychotria pubescens	490
Psychotria tennuifolia	485
Randia aculeata	175
Rensonia salvadorica	590
Sarcostema sp.	525
Serjania goniocarpa	540
Smilax sp.	145
Solanum erianthum	390
Spondius mombin	255
Stizophyllum perforatum	560
Swietenia macrophylla	915
Ternstroemia tepezapote	605
Thevetia ahoui	250
Trema micrantha	85
Trichachne sp.	600
Trophis racemosa	495
Vitex glaumeri	635
Vitis tilifolia	610
Zamia loddigesii	345

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