THE DISTRIBUTION AND MOVEMENT OF TROPICAL PASTURE AND WEED SPECIES IN RELATION TO ENVIRONMENT

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ABSTRACT

Experimentation was conducted at the Hawaii Agricultural Experiment Station, Kauai Branch, on a steep, wetland area following jungle clearing, reseeding and fertilization. The objective of the experiment was to test the usefulness of the ecological approach to pasture research and management in such a land development system. The important phases of the research program included, the verification of evident distribution patterns of certain forage and weed species; the collection of vegetation and environmental data in order to relate these patterns of growth to gradients of environmental parameters; and the study of sward dynamics and productivity, identifying the weed species most reliably indicating sward degeneration.

Mapping of species distribution patterns was facilitated by the use of data collected from belt transects and aerial and ground photography. Of the improved forage species studied *Stylosanthes guyanensis* was the only species dominant at ridgetop locations and on the shallow soils of spurs and steep, eroded areas. From the multiple regression analysis, it was the higher soil pH and shallower soil profile that most aptly distinguished the conditions at these locations from those further down the slope. Another important community component at those sites was the weedy association of *Paspalum conjugatum* and *Setaria geniculata*. Its distribution also closely corresponded to the shallower soil profiles and lower soil moisture regimes. Of the other, more woody weed species found at these ridgetop locations, *Melastoma malabathricum*, *Elephantopus mollis*, *Lantana camara* and *Stachytarpheta urticaefolia* were the more dominant. They all showed distribution

patterns closely related to water extractable soil silicon among other environmental parameters.

At locations further down the slope and in the valley bottoms, the more productive sward of improved species was dominated by Panicum maximum (var. trichoglume) and Desmodium intortum. In the case of Panicum maximum, distribution was more reliably influenced by variations in soil moisture, soil nitrogen and exchangeable soil manganese. The distribution patterns of the forage legume, Desmodium intortum, more closely corresponded to the variation in total soil nitrogen and soil calcium. The weed species occuring most frequently at those sites were Commelina diffusa, whose occurrence was closely related to the lower soil pH conditions and Erechtites hieracifolia, which exhibited a more varied distribution pattern, corresponding to higher total soil nitrogen and soil moisture conditions.

Seasonal productivity of improved forage species and dominance of weed components were influenced by grazing management and a natural decline in soil fertility. The contribution of Panicum maximum (var. trichoglume) declined from 30% to 10% of the total forage yield of the sward, only to recover to its original dominance after an extended rest period during the winter months. Its annual dry matter yield averaged 7000 kgm/ha, going as high as 12,000 kgm/ha. A similar trend of productivity was exhibited by Desmodium intortum whose annual dry matter production approached 3000 kgm/ha or 15-20% of the total yield of the sward. Stylosanthes guyanensis was only readily utilized during periods of heavy grazing. The most reliable indicator of sward condition was the weedy grass association of Paspalum conjugatum and

Setaria geniculata. After each heavy grazing period the contribution of this association increased, only to decrease when the more vigorous forage species responded to the rest period. Under the conditions of these humid wetlands, other weed species such as *Lantana camara*, *Psidium guajava*, *Elephantopus mollis*, *Commelina diffusa*, *Erechtites hieracifolia*, *Cuphea carthagenensis* and *Ageratum conyzoides* were also excellent indicators of environmental conditions favoring the decline in productivity of improved forage species.

No clear pattern of seasonal liveweight gain by the grazing animals was evident, except for the drop in production during the wet season and during the stress periods of summer.

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CHAPTER I. INTRODUCTION

The tropical region contains almost two thirds of the world's population, of which a great proportion suffers from malnutrition or under nutrition. With a rapidly increasing need for greater food production, especially protein, and more efficient use of available lands in this region, we must learn more about the land and environment in which we will manage our plant or animal-plant systems. The more productive and cultivable lands should be more efficiently used for increased production of cereals, feed grains and proteinaceous seed crops such as soybean and ground-nuts rather than pastures for animal production. Many of the tropical areas left for pasture development are those posing limitations, and management decisions require consideration of the economic and practical feasibility of land clearing, re-seeding, fertilization and subsequent follow-up renovation and management. Under such conditions we must design systems of land development which integrate specialized techniques at each stage of the development program. Although this study will deal mainly with the use of an ecological approach to species evaluation and pasture management, an overall view of the whole land development program is necessary to appreciate the importance of such a study. The factors and steps in this systematic approach to land development are:

A. <u>Land Clearing</u>

1. Mechanical clearing of weeds and brush entails high operational costs. It is only practically feasible on less rugged land. Consideration must be given to preventing soil removal in the

process of, or as a result of clearing, exposing bare ground to erosion.

2. Chemical clearing involves using aerial or ground-rig treatments to kill or desiccate the vegetation sufficiently to allow clearing by fire, or on more accessible areas, to facilitate mechanical clearing.

B. Sowing of Improved Species

Once the original, undesirable and unproductive vegetation has been removed, more productive species must be introduced. In the case of land clearing for pasture development, improved forage species are sown and managed so as to prevent the ecological shift back in the direction of the original climax community. To do this, the steps after land clearing include seed-bed preparation, seed treatment and the actual sowing of the seed.

The degree of seed-bed preparation depends on the environment and the economics of the particular situation. Procedures range from intensive to zero land preparation. Next there is the consideration of seed treatment. In the case of legumes, effective inoculation and seed pelleting is essential for reliable and vigorous establishment. In some legumes treatment for hardseededness is required. Other important considerations before sowing include time of sowing, seed quality, seeding rate, method of sowing and fertilizer requirements.

C. Subsequent Management and Renovation

Once the range or pasture has been improved or established we must be able to identify indications of mismanagement, overgrazing or undergrazing. This is where the ecological approach is important.

Ecological analysis is basically a determination of the cause-effect relationship in which various factors are causitive, and the effect is expressed as plant response. Plant species are the best indicators of the nature of the environment. The environment in question is obviously the most suited to the more dominant species. By mismanagement of the more palatable and nutritious species there is a replacement by less desirable communities. It is the early identification of this trend that is important in pasture and range management.

Detailed ecological studies of ranges and pastures enable us to evaluate improved species as regards their adaptability and to determine which weed species are reliable indicators of sward decline. Such studies will also help us explain and avoid the failures or disappointing performances of some species which show promise in one area but fail in another area with only superficial environmental similarities. By knowing more about the adaptability of a species, we can help reduce current high costs of improved pasture seed mixes by being able to reduce the number of species in a mix and also to distribute the seed of the species in areas of most suitable microenvironment.

The objectives of this study were to examine the usefulness of the ecological approach to evaluate the adaptability of improved pasture species, to study the dynamics and productivity of the grazed sward and to identify species which indicate degeneration of pasture quality. Computation of the data involving the more important environmental factors, their interactions and the influence of the grazing animal, help to explain why only a few of the improved species do persist and why some species are dominant in certain areas or grow in association with certain weed species.

CHAPTER II. LITERATUVE REVIEW

This study on the use of ecological approach to pasture and range management and species evaluation involved: (1) the recognition of species distribution patterns, (2) the measurement of environmental parameters, (3) the verification of relationships between such species distribution patterns and environmental factors, and (4) dynamics of the sward components. The literature contains considerable work on the individual aspects of the systems approach to land clearing, re-seeding and subsequent management. Unfortunately very little has been done on the integration of these aspects into a manageable system.

Use of Herbicides for Land Clearing

Such workers as Motooka, Plucknett, et al. (1967), Motooka, Saiki, et al. (1967), Ripperton and Hanson (1952), Little and Ivens (1965), and Romancier (1965), have documented the use of herbicides in the process of land clearing for pasture establishment, range improvement or the maintenance of powerline right-of-ways. These works are confined to the tropics and sub-tropics where species and management problems are unique. Particular reference should be made to the works of Motooka, Plucknett, et al. (1967) and Motooka, Saiki, et al. (1967). These papers contain the essential steps leading up to this particular ecological study. The procedures outlined include the initial indexing of a range of combinations of systemmic and contact herbicides as to their effectiveness in controlling the brush species in question. Once a particular herbicide treatment was found superior, large scale aerial application took place followed by re-treatment, burning and subsequent seeding of improved forage species.

Special Sowing Problems

The problems involved in seed treatment before sowing or broadcasting have been studied. Techniques of legume seed inoculation and pelleting have been documented by such workers as Brockwell (1962, 1963), Hastings and Drake (1963), and Loneragan, et al. (1955), under temperate conditions and more recently in the tropics and sub-tropics by Norris (1965, 1967), Dawson (1967) and Plucknett (1971). As well as actual seed treatment, 'package' preparation and distribution of vegetatively propagated grass species such as pangola grass (*Digitaria decumbens* Stent), kikuyu grass (*Pennisetum clandestinum* Hochst.) and para grass (*Brachiaria mutica* (Forsk.) Stapf), appear to have a potential in such land development systems (Nicholls and Plucknett, 1971). In areas where much detailed research has been done on species response to the environment, specific seed mixes can be suggested, but as is the general rule, a 'shot-gun' mix is used to cover all possible environmental habitats (Motooka, Plucknett, et al. 1967 and Harrison, 1969).

Identification of Vegetation Patterns

In studying the distribution patterns of plant communities, workers have used methods ranging from subjective, diagrammatic techniques to more objective classification methods. All approaches have proved time consuming, resulting in more recent intensification of studies involving techniques using multi-enhancement photography.

For large scale vegetation analyses the basic sampling unit used has been the line transect. Bauer (1936, 1943) was the first to appreciate this unit in studies on the composition of vegetation in chaparral. Edwards (1950) devised and used a line intercept method in Kenyan grassland studies. Other techniques, (Anderson, 1942; Parker and Savage, 1944; and Roe, 1947), have also been given the name line intercept, but the measurements were actually within a narrow belt transect. Even though the apparatus consists of a line, measurements within a quadrat centered on this line were finally expressed not in units of length but area.

Dansereau (1943) set up a diagrammatic technique of recording plant types along line transects. The symbols he selected represented plant size, height and shape (Dansereau, 1943; 1946; and 1947). Many other ecologists have published semi-diagrammatic transects of vegetation to show relations to topography (Dachnowsky-Stokes, 1912; Hough and Forbes, 1943; Beard, 1944; and Egler, 1948). These methods cited are hardly statistical but are means which graphically represented species distribution patterns. Later work by Goodall (1954) set up objective methods for the classification of vegetation. He stated that for an objective description and classification of vegetation, the first requirement is detailed data collection from a representative set of samples. His method of subdividing the quadrats into homogenous groups as regard to species associations was necessarily the basis for the association analyses described by Williams and his co-workers (Williams and Lambert, 1959, 1960, 1961; Lambert and Williams, 1962 in the heathland vegetation of England, and later used by Sarimento and Monasterio, 1969 in studying the Savanna vegetation of the Venezuelan Llanos).

The use of aerial and ground photography as an approach to vegetation is a relatively new science. Infra-red black and white and color photography has been used by workers in certain aspects of resource management and crop disease studies. Shay (1967) suggested the use of remote sensing in agriculture in determining crop acreages, surveying land use, soil surveys, rangeland surveys and a determination of crop conditions. It is already an important tool in identification of crop disease and insect damage (Norman and Fritz, 1965, and Skaptason, 1969) and in the identification of farm crops (Goodman, 1959).

Despite the slow rate at which good aerial photography has become available to range managers, they were among the first to use aerial photography in resource surveys (Poulton, 1968). Range technicians quickly found that they could do more consistent and accurate mapping of resource characteristics, estimate parameters for sampling more precisely, and perform necessary field work more efficiently (Reid, *et al.*, 1942; Clouston, 1950). However the use of color images is relatively new and the added benefit has been noted by several workers (Driscoll, 1971; Heller, 1970; Hoffer, *et al.*, 1966; Holmes and Hoffer, 1966).

Infra-red color film has the advantage of portraying in discriminant color images, differences among subjects in their reflectance of near infra-red radiation not observable to the unaided eye. This film is a false-color, reversal film. It differs from the ordinary color film in that the three sensitized layers are sensitive to green, red and near infra-red radiation instead of the usual blue, green and red. Since all three layers are also sensitive to blue light, the yellow Wratten 12 filter (or equivalent) is used to absorb that part of the spectrum. When exposed and processed properly, this combination of sensitizations and dyes produces false color for most natural objects.

For example, rapidly growing green vegetation produces an image in shades of magenta or red because of a relatively strong near-infra-red reflectance. Bare soil or mature, drying vegetation appears as shades of cyan or blue because of little near-infra-red reflectance.

The Influence of Environmental Parameters

The next step in such an ecological survey is to measure the environmental parameters which may have combined to influence such vegetation patterns. There is a conflict of beliefs among ecologists as to the true influence of environmental factors on plant growth and distribution.

The many soil factors which could influence plant growth and distribution have been the most widely studied group of environmental factors. Robson (1969) found that total soil phosphorus and soil texture were related to pH and were correlated equally well with the distribution of annual medic species. Andrew and Hely (1960), Heyn (1963), and Loveday (1964) concluded that the distribution of medic species depended on soil texture and available nutrients. In an attempt to study the soil factors related to the successional trends of species on the Transvaal Highveld, Davidson (1962) found that the gradual decrease in inorganic nitrogen influenced the rate of succession in the subsere. Apart from pasture and range species of vegetation, Haig (1929) related the growth of Pinus species to such soil factors as percent silt and clay in the A-horizon and to soil nitrogen, while Auten (1945) related the growth of yellow poplar to thickness of the A-horizon.

As well as these factors more directly related to soil fertility we also have to consider factors such as soil temperature. Soil temperature has its immediate effect on seed germination, root development, elongation, and rate of absorption of nutrients. Also it affects soil moisture, soil microorganisms such as Rhizobium (Robson, 1969 and Gibson, 1966) and soil temperature at the immediate ground surface. Soil surface temperature influences not only the entire diurnal increase in temperature but also the convectional currents of air which are of great importance to plants. Shreve (1924) showed how soil temperature was influenced by altitude and slope exposure, stating that this could be one of the reasons why, in the temperate zone, different slopes have vastly different vegetation. This point makes it clear that very few of these environmental factors are independent but each actually depends on another.

Topographic factors most strongly influence soil and micro climatic factors. Shreve (1924), as previously mentioned, indicated how slope aspect influenced vegetation distribution in temperate regions. Differences were greatest when contrasting slopes were orientated one in the west of south direction and the other facing east of north. The controlling factors due to orientation differences were the differences between environmental conditions of opposed slopes rather than the overpowering weight of differences in a single condition. It could however be assumed that since nearly all dissimilarity of conditions must be related ultimately to the differences between the angle of incidence of the sun's rays on the north and south slopes, it appears that soil temperature-related factors are the conditions most closely connected with this effect. Auten (1945) in his prediction of site-index for yellow poplar from soil and topography data, indicated interesting distribution patterns of forest species depending on aspect, exposure and position on the slope. He suggested that the upper slope is usually of coarser textured soil and shallower than that of the lower slopes hence the upper areas are drier because their drainage and evaporation rates are greater and they have a lower water storage capacity. Also the upper slope is less sheltered from the wind and also it loses part of its soil moisture to the lower slopes by seepage.

Andrew and Hely (1960) and Hely (1962) indicated that soil drainage was an important determining factor in the distribution of some of the annual medics. The influence of soil drainage on availability of minor elements to some species and the subsequent effect on growth and distribution has been pointed out by such workers as Robson and Loneragan (unpublished); Marshall and Millington (1967); Piper (1931); Gravan, et al. (1965); Finn, et al. (1961); Aandahl (1948); Norton and Smith (1930). Aandahl (1948) explained the variation in total nitrogen content of soil by slope position, slope gradient, slope curvature and length of slope. Norton and Smith (1930) found a variation in soil profile characteristics with the slope of land surface; as the slope increased the depth of the profile decreased, texture changed from a heavy clay to a silt loam and structure from angular aggregates to subangular, small particles. On the chalk grassland areas of England, Perring (1959) associated various soil chemical factors with slope and exposure. He found that the distribution of soil calcium was strongly correlated with slope aspect. Soil calcium was higher in profiles on the northern exposures. Soil pH and phosphate content distribution were governed by slope and not by aspect; soil phosphate content was lower on greater slopes, soil pH increased with increased slope as did soil potassium.

One remaining pertinent factor found to influence soil condition is the tree drip-ring effect. Ebersohn and Lucas (1965) identified a positive correlation between growth of improved grasses under mature poplar box trees (Eucalyptus populnea), and the higher available phosphorus and exchangeable potassium of the soil in these locations. This was explained by the recycling of nutrients by the deeper-rooted tree species, making such soil nutrients more available to the shallow rooted improved grass species which responded more readily than the native species. With the burning of brush species evident 'drip-ring' burning patterns have been recorded (Motooka, et al., 1967; and Nicholls, (unpublished). In the higher rainfall zones nutrient leaching from this ash could help to explain the subsequent enhancement of legume growth in these locations.

Relating Vegetation Patterns to Environmental Factors

The methods for determining the strength of the relationships between species distribution patterns and environmental factors have not been adequately documented. As was seen earlier such workers as Robson (1969), Andrew and Hely (1960), Heyn (1963), Loveday (1964), Davidson (1962), Haig (1929) and Auten (1945) were able to sort out soil factors in regard to their degree of influence on a particular growth habit of certain vegetation units. If we consider the environmental parameters as factors or cause variables and the vegetation parameters as subject or effect variables, there are several methods of relating these variables (Scott, 1969).

In studies of soil factors and micro-climatic environmental factors, the use of multivariate methods of analysis is appropriate since most of the factors are not independent but are interrelated in a complex way. Univariate analyses do not allow for both single variable effects as well as interactions of these variables. Although these techniques are mathematical, in practice they are often very useful for the simplification and consequent understanding of such a complex environmental situation. Norris (1970) outlined a number of these multivariate methods which could be applied to either or both soil and micro-climatic factors.

(a) Multiple Discriminant Analysis (or Canonical Analysis)

This is a method for selecting the most effective discriminators in a multivariate situation. Horton, et al. (1968) used this procedure to show that the top, slope and depression areas of a gilgaied landscape in Queensland were significantly different taken individually. This is because a univariate analysis ignores the dependence existing between variables which may well be a source of differentation. Little, et al. (1968) also used this approach in a similar situation as did Cooley and Lohnes (1962), Morrison (1967), Austin (1968) and Barkham and Norris (1970).

(b) Path Analysis

Scott (1966), Tukey (1954), Turner and Stevens (1959) and Scott and Billings (1964) provided another potentially useful method whereby the complicated net of interacting causes and effects can be simplified by depicting regression problems with a simple flow diagram. Not only does this method show whether the factor is significant in the statistical sense but as in regression analysis, it shows the quantitative effects of each factor. Path analysis can account for both linear and curvilinear relationships between variables.

(c) Ordination or Principal Component Analysis (P.C.A.)

Seal (1964) and Anderson (1958) arranged individuals on axes with positions determined by the variables and plotted on 'x' dimensional space. This method can be useful when the interrelationship of the variables with high loadings on a component are likely to suggest an hypothesis about the arrangement of the individuals on the component. Norris (1970) used this method to identify the nature of most of the variation in the separate soil and vegetation systems of some beechwoods of Cotswold Hills, England and subsequently to explain much of the change in the vegetation system by variation in the soil system. Holland (1969) used P.C.A. to examine the variation of nutrients in a field. The components provided a useful summary of the variation and by use of a technique similar to that of Barkham and Norris (1970), these components were related to the variation of features other than the nutrients. The (d) Numerical Classification of Lance and Williams (1967, 1968) and the P.C.A. are complementary. However for P.C.A., if the data is clustered (i.e. markedly heterogeneous), these clusters may not be apparent from inspection of the components. When a situation is thought to be heterogeneous, it may be advisable to use the Numerical Classification as a initial technique and then do a P.C.A. of the resulting groups. The problem has been discussed by Lance and Williams (1967).

Even though these methods of relating vegetation parameters to environmental factors can be grouped as such, they all rely on modified usage of multiple regression and correlation analyses.

Sward Dynamics

Literature on the dynamics of sward components is scarce. By superimposing the influence of the grazing animal over the natural seasonal fluctuations in productivity and competitive characteristics of certain species, one can detect rapid successional trends within a sward. Such a trend will not be so rapid in regions where conditions for plant growth are not as conducive as those in the humid tropics (Sampson, 1919). Conditions of high temperature and moisture in the tropics favor vigorous invasion of species once the existing vegetation has been removed, or some other aspect of the environment gradually swings in favor of another species. This is especially so in improved pastures. If a pasture is overgrazed or heavily trampled, exposing bare ground, weed species will quickly spread and unless control measures are taken the dominant components of a community will change rapidly. If the fertility of the pasture or range is allowed to decrease, conditions no longer favor the improved forage species. The recognition of this replacement of one type of plant cover by another is important. Incoming, generally weaker species are good indicators of succession from the more stable communities on overgrazed or otherwise poorly managed lands. The recognition of these indicator species is necessary for good range or pasture management.

In order to evaluate improved species and to recognize species retrogression, periodic measurement of the individual contribution of each of the dominant species is necessary. Even though destructive sampling and sorting provide the most accurate determination of dry matter contribution of species, the time consuming nature of this method obviously limits the area able to be studied. Accurate visual estimates of dry matter contribution of species comes only from practice with the particular species to be studied and by comparison with destructive sampling and sorting. Indices for temperate species have been developed, but these will be different from sub-tropical and tropical species of different growth habits. 't Mannetje and Haydock (1963) developed indices for tropical species based on the rank method of de Vries (1933). This method differed from that of de Vries in the respect that the ranking of species is based on dry weight and not on bulk. A set of factors was used for weighing first, second and third ranks, and the botanical composition was expressed as dry weight percentage.

Species

A review of literature for such a study would not be complete without a short description of some of the more important tropical forage and weed species dominating the vegetation communities under consideration.

Panicum maximum Jacq. (var. trichoglume) Eyles, (green panic), is a fine stemmed variety of Guinea grass (P. maximum). It grows in tufts to a height of 1.5 - 2.0 m but normally 1.0 - 1.5 m. The seed head is a typical panicle borne on a slender stem and is exserted well above the foliage. Crowns of tussocks will develop to a diameter of 28 cm or so (Fox and Wilson, 1959). It possesses remarkable drought resistance, palatability and rapid growth response to rain. It is best adapted to the 600 - 1800 mm rainfall belts of the sub-tropics. Since its introduction from Africa, green panic has become naturalized throughout the tropical and subtropical world.

The climatic adaptability of green panic is complemented by a wide tolerance of soil conditions. It will grow in acid or alkaline soils (pH 5 to 8) but best results occur from slightly acid to neutral soils.

Management of green panic must be directed at protecting the crown region of the tussocks from grazing damage, especially if frosts are prevalent. Profuse flowering and seed setting every 6 weeks under suitable conditions leads to the possibility of managing the stand so that seed set and drop is encouraged at intervals throughout the life of the pasture. Green panic is very acceptable to cattle and will withstand shading beneath brush and trees. It provides strong competition to many tall weeds (Fox and Wilson, 1959).

Establishment of green panic is extremely easy, provided the seed stock is reliable. Good establishment with legume components has resulted in both prepared and ash seed-beds. Aerial establishment of this species has shown remarkable success (Motooka, Plucknett, et al., 1967). Because of its tussocky nature, green panic is compatible with all adapted tropical legumes, especially Desmodium intortum (Mill.) Urb. (intortum), Centrosema pubescens Benth. (centro), Phaseolus atropurpureus Mog. and Sesse ex DC. (siratro), Glycine wightii (R. Grah. ex Wight and Arn.) Verdcourt (Syn. G. javanica L.) (glycine), and Stylosanthes guyanensis (Aubl.) Swarts. (Stylo). In Queensland, in areas in which Medicago sativa L. is adapted, green panic is the dominant grass component of mixed pastures (Fox and Wilson, 1959).

Desmodium intortum (Mill.) Urb. (intortum) was first considered for use in cultivated agriculture in Hawaii where it was introduced from its native Central America in 1947 (Younge, et al., 1964). It is also an important legume in the wetter, coastal areas of northeastern Australia and other areas of the tropics (Bryan, 1969). It is naturally distributed in areas receiving at least 1000 mm of annual rainfall and its optimum use seems to be limited to high rainfall areas. In Australia it is recommended for use only in regions receiving at least 1000 mm of annual rainfall (Bryan, 1969). It has some cold tolerance, but day/night temperatures of 15/10° C to 18/13° C have been found to severely limit seedling growth. The optimum temperature for growth appears to be 30/25° C (Whiteman, 1968).

This perennial, prostrate legume is adapted to a wide variety of soils (Humphreys, 1969) from wetland to well-drained upland (Bryan, 1969), and on soils with a pH as low as 5.0 to 5.5. It has been reported that intortum is difficult to establish in a poorly-prepared seed bed, in which case vegetative cuttings should be used. However excellent establishment of intortum has resulted from aerial seeding into rugged terrain previously cleared by herbicides and fire alone, with no mechanical seed-bed preparation (Motooka, Plucknett, *et al.*, 1967). It is usually slow to establish in the first year since its seeds germinate slowly and early growth is slow, but after 6 weeks favorable conditions runners appear and the plants spread rapidly (Bryan, 1969; Younge, *et al.*, 1964). Inoculation of the seed is necessary even though much natural infection with ineffective strains of *Rhizobia* has been found to occur (Bryan, 1969). Intortum combines well with many of the sub-tropical and tropical grass species. It has been grown successfully with *Digitaria decumbens* Stent, *Chloris gayana* Kunth, *Brachiaria mutica* (Forsk.) Stapf, *Paspalum dilatatum* Poir, *Pennisetum purpureum* Schumach and *Panicum maximum* Jacq. among others (Bryan, 1969 and Fox and Wilson, 1959). In Hawaii (Younge, et al., 1964), a mixture of intortum with Digitaria decumbens yielded more than 22,400 kgm dry matter (D.M.)/ha/year, and grazing livestock produced gains of 896 kgm/ha/year. In another trial (Younge and Plucknett, 1965), a mixture of intortum and Digitaria decumbens receiving an initial application of 1,680 kgm P/ha and grazed by beef animals, produced liveweight gains of 1,304 kgm/ha/year, compared with 34 kgm/ha/year from unimproved pasture. Whitney (1966), Whitney, et al. (1967) and Bryan (1969) found intortum to be a capable fixer of atmospheric nitrogen - in the order of 380 kgm N/ha/year, of which 5% was transferred to the associated grass. Once well established, considerable leaf fall and stolon decay occur, producing a layer of organic material on the soil surface. This layer contributes to an increase in soil organic matter content, and it may be an important source of N for associated grasses (Murphy, 1972; and Bryan, 1969). Whitney, et al. (1967) estimated that fallen dead leaves supply N at a rate of 1.3 kgm/ha/week.

The response of intortum to different management practices (Whitney, 1970; Riveros and Wilson, 1970; and Jones, 1968) is due to the fact that it has large axillary vegetative buds that develop rapidly once the terminal bud is removed. With a low cutting height, most of the axillary buds are removed and, consequently, recovery is slower and persistence may be greatly reduced. With longer intervals between harvests, there is time for the axillary buds that remain to develop new top growth and for root carbohydrate reserves to be replenished (Bryan, 1966).

Stylosanthes guyanensis (Aubl.) Swarts. (stylo). The pan-tropical papilionate genus Stylosanthes is placed in the tribe

Hedysareae, which includes such familiar legumes as the groundnut (Arachis hypogaea) and Desmodium intortum. Stylo is a perennial and is a native of Brazil. It is generally tall and branched with hairy stems, narrow pointed leaves and compact spikes of small yellow flowers (Hutton, 1970). It is a heavily seeding species and shows excellent regeneration from seed. Seedling populations of stylo exhibit a wide range of forms. The general habit can range from stiffly erect to prostrate or near-creeping, while such characters as hairiness and degree of leafiness are highly variable. The successful introduction of the plant into diverse environments (Allen and Cowdry, 1961; Blouard and Thuriaux, 1962; Carre, 1962; Desneux, 1964; Foster, 1961; Gilchrist, 1967) can be attributed to this inherent morphological and associated physiological variability (Tuley, 1968).

Allowing for this variation in form, a typical single plant has a radial form of growth with prostrate, thin and pliable branches spreading out from the deep-rooted central axis. From the radial branches shorter and more leafy growth develops, the shoots being held vertically to a height of about 1 m above the ground. With age and increasing weight, this growth collapses on itself and a mat of tangled, lignified stems is formed, from which new, erect stems arise. The stems do not generally root at the nodes. Stylo exhibits a great adaptability to a wide range of soils and climates. It flourishes under an annual rainfall of over 2500 mm but can also survive in areas with as little as 650 mm and a 7 - 8 month dry season (Rains, 1963; Mosnier, 1963). Another factor which makes stylo a more easily adapted species is that it nodulates freely without seed inoculation, having affinity with the ubiquitous cowpea Rhizobium.

Stylo has a special ability to extract and accumulate phosphorus and calcium from soils low in these elements (Roberts, 1970; and Andrew and Robins, 1969). Many workers have indicated the value of stylo and *S. humilis* as dominant species on very poor soils where other legumes could not survive (Roberts, 1970; Andrew and Hegarty, 1969; Schofield, 1945; Sillar, 1967; Nwosu, 1960; Torsell, *et al.*, 1968; and Douglas, 1965).

Stylo's distribution extends well into the sub-tropics and it can survive light frosts (Gilchrist, 1967; Whyte, *et al.*, 1953). It is however, susceptible to yield reduction through shading. Stylo regenerates well from seedlings and continues to produce into the early part of the dry season, resulting in a more uniform pattern of annual growth than most other sub-tropical forages (Vivian, 1959; Rains, 1963; and Cadot, 1965).

Schofield (1945) found that stylo persisted well with *Brachiaria mutica* and *Pennisetum clandestinum* but was suppressed by *B. brizantha*, *Panicum maximum* var. typica, *P. maximum* var. coloratum, *Melinis minutiflora* and *Paspalum dilatatum*. Personal experience has shown stylo to be productive in grazed stands of pangola grass and to be extremely competitive with weed species on the poorer soils of ridge tops and road-sides.

Glycine wightii (R. Grah. ex Wight & Arn.) Verdcourt (Syn. *G. javanica* L.) (glycine). This tropical legume is indigenous to Africa. It is a vigorous, prostrate, creeping, vine-like perennial which roots at the nodes when in contact with the soil. It requires an annual precipitation of 750 - 1750 mm but can tolerate seasonal droughts due to its deep tap-root and strong lateral root system (Bray, *et al.*, 1969). It is one of the more frost tolerant of the tropical legumes, recovering rapidly with the return of warm weather.

As compared to most other tropical pasture legumes, glycine is very specific and demanding in its soil requirements (Murphy, 1972). It is intolerant to waterlogging, being adapted to deep, well-drained soils. It has a higher demand for P and K than most tropical legumes. Kyneur (1962) found that nodulation of glycine responded to an increase in soil phosphorus regime, making this species most sensitive to P deficiency in the establishment phase. Glycine seems to be more sensitive than most other tropical legumes to excessive amounts of soil Mn and Al, and its response to liming may result from the affect of lime on the availability of Al, Mn or P (Humphreys, 1969; Hutton, 1968; Norris, 1967; and Neme and Lovadini, 1967). Inoculation of the seed is essential, but even when inoculated with the most effective Rhizobium strains, the seedlings often have poor nodulation for 2 - 3 months after emergence.

Glycine is compatible with a wide range of grass species - Chloris gayana, Pennisetum clandestinum, P. purpureum, Panicum maximum, and Paspalum dilatatum (Murtagh and Wilson, 1962).

Paspalum conjugatum Bergius (Sour paspalum, Hilo grass in Hawaii). Hilo grass is a perennial, spreading by long creeping stolons which root at the nodes. It is widespread throughout the tropics and subtropics of both the Old and New World. It is adapted to the more humid tropics, and is common in natural pastures on moist, heavy soils in South America, (Whyte, et al., 1953), Hawaii and South-East Asia, where it has become a serious domestic and range weed pest (Neal, 1948).

Setaria geniculata (Lam.) Beauv. Knot-root foxtail is a perennial, rhizomatous grass. Its tough and wirey stems usually are erect but sometimes are almost prostrate and flattened. Leaves are rather tough, rough and with long hairs on the upper side near the base. Flowering heads are erect, dense, bristly, spikelike, rounded at the tips, 2 - 7 cm long, 1 cm thick, yellowish or brownish, usually slightly twisted; seed (mature floret) is about 1 mm long, wrinkled and plump.

This grass was originally from West Indies and is now found throughout the tropics of both hemispheres, in moist areas at low to medium altitudes. It is unpalatable and a very serious weed pest due to its persistent, knotty rhizomes and prolific seed habit (L. D. Whitney, et al., 1964).

Commelina diffusa Burm. f. Spreading dayflower is a member of the family Commelinaceae or Spiderwort family. It is a creeping, freely branching perennial with a fleshy stem, rooting at the nodes. Leaves are grass-like, lanceolate, green, smooth on both surfaces. The leaf sheath is thin and membranous. Stalked flowers are deep blue.

Short descriptions and reviews of the less dominant improved forage and weed species appear in Appendix III.

CHAPTER III. GENERAL MATERIALS AND METHODS

A project to control dense jungle brush in a clearance and forage establishment program was commenced in October, 1965. Procedures were set up, working on the assumption that the only economically feasible method of clearing these jungle wetlands (considering rugged terrain, dense vegetation, extensive area and labor involved) was through the use of aerially applied herbicides followed by burning, sowing of improved species and a system of grazing management to create a stable and highly productive pasture. The establishment phase of this trial was discussed by Motooka, Saiki, *et al.* (1967) and Motooka, Plucknett, *et al.* (1967). It is evident that of the improved species remaining after three years of intermittent grazing, there are definite patterns of distribution throughout the area where the topography offers a variety of slopes, slope aspects, soil moisture and nutrient gradients, soil surface temperatures and soil depths.

Most of the field data was collected from an established pasture at the Kauai Branch Station of the Hawaii Agricultural Experiment Station, University of Hawaii. The area is at an elevation of 180 meters above sea-level, on a soil characterized as a Typic Gibbsihumox. The twenty hectare area studied was originally vegetated by 'jungle' species such as false staghorn fern (*Dicranopteris linearis* Burm.) and Banks melastoma (*Melastoma malabathricum* L.). Less prevalent species were ohia (*Metrosideros collina* subspecies *polymorpha* (Forst.)), guava (*Psidium guajava* L.), pandanus (*Pandanus odoratissimus* (L.f.)), tree fern (*Sadleria* sp.), java plum (*Syzygium cumini* (L.) Druce), hau (*Hibiscus tiliaceus* L.), downy rosemyrtle (*Rhodomyrtus tomentosa*

FIGURE 1. EXPERIMENTAL SITE AT HAWAII AGRICULTURAL EXPERIMENT STATION, KAUAI BRANCH, SHOWING GENERAL TERRAIN.

(Ait.) Hassk.), lace fern (Stenoloma chinensis), Boston fern (Nephrolepis exultata) and lantana (Lantana camara (L.)).

In 1965-66 two aerial applications of 4.48 kgm/ha of silvex, 2-(2,4,5-trichlorophenoxy) priopicnic acid, were applied at 6 month intervals (October 2, 1965 and June 1, 1966). The area was burned in 1966 to produce a good ash seed-bed. Twelve pasture legume species and varieties along with two grass species were aerially sown into the ash together with the fertilizer. The legume seed together with the appropriate strains of Rhizobia was pelleted with T.V.A. slag using methyl ethyl cellulose ('Cellophas A') as the adhesive. Annual applications of fertilizer were made up to June, 1970. See Table 1 for a list of species and Table 2 for fertilizers used. After the planting date (October 13, 1966) a twelve month establishment period was allowed followed by a 9 month period of continuous grazing. In June, 1969 the area was subdivided and the three sections were rotationally grazed on a 3 week on, 6 week off basis (See Table 2).

Further field observations and data collecting took place on adjacent, freshly burnt jungle area of similar topographic and climatic nature. Species distribution patterns and some soil profiles associated with these patterns were also studied on State land in the Hanalei district in north Kauai where a large area was accidentally burned in 1967 and subsequently reseeded with pasture species.

Laboratory analyses, green-house and growth chamber trials took place at the Kauai Branch Station facilities.

Soil: The soils of both the experimental site at the Kauai Branch Station and the adjacent, freshly burned area of State land fall into the Halii series. Because of the moist nature of this

TABLE 1. SPECIES USED IN AERIAL SEEDING

SPECIES	RATE (kgm/ha)
Glycine wightii (Clarence)	0.56
Glycine wightii (Cooper)	0.56
Glycine wightii (Tinaroo)	0.56
Glycine wightii (Early flowering)	0.56
Desmodium intortum	0.84
Stylosanthes guyanensis	1.12
Phaseolus atropurpureus	0.56
Centrosema pubescens	1.12
Lotononis bainesii	0.56
Trifolium repens (N.Z. Mother white clover)	1.12
Trifolium repens (N.Z. white clover)	1.12
Trifolium repens (Ladino white clover)	1.12
P. maximum var. trichoglume (Green panic)	2.24
Cynodon dactylon (Bermuda NK-37)	2.24

Pangola (Digitaria decumbens) cuttings were distributed from the top of the south-facing slope and covered with a tractor blade.

TABLE 2. CALENDAR OF JUNGLE TO PASTURE CONVERSION

DATE	TREATMENT
Oct. 2, 1965	First silvex application (4.48 kgm/ha)
Feb. 4, 1966	First burn (small area in center of valley)
June 1, 1966	Second silvex application (4.48 kgm/ha)
Oct. 3, 1966	Second burn (most of the area)
Oct. 13, 1966	Aerial seeding (Table 1) + 224 kgm/ha treble superphosphate
Dec. 22, 1966	Aerial fertilization, 224 kgm/ha 18:46:0
Nov. 7, 1967	Start of 9 month continuous grazing
June 27, 1968	Aerial fertilization, 224 kgm/ha 7:30:20
Aug. 6, 1969	Start of 6 month grazing
June 20, 1970	Aerial fertilization, 224 kgm/ha 7:30:20
July 9, 1970	Start of rotational grazing system
March 2, 1970 July 23, 1970 Sept. 28, 1970 Jan. 9, 1971 April 16, 1971 July 18, 1971 Dec. 20, 1971 July 11, 1972	Sampling Dates

soil and its high proportion of humus it belongs to the suborder humox. Because they contain much gibbsite (or bauxite) they can further be classified in the great soil group of gibbsihumox. A more complete description of this soil would be: a deep, well drained, aluminous, ferruginous latosol, Halii soil (Typic Gibbsihumox).

The soils of the Hanalei region are classed as highly weathered, gently sloping, Kaena silty clays rising up into rough broken land of residual material. It is classified as an Hihimanu soil (Ustoxic Humitropepts).

Elevation: The area at or adjacent to the Kauai Branch Station is at approximately 180 meters while that at Hanalei is from 120-450 meters above sea level.

Topography: The main study area at the Kauai Branch Station and adjacent locations was a steep-sided valley, with distinct north and south facing slopes. The slopes were up to 70%.

The Hanalei area had a similar topography with similar but longer slopes. At higher elevations the slopes approached 80-85%.

Rainfall: Both locations have a similar annual rainfall of approximately 2,300 mm, with a distinct winter maximum (Table 3).

Wind: The prevailing wind is a N.E. trade wind with the possibility of strong southerly winds in January through March.

Seed: Seeds of improved pasture species and legume inoculum for green-house, growth-chamber and field experiments were obtained from Wright-Stephenson Seed Company, Brisbane, Australia.

Sampling transects: From Figure 2 it is evident that the valley provides slopes with approximate north and south aspects. The transects shown in the photograph (T1, T2, T3, T4) were located by

TABLE 3. MONTHLY DISTRIBUTION OF TEMPERATURE AND RAINFALL AT THE HAWAII AGRICULTURAL EXPERIMENT STATION, KAUAI BRANCH

	RAINFALL (cm)	TEMPERATURE (°C)	
		AVERAGE MAX.	AVERAGE MIN.
Jan.	23.1	23.5	17.0
Feb.	17.1	23.5	17.5
March	23.6	23.5	18.0
April	27.2	23.5	18.0
May	18.3	25.5	19.5
June	11.9	26.0	20.5
July	16.3	26.0	20.5
Aug.	14.9	26.0	20.5
Sept.	12.4	26.0	20.5
Oct.	20.8	26.0	20.5
Nov.	28.5	25.5	20.0
Dec.	24.4	24.5	20.0
Annual Max.	308.2	25.5	20.0
Annual Min.	175.5	24.5	18.5
Annual Mean	235.5	25.0	19.5

randomly selecting an azimuth for the first transect T1 and then running the others parallel at equal distances apart. A surveyor's transit was used to facilitate the setting up of the transects.

On each transect five steel posts were located on each slope in such a manner that the first post on top of the south-facing slope was at the same elevation as the first post on top of the north-facing slope and so on down the two slope aspects. Once again the transit was used to facilitate the setting up of these 10 sites on each of the four transects. The north-facing slope was divided into four equal parts and from the resulting five sites on this slope a level was directed to the opposite slope, thus locating the corresponding five points.

These 40 sampling sites were used to gather data on soil physical and chemical factors, soil surface temperature, forage productivity and species dynamics.

Photography: Both aerial and ground photographs of the valley situation were taken using an array of film types. Before and after each grazing, sampling sites and overall grazing and regrowth patterns were photographed with black and white film.

(a) Kodak Infra red black and white

(b) Kodak Infra red color - Kodak Ektachrome
I.R. film (IE 135). Processed by Kodak Process EA-5 or E-4.

(c) Real Color film - Kodachrome II and Kodachrome - X

(d) Regular Black and White film - Kodak Panatomic - X

Filter for Infra-red color photography: Hoya K2 Yellow filter.

Soil Analysis

Soil chemical and physical properties where analyzed by the usual methods (Appendix I). Factors studied included, soil moisture, soil pH, total soil nitrogen, extractable soil phosphorus, exchangeable soil potassium, calcium, magnesium and manganese, and water extractable silicon. The soil samples were taken along valley transects and from the drip ring of dead trees.

Plant Analysis

The procedures for plant analyses can be found in Appendix I. The plant analyses included: crude protein, plant phosphorus, potassium, calcium, magnesium, manganese, zinc and iron. The forage species considered were: Stylosanthes guyanensis, Desmodium intortum, Centrosema pubescens, Panicum maximum (var. trichoglume), Melinus minutiflora, Paspalum conjugatum and Digitaria decumbens. After sampling and drying, plant material was ground in a Wiley mill using a #20 mesh sieve. The samples were re-dried at 75° C for at least two hours prior to weighing for the analyses described in Appendix I. The results of this study can be found in Appendix IV.

CHAPTER IV. DISTRIBUTION OF PLANT COMMUNITIES

A plant genus or species may be dominant in a particular environment because it has a competitive advantage over others, in relation to the limiting factors for plant growth in that environment. Within a specific area there are many possible interrelationships of environmental components, each favoring a particular species or species association more than the next. In this way the vegetation of this area may consist of distinct patterns which are results of plant response to a certain environment.

In studying species distribution patterns over an extensive area we must use a sampling method which is both practical and statistically sound. The greater the number of samples taken, the more accurate will be our estimation of the population but too many samples will restrict the extent of the study. Workers in this field have used a range of sampling techniques to record and plot vegetation, from the systematic grid pattern of Williams and Lambert (1959, 1960, 1961) and Lambert and Williams (1962) to completely randomized point or line transect sampling systems of Bauer (1936, 1943), Edwards (1950), Anderson (1942), Parker and Savage (1944), Roe (1947), Dansereau (1943, 1946, 1947), Dacknowsky - Stokes (1912), Hough and Forbes (1943), Beard (1944) and Egler (1948). A relatively new tool in studying vegetation resources is multispectrum aerial and oblique photography (Shay, 1967; Goodman, 1959; Poulton, 1968; Reid, _et al._, 1942; Clouston, 1950; Driscoll, 1971; Heller, 1970; Hoffer, _et al._, 1966 and Holmes and Hoffer, 1966).

Once the data on such vegetation patterns has been collected, accurate and efficient interpretation is necessary. Methods of handling such data have been documented, ranging from the subjective, descriptive techniques of Dansereau (1943, 1946 and 1947) and his co-workers in the earlier years of plant ecology, to the more objective classification techniques of Goodall (1954) and later Williams and Lambert (1959, 1960 and 1961).

To supplement the earlier introductory description of the vegetation existing in the experimental area before land clearing procedures were commenced, reference should be made to Moomaw and Takahashi (1960). These workers did a detailed vegetation survey of an adjacent bauxitic area both before and after burning. No reseeding practices were carried out. They recognized three species associations in the regrowth after burning. The ridge-top Setaria-Paspalum association; a Setaria-Nephrolepis association at mid-slope, and an association of woody species in the valley bottom. No attempt was made to relate these patterns to aspects of the environment.

After the procedures of land clearing and reseeding of the experimental area (Motooka, Plucknett, et al., 1967), the improved forage and weed species soon exhibited distinct patterns of distribution. The species and species associations studied in more detail were: Stylosanthes guyanensis, Desmodium intortum, Panicum maximum (var. trichoglume), Paspalum conjugatum - Setaria geniculata association, and Commelina diffusa. Distribution graphs of other less dominant weeds and improved species are represented in Figure 8.

MATERIALS AND METHODS

Transects: The valley provided slopes with approximate north and south aspects. To study the distribution and movement of species and to provide soil, temperature and plant sampling sites, thirteen (13) parallel transects across the valley were set up (Figure 2). The methods used to set up such a set of sites were described in the 'General Materials and Methods'.

The 'belt' transect is a name given to a modification of the line transect method of sampling vegetation. As one of the aims of this study was to measure species movement up and down the slope or their removal from or invasion of the sward, it was decided to use a 'belt' method of sampling. This 'belt' is made up of a 'rolling' quadrat, one meter square, along each transect. At each quadrat position along the transect, presence and absence data were recorded for each weed and improved species. This provided a means of mapping the distribution patterns of particular species at different locations along each transect. These data were mapped in the form of bar graphs along each transect. The bar graphs represented the distance along the transect within which the particular species was located.

Aerial and Ground Photography: Before each destructive sampling of vegetation, black and white photographs were taken of each sampling site. This photographic record aided subsequent description of pasture condition before and after each grazing period.

In an attempt to identify grazing patterns, black and white and color infra-red photographs were taken from opposite slopes. To aid the identification of distribution patterns of pasture and weed species, aerial and oblique infra-red color and true color photography were used. These photographs were taken from adjacent slopes and from

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FIGURE 2. AERIAL VIEW OF EXPERIMENTAL AREA, SHOWING LOCATIONS OF SAMPLING TRANSECTS.

an altitude of 450-600 m. These photographs were used in conjunction with those taken from the ground and visual ground-truth observations in order to set up a vegetation mapping system of the experimental area.

RESULTS AND DISCUSSION

The diagrammatical representation of species distribution patterns along belt transects are shown in Figures 3 to 8. These figures illustrate the presence of the more dominant species or species associations as measured in a total of 2,103 quadrats along the 13 valley transects. The dark bars represent the length of the belt transect in which each species was recorded.

Stylosanthes guyanensis. It is evident from Figure 3 that stylo is most commonly found on the tops of the slopes and ridges. Along transect 1 stylo was found all the way to the stream, whereas on other transects it was not found towards the bottom of the slope. Transect 1 lies on a very steep escarpment where severe soil erosion has removed everything except rocky material. Here stylo had the competitive advantage and formed a pure sward. Along transects 2, 3, 5, 6, 7, 8, 9, small areas of stylo appeared towards the bottom of the slope. In actual fact these locations corresponded to the points of interception of spurs and the transects. On these spur tops, conditions are like those found on the tops of the slopes and tend to favor stylo and weed species more than the more vigorous improved species. This association of stylo and weedy grass and brush species is indicated in Figure 8.

Desmodium intortum. Figure 4 illustrates the distribution pattern of intortum. Its general pattern was toward the middle section and

Stylosanthes guyanensis

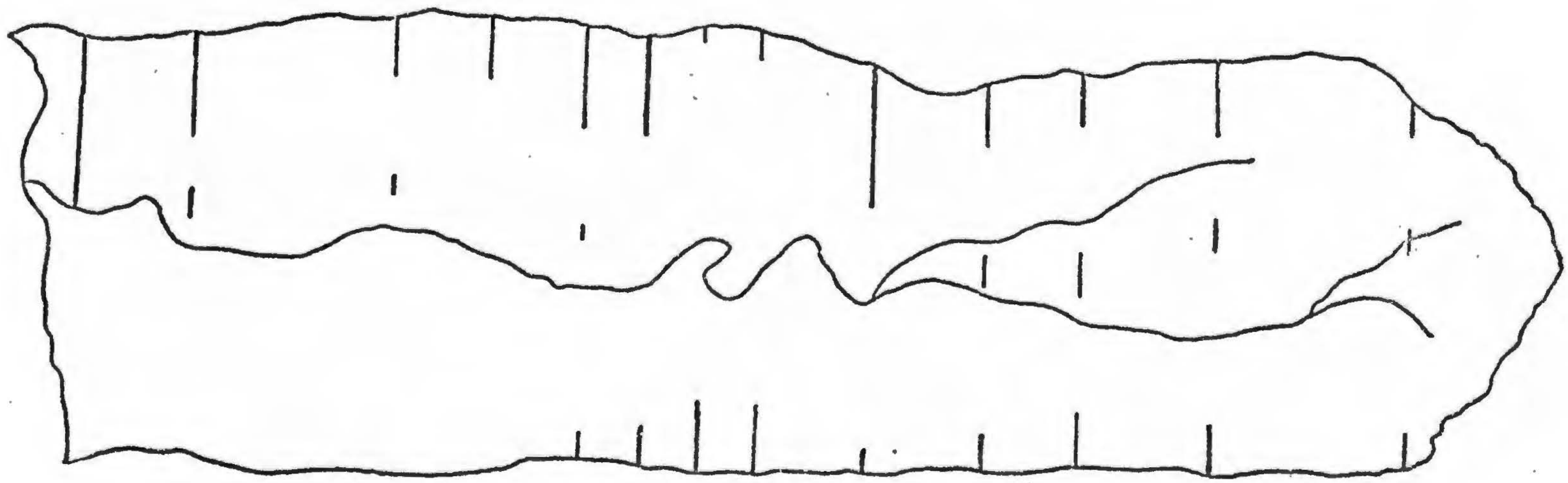

FIGURE 3. DISTRIBUTION OF PASTURE LEGUME *Stylosanthes guyanensis* ALONG SAMPLING TRANSECTS.

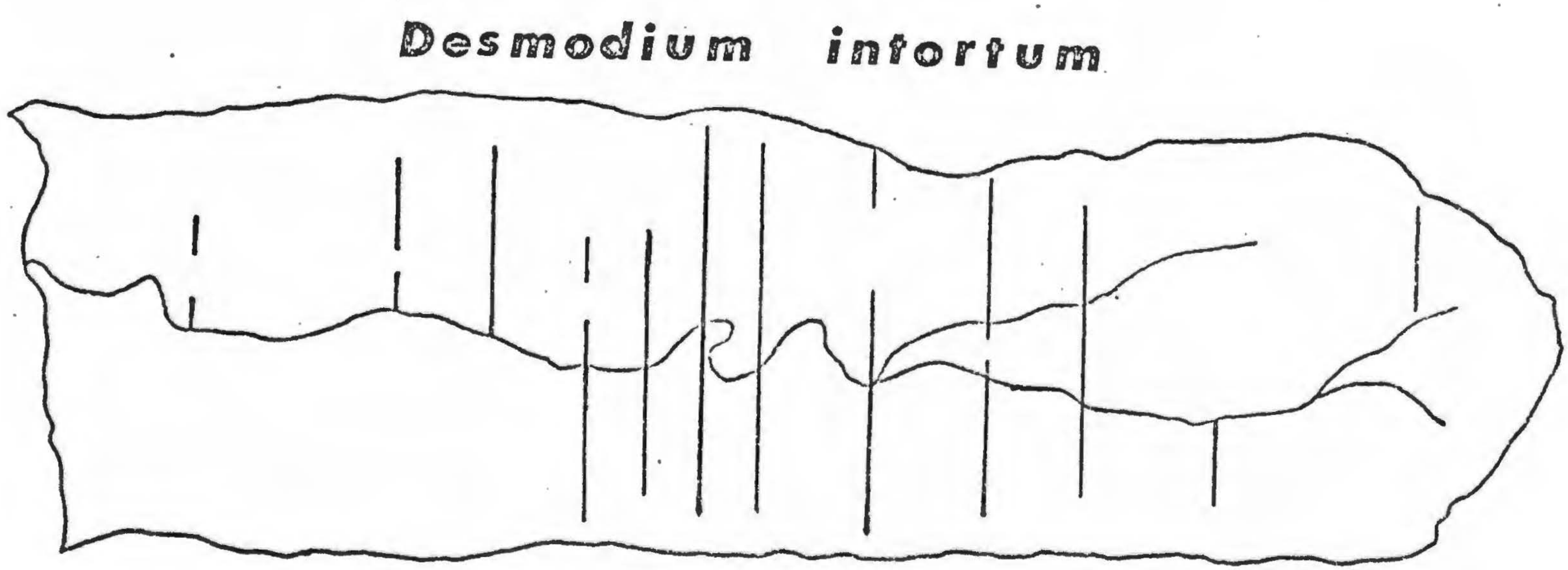

FIGURE 4. DISTRIBUTION OF PASTURE LEGUME *Desmodium intortum* ALONG SAMPLING TRANSECTS.

bottom of the slopes. As will be seen in Chapter V the micro-environment was more favorable for growth of the more vigorous improved species in these locations. Where intortum was found on the ridge tops, growth was poor and there was evidence of nutrient deficiencies. With further weakening of intortum stands by periodic grazing, stylo with its competitive advantage eventually took over and became dominant. The opposite was true for stylo seedlings that came up in areas on the lower slopes. They were quickly shaded out by the species that were more competitive at these locations.

Panicum maximum var. trichoglume. As can be seen from Figure 5, green panic and intortum had a similar distribution pattern. Table 7 illustrates the close relationship between these two improved species. Their similarity in response to the same site factors will be made more evident in Chapter VI. It is seen from Figure 53 that in the regions of transects 8 and 9 where pangola grass (Digitaria decumbens) was the dominant introduced grass, green panic was not able to compete and disappeared from the sward.

Paspalum conjugatum - Setaria geniculata association. This particular weedy grass community was considered important from the standpoint of having a distinct distribution pattern, and as will be seen later, as a valuable indicator of sward condition. It is evident from Figure 6 that the pattern of distribution is similar to that of stylo, being confined to the upper slopes and ridges. Figure 8 illustrates the close relationships between this weedy grass community and the improved forage legume, stylo. It was noticed throughout the period of data collection that following severe overgrazing, this weedy grass association appeared, even toward the bottom of the slope.

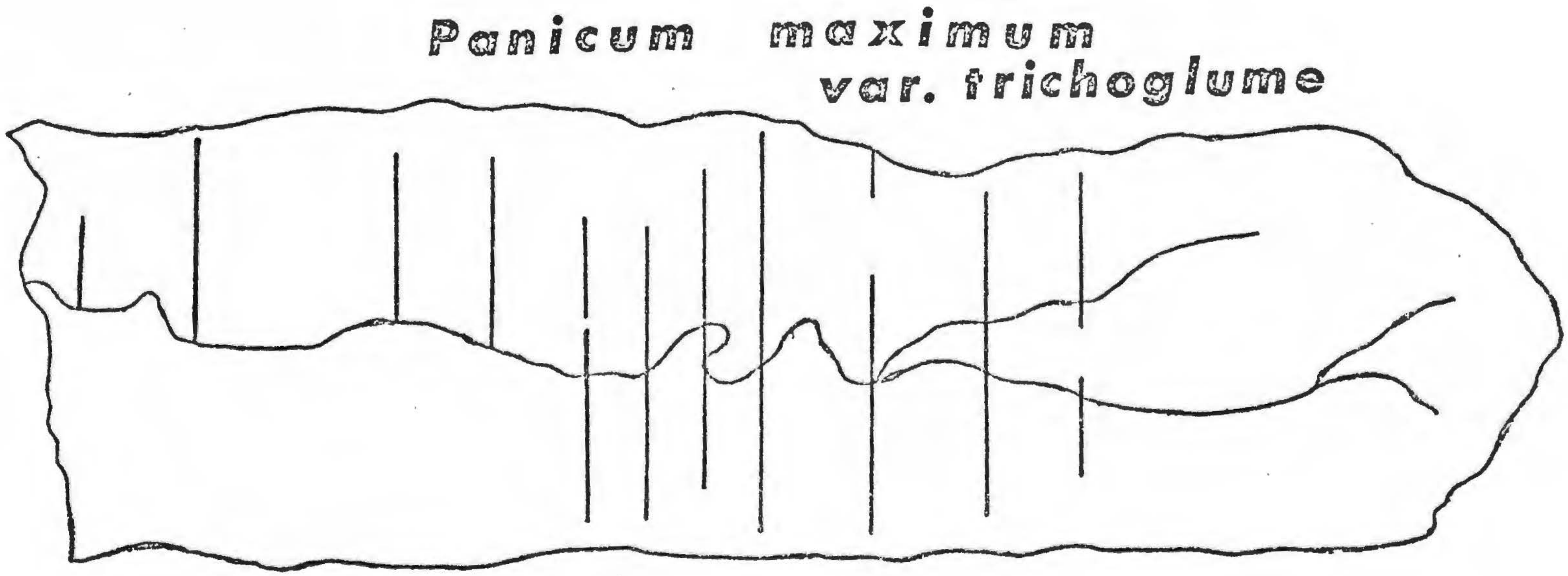

FIGURE 5. DISTRIBUTION OF PASTURE GRASS Panicum maximum (var. trichoglume) ALONG SAMPLING TRANSECTS.

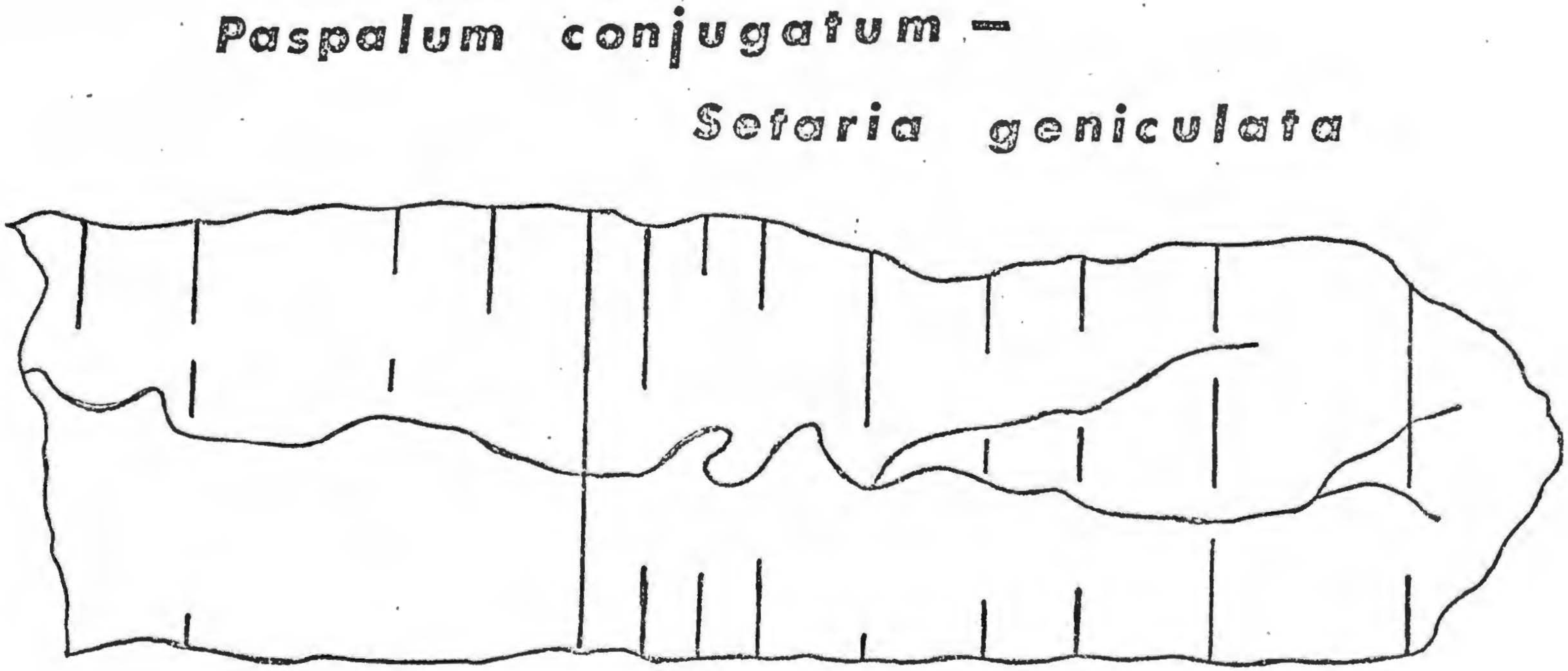

FIGURE 6. DISTRIBUTION OF WEEDY GRASS ASSOCIATION OF Paspalum conjugatum AND Setaria geniculata ALONG SAMPLING TRANSECTS.

However as will be seen later, with an adequate rest period, the superior competitive ability of the improved species forced out these less vigorous, weedy grasses.

Commelina diffusa. Another weed species which exhibited a distinct pattern of distribution was spreading dayflower (Figure 5). This species remained in association with the intortum/green panic community from mid-slope to the valley bottom (Figure 8). Spreading dayflower, although always present, especially during the wet winters, was more dominant after overgrazing, less so after periods of rest.

The data on the remaining weedy species in Figure 8 (lantana, Banks melastoma, Hawaiian elephantsfoot (Elephantopus), stachytarpheta and American burnweed) were not collected over all of the 13 transects, but only from transects T1 - T4. It is evident from this series of graphs that the more woody, perennial weed species, namely lantana, Banks melastoma, elephantopus and stachytapheta, are confined to the tops of the slopes and ridges, in association with stylo. The remaining annual weed, American burnweed, is found more toward the bottom of the slopes and valley bottoms in association with intortum and green panic.

In an effort to identify vegetation patterns and evidence of grazing patterns, multispectral photography was used. Infra-red color, infra-red black and white, regular black and white and true color photography made it possible to identify patterns on a large scale.

Infra-red color photography enabled detection of definite differences in vegetation patterns. From Figure 9 it is evident that the different tones of pink represent distinct vegetation groups. Figure 9 (a) is an aerial view taken from 450 m. The grey-pink regions

Commelina diffusa

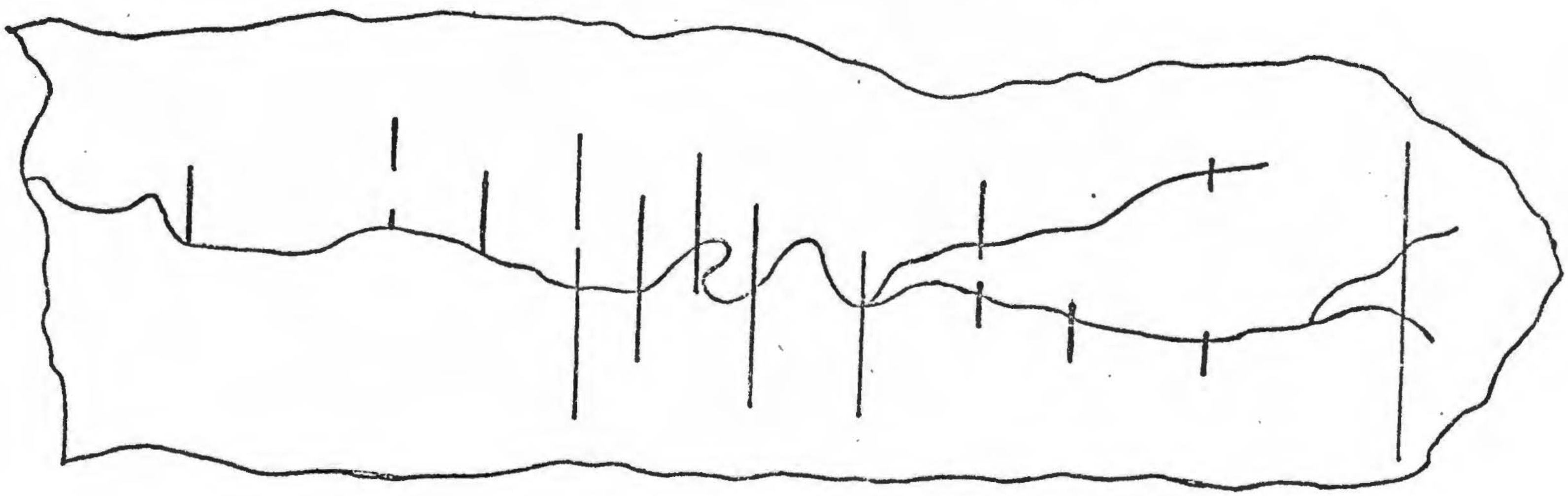

FIGURE 7. DISTRIBUTION OF THE WEED Commelina diffusa ALONG SAMPLING TRANSECTS.

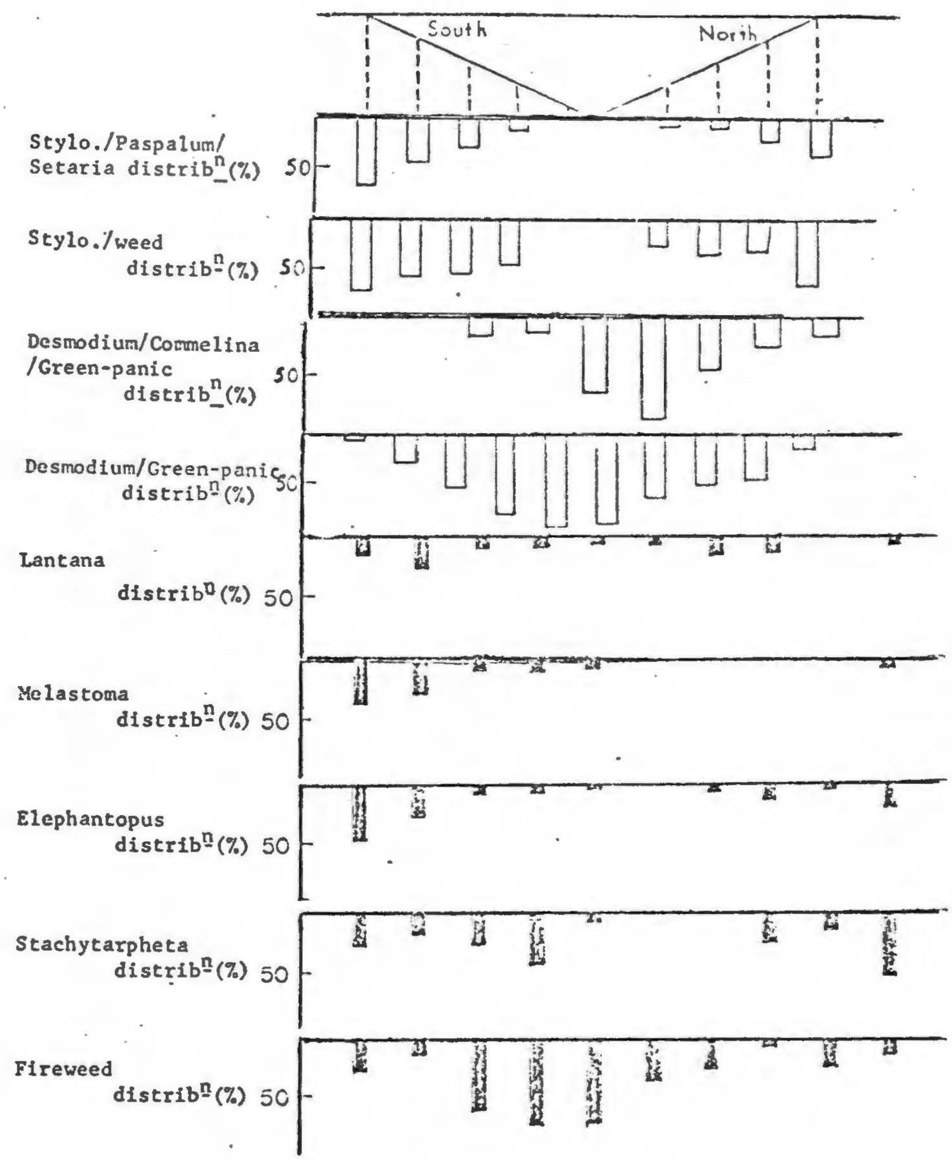

FIGURE 8. DISTRIBUTION PATTERNS OF SOME OF THE MORE COMMON WEED SPECIES AND THEIR ASSOCIATIONS WITH IMPROVED FORAGE SPECIES. FREQUENCY IS EXPRESSED AS PERCENT OCCURRENCE IN TOTAL NUMBER OF QUADRATS SAMPLED.

represent the open sward of green panic and intortum while the medium pink-red areas on the tops of the slopes represent the stylo - grassy weed community. The darker, pink-red clusters obviously represent Psidium guajava in the valley bottoms and ohia (Meterosideros collina sub-species polymorpha) on the upper slopes. The white areas are kukui (Aleurites moluccana) trees, generally in gulleys where there is adequate moisture. There is a similar trend in Figures 9 (b) and (c) with the shorter, narrow-leaf forage associations showing up as a lighter pink, taller, weedy brush (Melastoma malabathricum) medium pink-red and taller, more dense ohia and java plum (Syzygium cumini) a darker red. Because of the oblique angle of incidence represented in Figure 9 (d) the grass dominant sward appears to be more grey with the brushy weeds still dark pink-red.

It is evident from this group of photographs that with limited ground-truth work, the interpretation of larger scale, aerial surveys, using infra-red color film, would be relatively simple and would supply valuable ecological data.

Figure 10 illustrates the value of infra-red black and white photography in detecting grazing patterns. The area on the left had just been grazed for 4 weeks whereas that on the right had been rested for 5 weeks after grazing. From above, through the naked eye, this contrast was not so evident. However a ground-truth survey made it evident that the area on the left had been subjected to considerable overgrazing and trampling damage. If this type of photography could be used in conjunction with color photography on larger scale pasture or range aerial surveys, much time, labor and natural resources could be saved.

(a)

(b)

FIGURE 9. (a) (b) AERIAL COLOR, INFRA-RED PHOTOGRAPHY SHOWING DIFFERENTIAL COLOR IMAGES OF WEED AND FORAGE SPECIES.

(c)

(d)

FIGURE 9. (c) (d) AERIAL AND OBLIQUE COLOR, INFRA-RED PHOTOGRAPHY SHOWING DIFFERENTIAL COLOR IMAGES OF WEED AND FORAGE SPECIES.

FIGURE 10. OBLIQUE BLACK AND WHITE, INFRA-RED PHOTOGRAPHY SHOWING GRAZING PATTERNS. HEAVILY GRAZED SECTION ON LEFT AND SECTION AFTER A FIVE WEEK REST PERIOD ON RIGHT.

Two remaining situations caused deviations from the overall pattern of species distribution. One was the tree drip-ring effect. Following burning there was an evident pattern of white ash beneath charred trees (Figure 11). This pattern remained until the first rainfall. As will be seen later in Chapter V, considerable leaching of water soluble nutrients occurred from this ash residue. The possible enhancement of soil fertility conditions in the tree drip-ring because of this phenomena as well as that of nutrient recycling by the deep rooting tree species, lead to the more vigorous growth of legume forage species at these locations (Figure 12). In particular, Glycine wightii seems to be more adapted to such sites. This species is noted for its difficulty to become established. The improved environment in the vicinity of these dead trees obviously enhanced its competing powers. Another explanation may lie in the fact that owing to the climbing habit of glycine, such physical supports have protected it from the grazing animal.

The second effect is that caused by staghorn fern residues (Dicranopteris linearis). Explanation of this effect is much more complex. Even 2 to 3 years after burning of this vegetation, very little revegetation by other species occurs even where only a light layer of residue remains (Figures 13 and 14). It is possible that some organic compound may be leached from the burnt rhizomes, a compound that inhibits seed germination or seedling growth. As will be seen in Chapter V, the ash from such a burning is very low in most water soluble minerals. More detailed study of this problem is needed, especially considering the vast areas of Hawaii and the tropics that are covered with weedy fern. A simplified explanation from such

FIGURE 11. BURNING PATTERN IN DRIP RING OF TREE.

FIGURE 12. DIFFERENTIAL GROWTH PATTERNS OF LEGUMES IN THE TREE DRIP RINGS.

FIGURE 13. STAGHORN FERN RESIDUE LEFT AFTER BURNING.

FIGURE 14. GROWTH OF Stylosanthes guyanensis ON STAGHORN FERN RESIDUE FOUR YEARS AFTER BURNING.

revegetation failures may be that the extreme density of underground rhizomes remaining after burning simply does not allow seedlings to survive. It may also be that this mass of underground tissue may be exuding substances phytotoxic to most other species and that gradually this material is leached away, enabling seedlings of more tolerant species to take hold after some period of time. The only improved forage species showing considerable adaptation to such conditions was stylo (Figure 14). Weak seedling growth of other improved species did occur after several months. American burnweed seedlings were the most tolerant weed seedlings emerging on this mulch.

SUMMARY AND CONCLUSION

In an effort to verify and map the evident distribution patterns of forage and weed species over the sloping terrain of the experimental area, data were collected and observations were made through the use of both transects and aerial and ground photography.

Of the improved species studied, Stylosanthes guyanensis was the only improved forage species dominant at ridge-top locations and on the shallow soils of spurs and steep, eroded areas. Other important community components at these locations were the weedy associations of Paspalum conjugatum, Setaria geniculata, Melastoma malabathricum, Elephantopus mollis, Lantana camara and Stachytarpheta urticaefolia.

At locations further down the slope and in the valley bottoms the more productive sward of improved species was dominated by Panicum maximum (var. trichoglume) and Desmodium intortum. The weed species occurring most frequently at these sites were Commelina diffusa and the annual, Erechtites hieracifolia. These species were particularly

Two isolated situations were recognized which caused deviations from the overall pattern of species distribution. One was the enhanced growth of legumes in the drip-ring of dead trees and the other was the depressed plant growth on the burned mulch of Dicranopteris linearis.

Aerial and oblique infra-red color photography enabled the large scale identification of forage and brushy weed communities. By using infra-red black and white photography it was possible to identify patterns of grazing intensities. With increased use of such a device, more reliable indices can be set up for different species and species communities, making infra-red photography an extremely useful tool in future pasture and range management programs.

CHAPTER V. ENVIRONMENTAL FACTORS

There is a conflict of opinion among ecologists as to the true influence of environmental factors on plant growth and distribution. Many such as Etter (1943), Braun-Blanquet (1932) and Curtis (1955) believe that edaphic factors have very little influence on the structure of a plant community. However, several other workers such as Shreve (1924), Auten (1945), Norris (1959), Andrew and Hely (1960), Heyn (1963), Loveday (1964), Horton, et al. (1968), Robson (1969) and Hallsworth (1969) think that edaphic factors have a stronger influence than climatic factors. A more realistic approach to such a study would be to include both schools of thought and to weigh all possible interactions of both climatic and edaphic factors against species patterns of distribution (Went, 1953; McMillan, 1956; Maycock and Curtis, 1960; Scott and Billings, 1964; Gillison, 1968).

The factors most widely studied regarding influence on plant growth and distribution are soil nutrient parameters (Robson, 1969; Andrew and Hely, 1960; Heyn, 1963; Loveday, 1964; Davidson, 1962; Haig, 1929 and Auten, 1945); soil temperature (Robson, 1969; Gibson, 1966 and Shreve, 1924); topographic slope factors (Shreve, 1924; Auten, 1945; Andres and Hely, 1960; Marshall and Millington, 1967; Graven, et al., 1965; Finn, et al., 1961; Aandahl, 1948; and Perring, 1959); and the tree drip-ring effect (Ebersohn and Lucas, 1965).

Even though we may measure the complete set of habitat factors, the amount or intensity of any particular factor necessary to cause a structural response within a community can only be determined by the plant itself. With this in mind we can see that a particular plant community may not be an indicator of a soil type alone, but may be an indicator of a combination of environmental factors.

The objective of this aspect of the study was to measure important trends for some of the more pertinent environmental parameters. It was impractical to attempt to collect data on all constituents of the environment.

MATERIALS AND METHODS

Soil samples

Soil samples from the established pasture area at the Kauai Branch Station were taken before any vegetation recording took place. An initial sampling and analysis trial was set up along one transect only. Two 15 cm diameter cores per site along the transect were taken to a depth of 20 cm. These samples were analyzed separately for N, P, K, Ca, Mg, Mn, water extractable silicon, pH and moisture content. The variation between samples taken from one site was very low. It was therefore decided to take two cores per site along each transect and bulk for subsequent macro- and micro-nutrient analysis, pH and moisture determinations. A similar sampling technique was adopted for the adjacent, freshly burnt area, where only one valley transect of ten sampling sites was used.

Soil samples in the 'drip-ring' of dead trees were collected from sites 60 cm apart on a diameter of the circle beneath the original canopy of the tree.

All samples were air-dried and sieved through a 20 mesh screen. Moisture factors were determined for each sample during the course of the analytical work. Soil pH measurements were performed using a

Beckman pH meter in a 1:1 soil-water paste which was allowed to equilibrate for about 24 hours. See Appendix I for details of soil analysis procedures.

Soil profile

At each of the 40 sites at the Kauai Branch Station and at selected locations at Hanalei, soil profile pits were dug. These profiles were about one meter deep and 90 cm wide, enabling data to be collected on the nature of existing profiles. Depth, structure, color and abnormalities of these horizons were recorded.

Slope

The slope of the land surface at each sampling site was recorded using a Haga altimeter. Both aspects of slope at each site were considered; namely, the degree of slope along the line of the transect (vertical) and that at right angles to this direction (horizontal).

Air temperature at the ground surface

In an effort to measure the variation of such a factor from one position on the slope to the next and from one slope to the other at different times of the day, 3 Taylor maximum-minimum mercury-in-glass thermometers were set up at equal intervals on one north- and one south-facing slope. In order to protect these instruments from cattle, a heavy metal case was constructed about each thermometer such that adequate air circulation across the instrument was possible (see Figure 15). The casing was painted with silver paint for protection against rust as well as heat build up and transmission through the air to the thermometer. Temperatures were read daily, recording daily maximum and minimum temperatures and the temperatures at 8 a.m. and 4 p.m.

FIGURE 15. APPARATUS USED FOR MEASUREMENT OF TEMPERATURE AT THE GROUND SURFACE. METAL PROTECTIVE CASING SURROUNDING TAYLOR MAXIMUM - MINIMUM THERMOMETER.

'Drip-ring' effect

Soil samples were taken at 60 cm intervals along the diameters of the 'drip-ring' of dead ohia trees for subsequent nutrient analyses. In an attempt to determine the nature of nutrient recycling by the burning of brush species, samples of ohia, guava, Java plum, melastoma and false staghorn fern were burned under controlled conditions. The water soluble fraction of this ash was analyzed for micro-nutrients. The water soluble fraction was extracted by leaching 10 gms of ash in a Buchner funnel with 230 ml portions of distilled water until the equivalent of 1840 ml of water was used. Each 230 ml leachate fraction was stored separately in plastic vials for separate analyses. These amounts of ash and water used resulted from considering the following information. Firstly, the average concentration of ash residue after burning these brush species in the field was about 1 kg of ash per square meter of the tree 'drip-ring'. From this, the amount to be used per Buchner funnel to simulate field conditions in the laboratory was calculated. Secondly, the average monthly rainfall was taken as being 20 cm. From this the equivalent of the total rainfall simulated in the laboratory was calculated and divided into 2.5 cm increments.

RESULTS AND DISCUSSION

Soil Moisture, Nutrients and pH

I. Along Valley Transects

In addition to soil moisture measurements, soil chemical properties tested were: total soil nitrogen, extractable phosphorus, exchangeable potassium, calcium, magnesium, manganese, water-extractable silicon, and pH (in suspensions of 1:1 soil:water, 1:1 soil:1N potassium chloride and 1:1 soil:1N potassium sulphate). Methods used in these analyses are outlined in Appendix I.

Soil Moisture (% O.D. soil): It is evident from Figure 16 that there was a soil moisture gradient along all valley transects sampled.

The explanation for this increase in soil moisture as one goes down the slope cannot be limited to one factor. The dominant factor would be the downward movement of drainage water through the surface horizons of the soil parallel to the soil surface. Also as was seen from the soil surface temperature and soil profile data, the drying influence of wind and the lower water storage capacities of the shallower, surface horizon of the profiles higher up the slope could also help to explain the trends. More humid, still conditions at the valley bottoms may also help the soil to maintain a higher soil moisture content.

This trend was consistently independent of the time of year the sample was taken. Transect T2 was sampled early in summer (June, 1969) and transects T1, T3 and T4 were sampled in December 1969, in the middle of the wet season. Transect T5 was sampled in December 1971. T2 had a lower overall soil moisture content due to the drying out of the soil during summer.

Soil Nutrients

(a) Total Nitrogen (% O.D. soil). It is evident from Figure 17 that there was an increase in total soil nitrogen going down the slope. This could be explained in several ways; however, there is little doubt that it is a response to a combination of factors. On going down the slope there is a similar trend in soil moisture and other soil nutrients, making conditions more suitable for soil micro-organism activity and

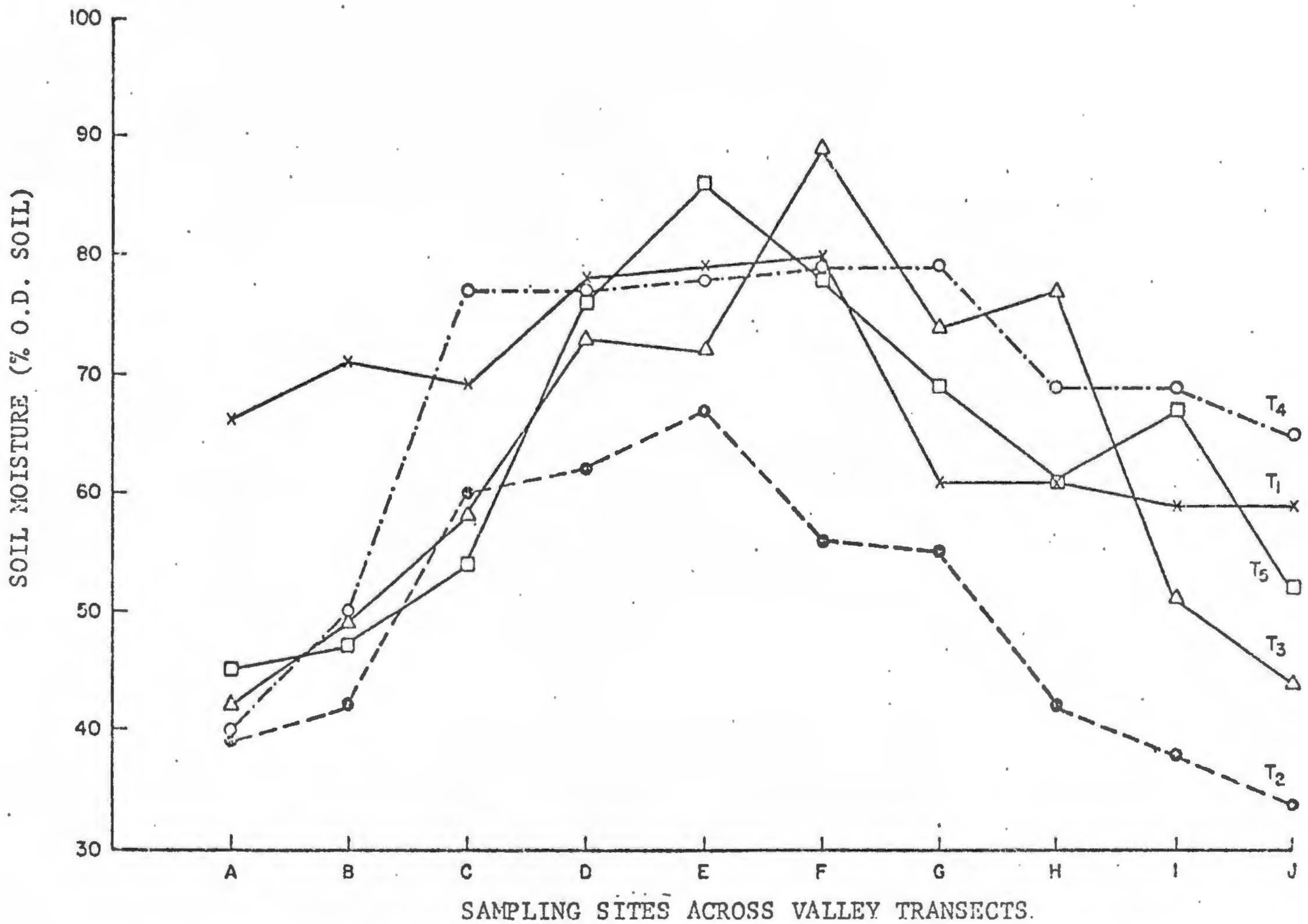

FIGURE 16. THE GRADIENT OF SOIL MOISTURE ALONG A SERIES OF VALLEY TRANSECTS. SITE 'A' IS AT THE TOP OF THE SOUTH FACING SLOPE AND 'J' AT THE TOP OF THE NORTH FACING SLOPE.

plant growth. The more vigorous plant growth provides more organic matter for nitrification and a stronger legume component which could enhance the soil nitrogen supply by actively fixing atmospheric nitrogen.

The higher values of total N at all points along transects T2 and T5 can be explained by the fact that these samples were analyzed soon after sampling and therefore at a higher soil moisture content. The samples from the other transects were stored for some time before analysis, thus explaining the lower soil nitrogen levels.

(b) Extractable soil phosphorus (ppm O.D. soil). Figure 18(a) represents the mean values of extractable soil P from corresponding sites on all five transects. The three histograms represent the mean value of extractable P at sites grouped thus: A through B, C through H and I through J respectively. There was little evident variation of these mean values along the valley transects.

(c) Exchangeable soil calcium (m.e./100 gms O.D. soil). Figure 18(c) represents the mean trend of exchangeable soil calcium along the valley transects. There were generally higher values towards the bottom of the slopes. There was considerable variation in actual results. The highest values recorded were between 2 to 3 m.e./100 gms at positions near the valley bottom and the lowest was 0.1 m.e./100 gms at a site on the top of the slope.

(d) Exchangeable soil magnesium (m.e./100 gms O.D. soil). It is evident from Figure 18(d) that in the case of exchangeable magnesium, the increase going down the slope was more significant than the trend for exchangeable calcium. The locations at the top of the slope had a mean value of about 0.5 m.e./100 gms, whereas the sites lower on the slope had a mean value of 1.5 m.e./100 gms with an actual high of

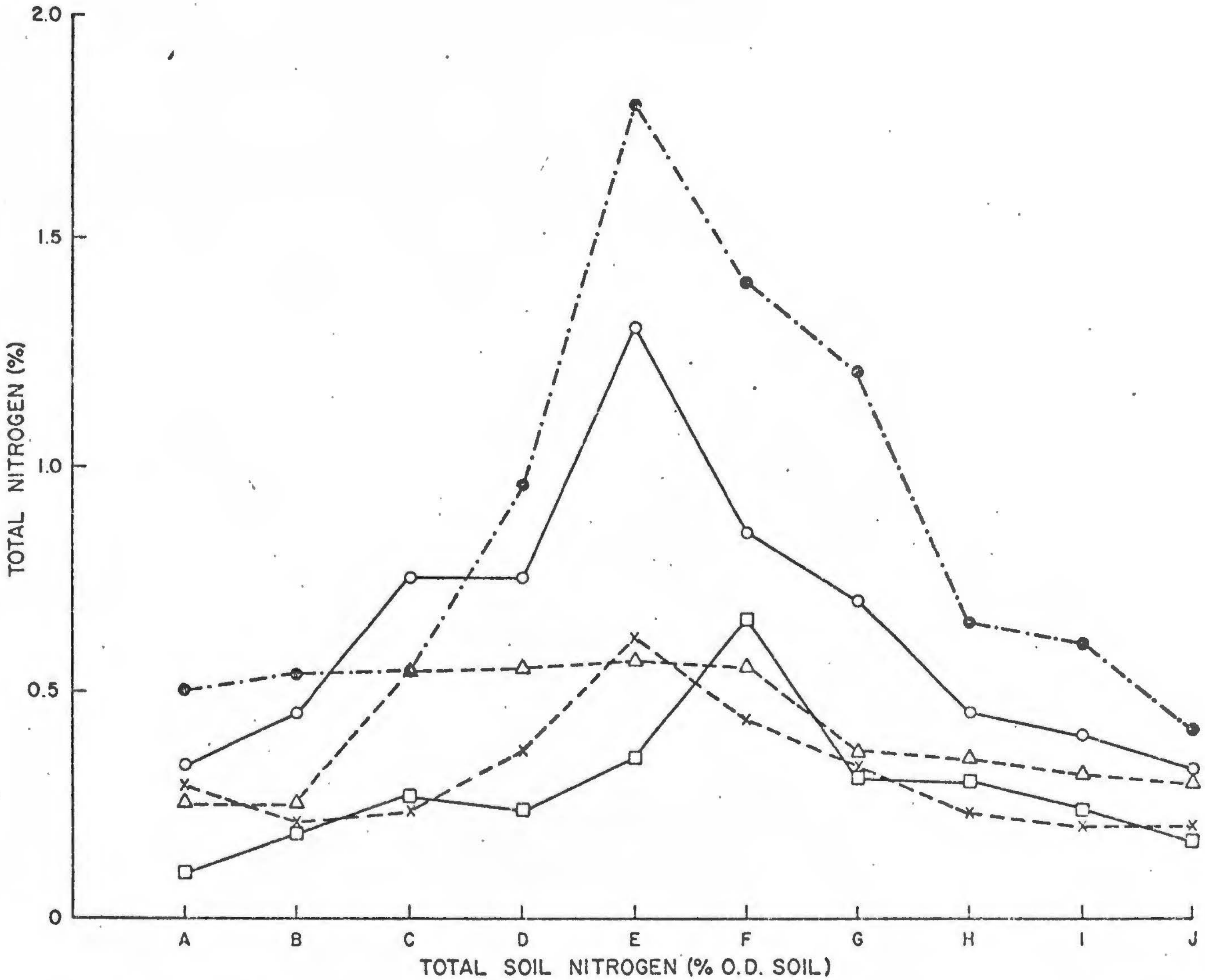

FIGURE 17. THE GRADIENT OF TOTAL SOIL NITROGEN (% O.D. SOIL) ALONG A SERIES OF VALLEY TRANSECTS.

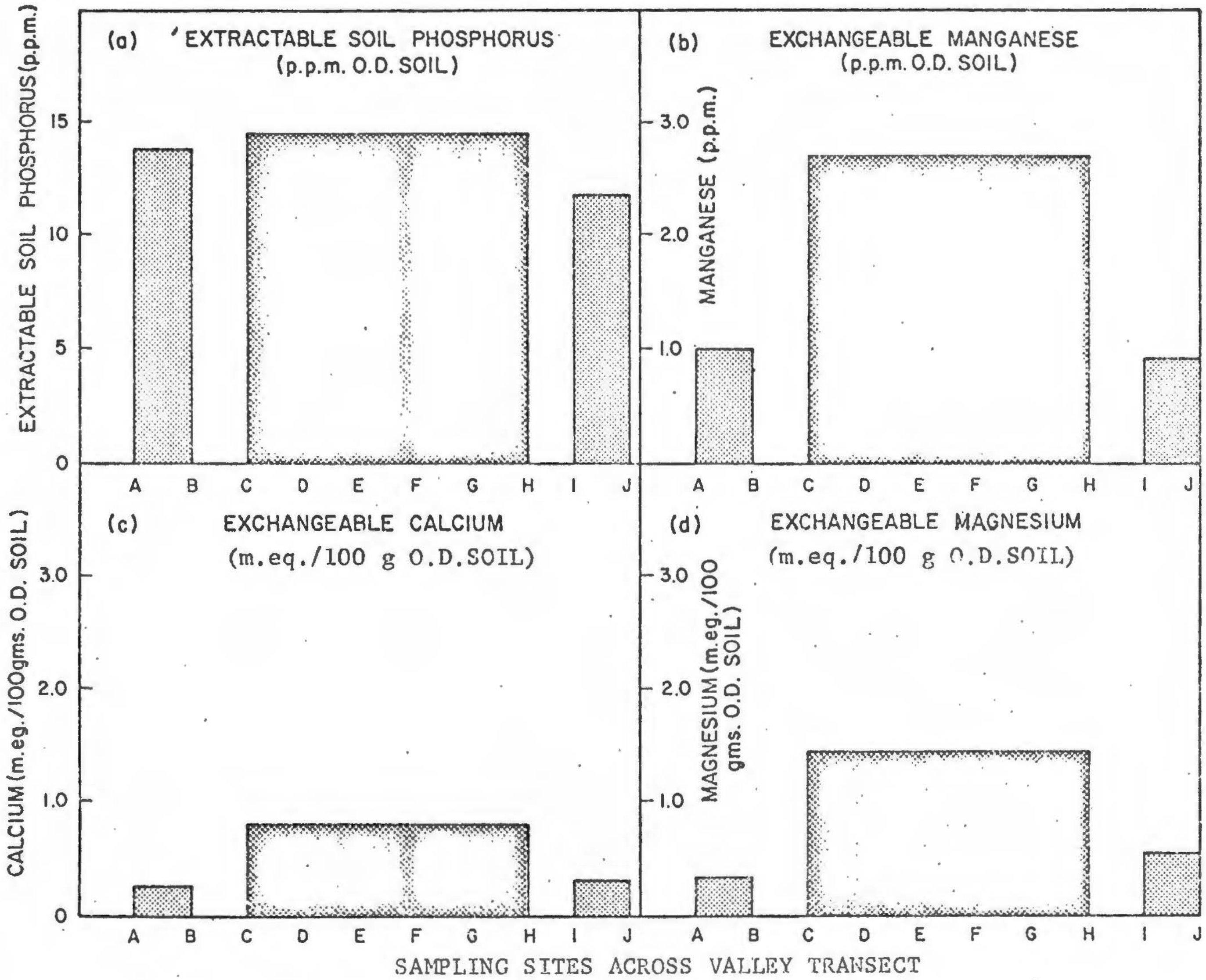

FIGURE 18. MEAN EXTRACTABLE SOIL PHOSPHORUS AND EXTRACTABLE SOIL MANGANESE, CALCIUM AND MAGNESIUM, IN SOIL SAMPLES.

2.8 m.e./100 gms at one location near the valley bottom.

(e) Exchangeable soil manganese (ppm O.D. soil). Figure 18(b) represents the mean values for exchangeable soil manganese along the valley transects. Once again this general trend of mean values seems significant. The range is from a low mean of 1 ppm at locations on the top of the slope to a high mean of 2.5-3.0 ppm in samples toward the valley bottom. Actual low and high values recorded were 0.3 ppm and 5 ppm respectively.

(f) Exchangeable soil potassium (m.e./100 gms O.D. soil). The results based on the analyses for exchangeable soil potassium were extremely variable. The values were well below the range of 0.2-0.8 m.e/100 gms recorded for soils of the same series. Up until 1970-71 no potassium was included in the fertilizer mix and intortum exhibited typical potassium deficiency symptoms. The addition of K in the fertilizer mix in 1970 removed this symptom but at the end of the 1971 wet season the deficiency showed up again. The mean exchangeable potassium in the soil samples was 0.06 m.eq./100 gms.

The high rainfall and the permeable nature of this soil, with movement of exchangeable bases down the profile as well as along horizons at a direction parallel to the soil surface, may help to explain the relatively low values of these soil nutrients as well as the increasing values in samples located further down the slope.

(g) Water extractable soil silicon (ppm O.D. soil). The values for water extractable silicon in the soil showed considerable variability along the valley transects, and the overall mean of all samples taken was 11 ppm with a range of from 6 to 20 ppm. These values are rather high compared with those reported by Fox, Silva, et al. (1967). These high and variable results could have resulted from the inability of the apparatus available to centrifuge some samples to the sparkling-clear stage essential for good colorimetric analysis.

Soil pH. Firstly considering soil pH as measured in a 1:1 slurry of soil and water, it is evident from Figure 19 that there was a general decrease in pH toward the valley bottom. The mean value was 4.8 with a mean high of 5.1 on the tops of the slopes and a mean low of 4.6 toward the valley bottom. Transect T2 once again supplied the more stable results since pH was determined soon after sample preparation.

The pH measured in 1:1 slurry of soil and each of a 1N KCl and 1N K_2SO_4 solution showed somewhat less consistency in variation down the slope. The mean pH in KCl was 4.6 while in K_2SO_4 it was 5.1. The purpose of testing soil pH in these salt solutions was to calculate delta pH (pH) values. Delta pH is a means used to determine net charge of soil colloids Mekaru and Uehara (1972). From the variable data collected along the valley transects pH K_2SO_4 values were positive whereas pH KCl values were generally negative. Because of the inconsistency of these pH values it was decided to use only actual soil pH values in water, KCl and K_2SO_4 and not to use the pH term in later analyses. Actual pH values in water, KCl and K_2SO_4 are available in Table 4.

II. In the Tree Drip Ring

In an effort to explain the enhanced growth of legumes in the immediate vicinity of dead trees, several soil factors were measured in the drip ring.

Soil Moisture (% O.D. soil). From Figure 20 it was evident that there is a decrease in the soil moisture as we approached the trunk of larger, dead trees. This trend was consistent for the three drip rings

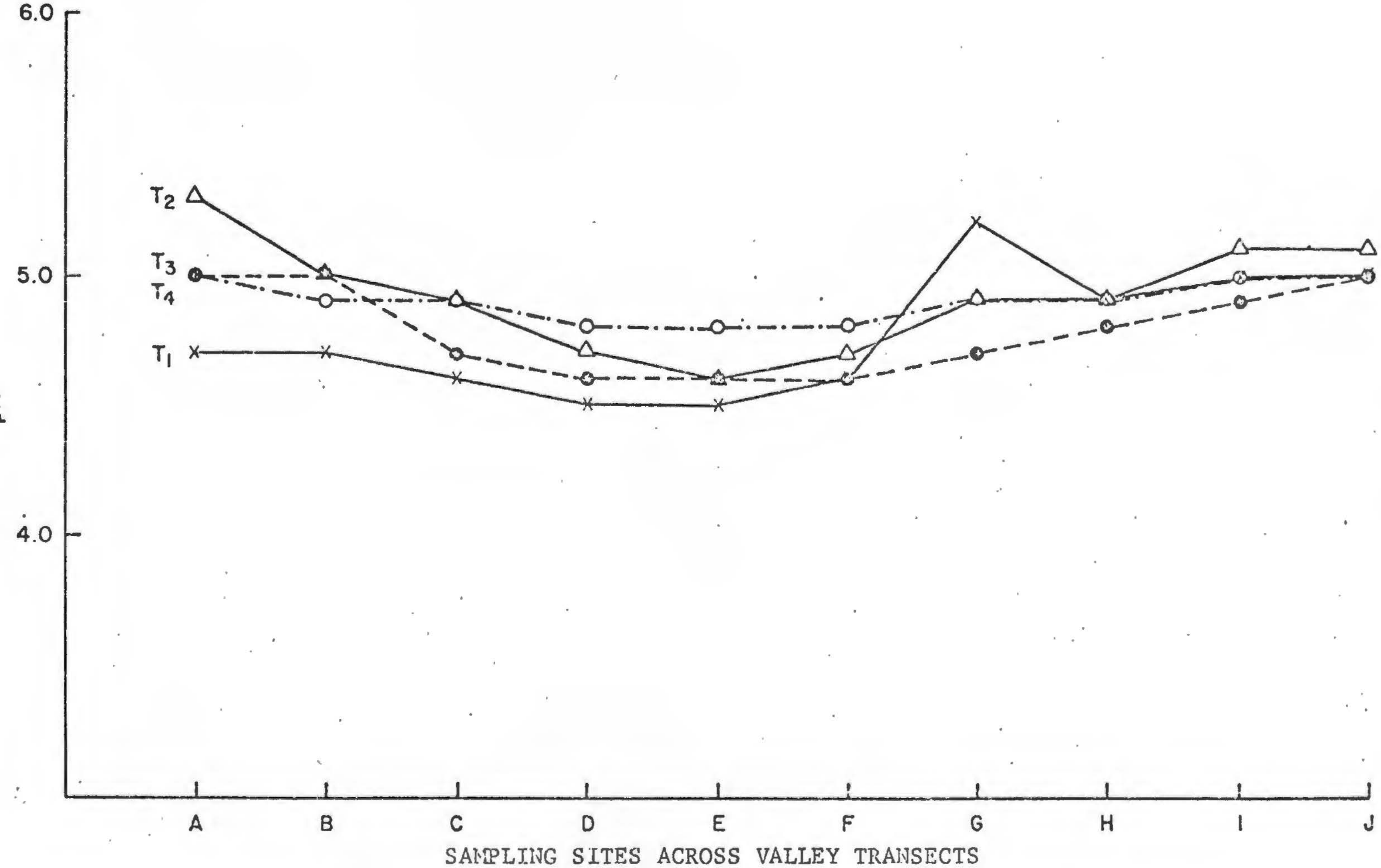

FIGURE 19. THE GRADIENT OF SOIL pH (IN WATER) OF SOIL SAMPLES TAKEN ALONG FOUR VALLEY TRANSECTS.

TABLE 4. MEAN SOIL pH ALONG THE VALLEY TRANSECT

		pH H_2O	pH KCl	pH K_2SO_4
Top of South-facing Slope	A	5.0	4.6	5.1
	B	4.9	4.7	5.1
	C	4.8	4.6	5.1
	D	4.7	4.6	5.1
	E	4.6	4.6	5.2
	F	4.7	4.7	5.2
	G	4.8	4.7	5.2
	H	4.9	4.6	5.1
	I	5.0	4.7	5.2
Top of North-facing Slope	J	5.1	4.6	5.1

sampled. It was initially thought that transpirational losses of soil moisture through vigorous legume growth, accumulating around these trees may be an explanation. However, on removal of this vegetation and after two years, the same soil moisture trend was evident. Curves a, b, and c in Figure 20 represent the trend of drip ring soil moisture following burning and before revegetation of improved species. One explanation for this might be that drainage of soil water could be enhanced by root channels especially those of the larger roots originating from the base of the trunk.

Total Soil Nitrogen (% O.D. soil). The trend of total soil nitrogen across the diameter of the tree drip ring was not as marked as that of the other soil nutrients recorded (Figure 21). The mean value of 0.5 - 0.6% N is somewhat higher than the mean values along transects T1, T3 and T4 in Figure 17 which were analyzed at the same time as the samples represented in Figure 21. This difference may be accounted for by the greater leaf fall and organic matter accumulation in the drip ring and also by the symbiotic fixation and transfer of atmospheric nitrogen by glycine, which was the dominant legume in the drip ring of the larger trees.

Extractable Soil Phosphorus (ppm O.D. soil). Figure 22 represents the trend of soil phosphorus along a diameter of the tree drip ring. Extractable soil phosphorus increases as one approaches the main trunk. This could be explained by the greater leaf and bark fall and thus organic matter accumulation closer to the trunk. This could also explain the higher overall content of soil phosphorus inside the drip ring as against samples taken along the transects, away from the influence of these trees.

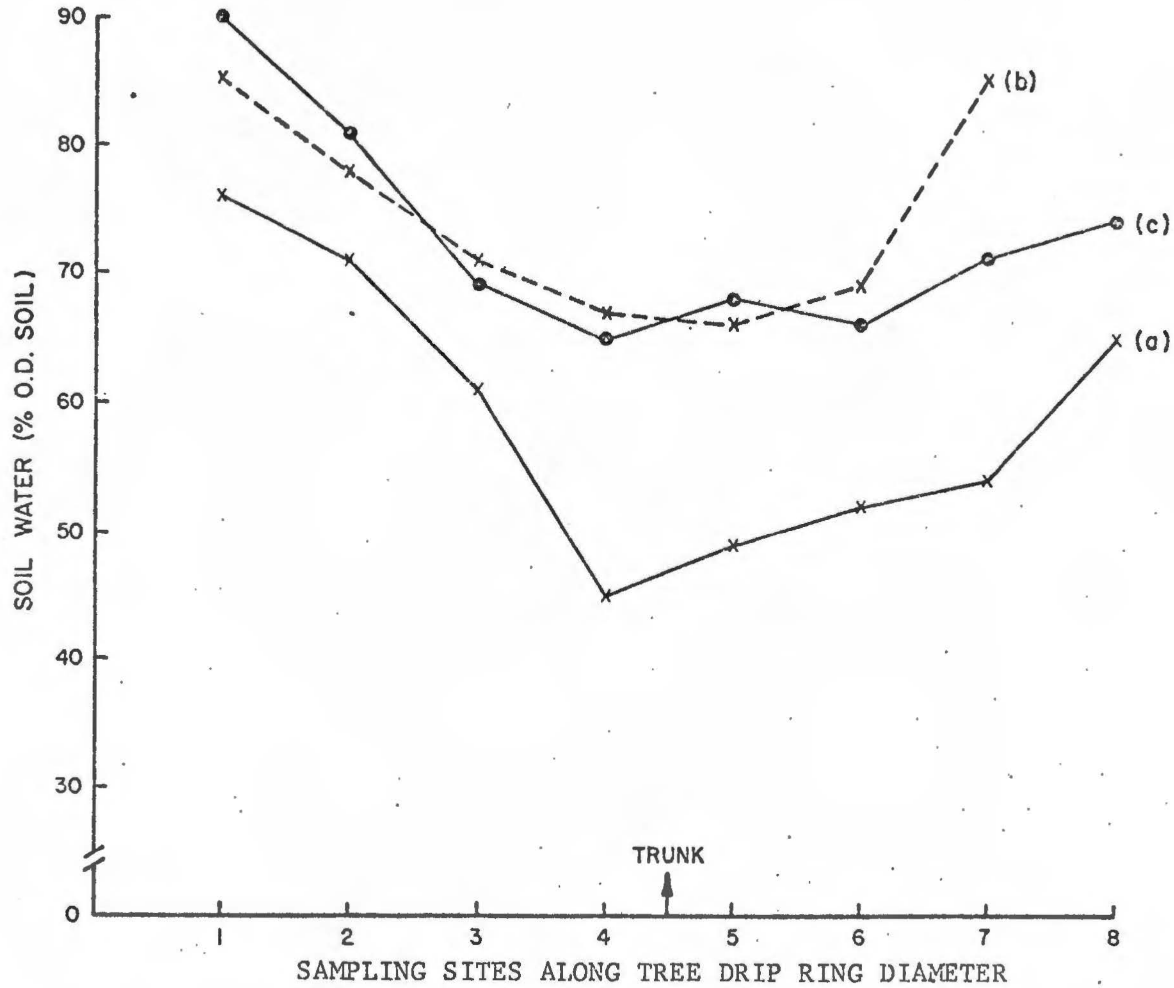

FIGURE 20. THE GRADIENT OF SOIL MOISTURE ALONG THREE DIAMETERS OF TREE DRIP RING.

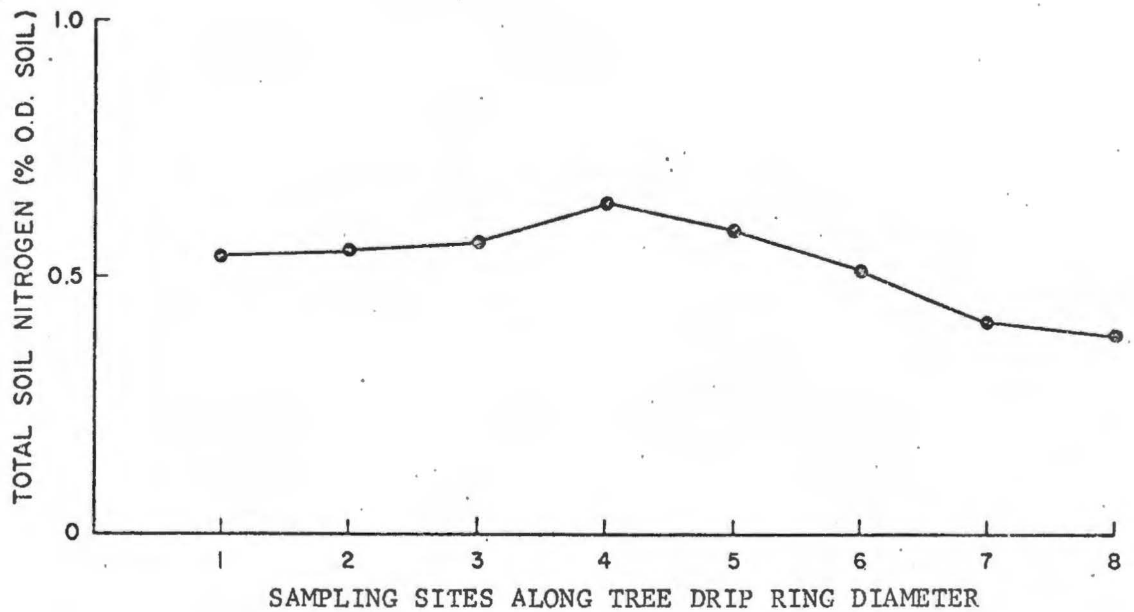

FIGURE 21. TOTAL SOIL NITROGEN ALONG ONE DIAMETER OF TREE DRIP RING.

Exchangeable Potassium (m.e./100 gms O.D. soil). Different to the low soil K values recorded along the open valley transects, the high values within the soil drip ring (0.1 - 0.15 as compared to 0.03 m.e./100 gms outside the drip ring) can be explained by the great amounts of K returned to the soil in the form of natural leaf fall and in the form of ash after burning. The significantly higher soil K values as one approaches the trunk could be explained by a greater accumulation of bark and leaf ash as well as natural leaf drop in this vicinity. High values of K in the ash leachate will be reported later in this discussion.

Exchangeable Calcium (m.e./100 gms O.D. soil). Figure 22 illustrates the trend of exchangeable calcium in soil samples taken along the diameter of the drip ring. The higher values near the trunk can be explained as for exchangeable K. There is a great difference once again in the mean calcium content of the soil in the drip ring (4 - 8 m.e./100 gms as compared to that outside, 0.25 - 0.75 m.e./100 gms). This is again attributable to the recycling and return of soil nutrients in the form of natural leaf drop and ash after firing.

Exchangeable Magnesium (m.e./100 gms O.D. soil). Figure 22 presents the trend of exchangeable soil magnesium along the diameter of the tree drip ring. The similar increase towards the trunk and the much higher mean drip ring values (6 - 10 as compared to 0.75 - 1.5 m.e./100 gms) can be explained as for the other nutrient elements.

Water Extractable Silicon (ppm O.D. soil). There seems to be a general increase in silicon as one approaches the main tree trunk (Figure 22). The range of from 20 - 38 ppm water extractable silicon is well above the mean value of 11 ppm found in soil samples outside

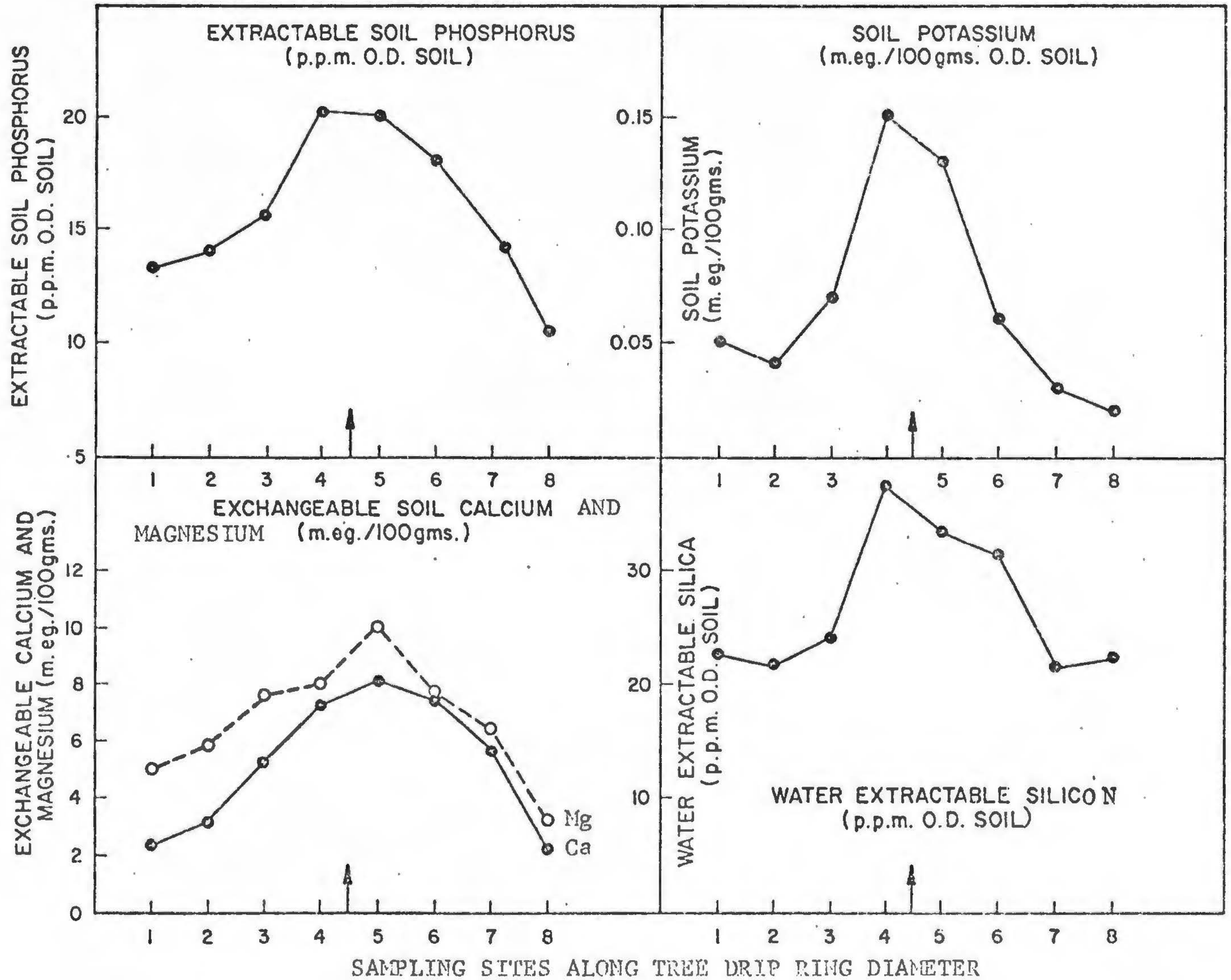

FIGURE 22. GRADIENTS OF EXTRACTABLE SOIL PHOSPHORUS, EXCHANGEABLE SOIL POTASSIUM, CALCIUM AND MAGNESIUM AND WATER EXTRACTABLE SILICON, ACROSS TREE DRIP RING DIAMETER.

the drip ring. This can be explained by the accumulation of silicon by the larger tree species and the greater amounts of leaf drop within the tree drip ring. Once again the discrepancy in these results compared to the much lower values for water extractable soil silicon given by Fox, Silva, et al. (1967) needs some explanation.

As well as collecting soil moisture and soil nutrient data along transects running through plant distribution patterns, such factors as the diurnal fluctuations of temperature at the soil surface, soil profile and variations in topographic aspects were studied.

Air Temperature at the Ground Surface. Daily maximum and minimum temperatures at 8 a.m. and 4 p.m. were recorded for a 12 month period. Since temperatures were recorded only along one valley transect no replication of readings is available. Data are graphically represented in Figures 23, 24, and 25. The 12 month period was divided into 4 periods, namely, February - April, May - July, August - October, November - January, roughly representing Spring, Summer, Fall and Winter, respectively. The daily readings for each time of day at each location were averaged to give the value on the graph representing each season.

Firstly considering the daily maximum temperature, it is obvious from Figure 23 that the south facing slope has the higher daily reading at all times of the year. The highest maximum temperature on this slope occurs between August and October and the lowest between November and January, as could be expected. It is evident that there is a lower maximum temperature at the ground surface on the tops of both slopes, compared to locations further down the slope. This could be explained by a 'shearing' or cooling effect of the wind across the top of the slopes leaving relatively still, warmer air at or near the valley bottom.

When considering the daily minimum temperature there appears very little fluctuation from one location to the next along the valley transect. This can be explained by the fact that the sun's orientation has no influence on the daily minimum temperature which occurs during the night hours. The lowest daily minimum occurred in the period February - April and the highest between August - October.

Figure 24 shows the trends of the temperature at the ground surface measured at about 8 a.m. It is evident that these morning temperatures are generally higher at locations on the north facing slopes. Different to the afternoon and daily maximum temperatures, the morning temperature is highest on the tops of both slopes. This can be explained by two factors. Firstly, early in the morning much of the valley bottoms and lower slopes are still in shadow and therefore much cooler. Secondly, the wind influence does not begin until early afternoon, explaining why there is no cooling effect on the top of the ridges in the early morning.

On considering the afternoon ground-surface temperatures in Figure 25, there is a reversal from the situation for the morning values. The highest values now occur on the north facing slopes, but with the cooling effect of the afternoon wind, the temperatures on the tops of the slopes are lower than those toward the valley bottom.

In the discussion on the soil moisture gradient down the slope, the consideration was given to the wind's cooling influence, and to the influence of the sun's orientation on the variation of daily maximum temperatures from one slope to another and from one position on a slope

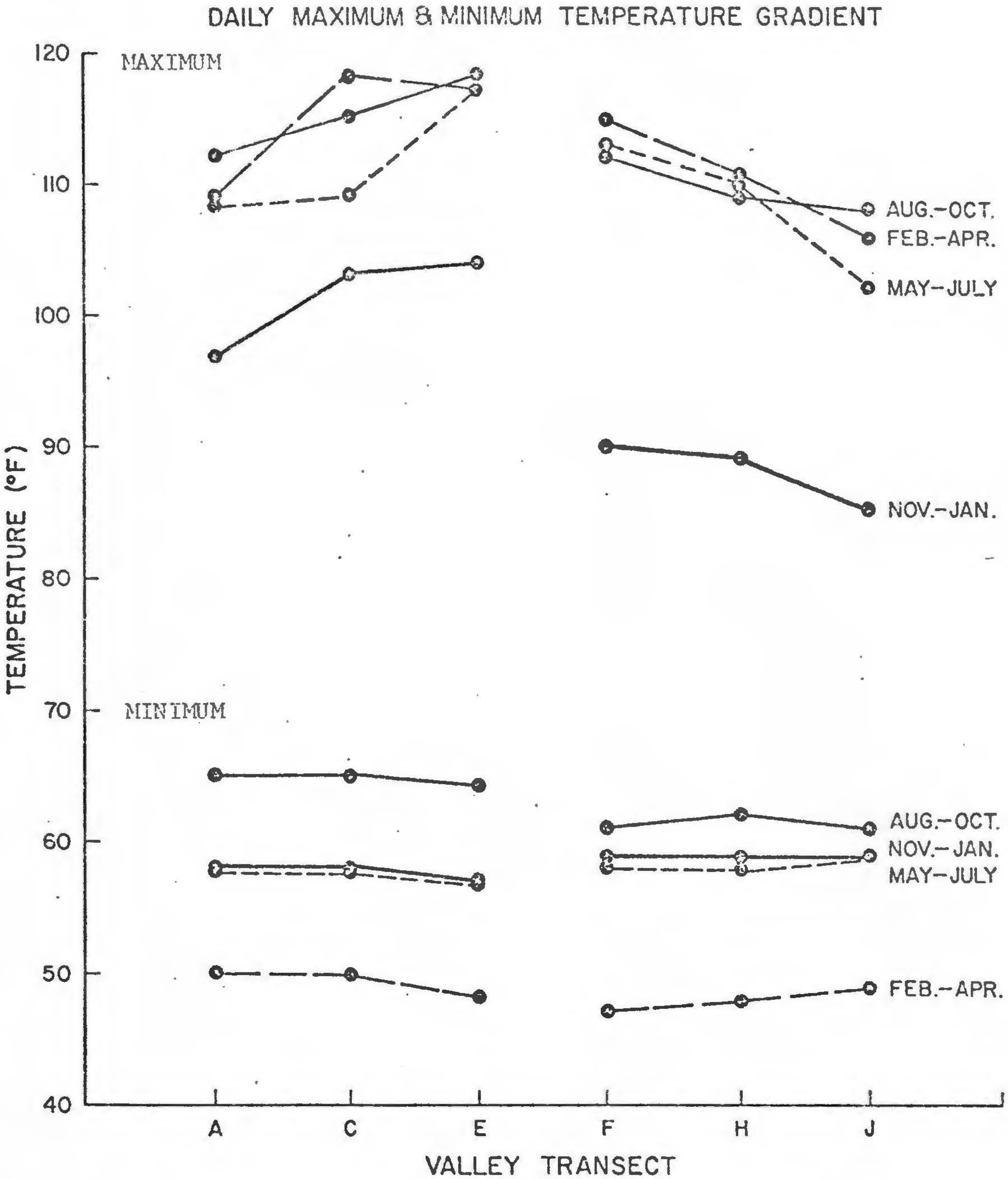

FIGURE 23. GRADIENTS OF THE DAILY MAXIMUM AND MINIMUM TEMPERATURES AT THE GROUND SURFACE ALONG THE VALLEY TRANSECT AT DIFFERENT PERIODS OF THE YEAR. 'A' IS AT THE TOP OF THE SOUTH-FACING SLOPE AND 'J' AT THE TOP OF THE NORTH-FACING SLOPE.

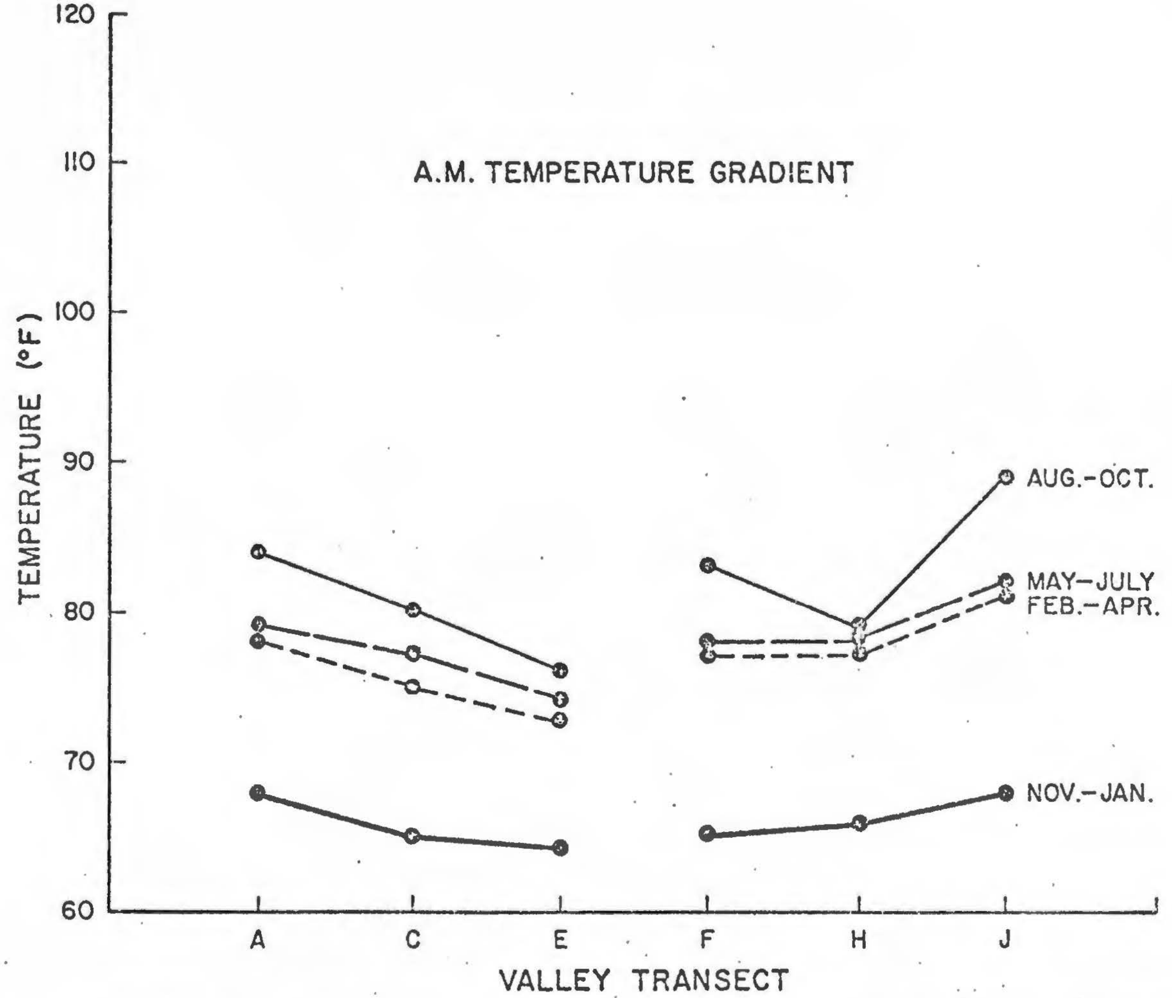

FIGURE 24. GRADIENTS OF MORNING TEMPERATURE AT THE GROUND SURFACE ALONG THE VALLEY TRANSECT AT DIFFERENT PERIODS OF THE YEAR. 'A' IS AT THE TOP OF THE SOUTH-FACING SLOPE AND 'J' IS AT THE TOP OF THE NORTH-FACING SLOPE.

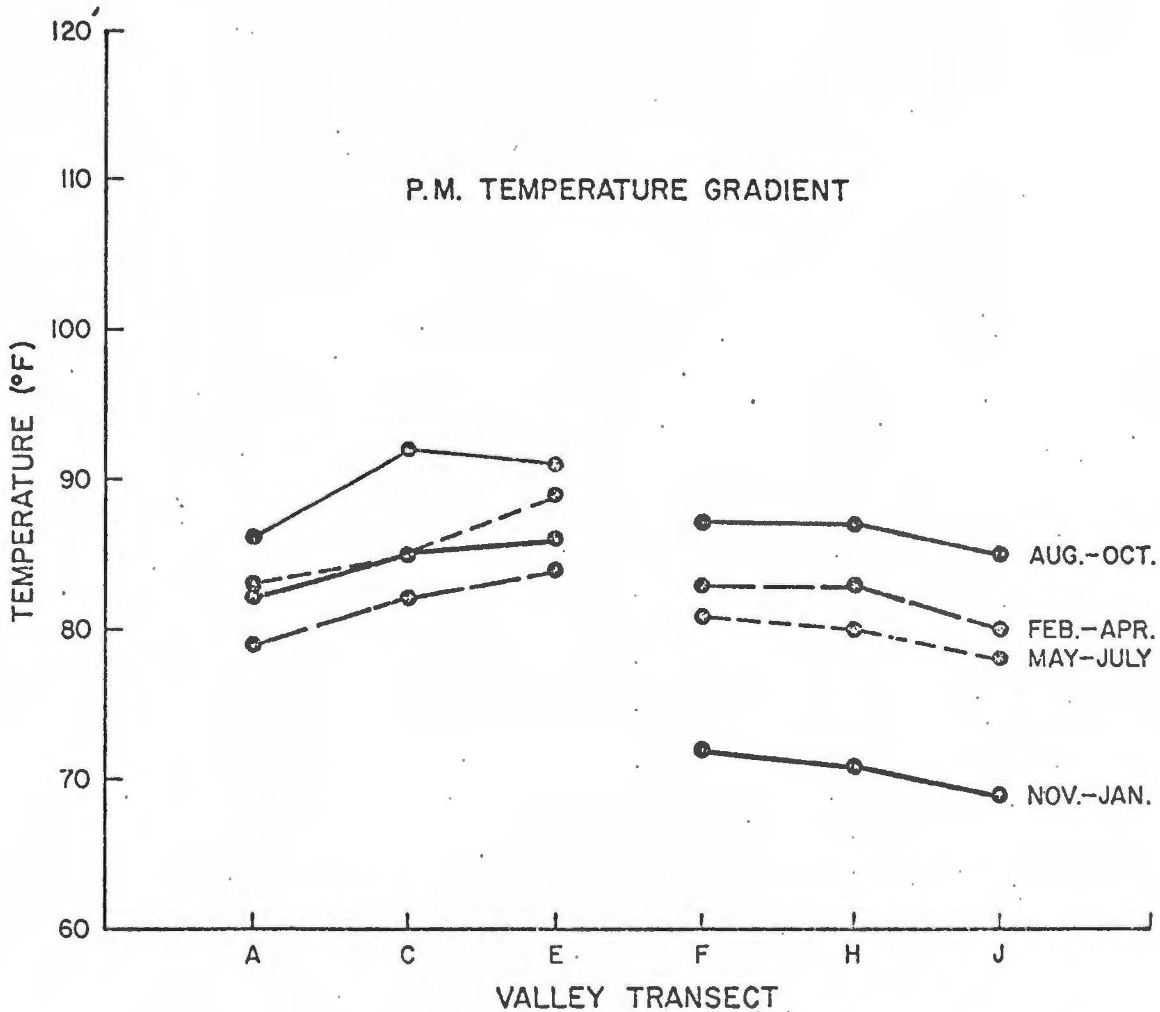

FIGURE 25. GRADIENTS OF AFTERNOON TEMPERATURE AT THE GROUND SURFACE ALONG THE VALLEY TRANSECT AT DIFFERENT PERIODS OF THE YEAR. 'A' IS AT THE TOP OF THE SOUTH-FACING SLOPE AND 'J' IS AT THE TOP OF THE NORTH-FACING SLOPE.

to another.

Soil Profile

As can be seen from Figure 26, the thickness of the A-horizon increases going down the slope. If we take the A_1 horizon as being that shallow layer, high in organic material, overlying the A_2 horizon, the thickness of the latter varies from as shallow as 12.0 cm at the top of the slope to as much as 60 cm at locations lower on the slope. This gradation can be explained by the gradual shift of surface soil material down the slope. This shift would generally be caused by the movement of surface water down the slope. Because the area has always been stabilized by some form of vegetation, there was no evidence of mass movement of soil. The same situation is found on the numerous spurs or ridges, the shoulders of which have a shallow profile compared with that at locations further down the slope. It also appears that generally, the amount of large, rock-like aggregates is greater in the profiles taken at locations near the top of the slope and on the ridge tops, decreasing once again toward the valley bottom. Also the clay content and friability increased as one goes down the slope.

Therefore, locations toward the middle and lower areas of the slope, with their deeper profiles of higher moisture and mineral content, are more conducive to growth of the more vigorous, fertility-responsive species such as green panic and intortum. On the other hand, profile conditions on the ridge tops, with the lower soil moisture and clay contents and the shallower rooting zone, are less conducive to the growth of these species. Species of lower fertility requirements such as stylo, sour paspalum and knot-root foxtail can thus survive and produce with a competitive advantage at these locations.

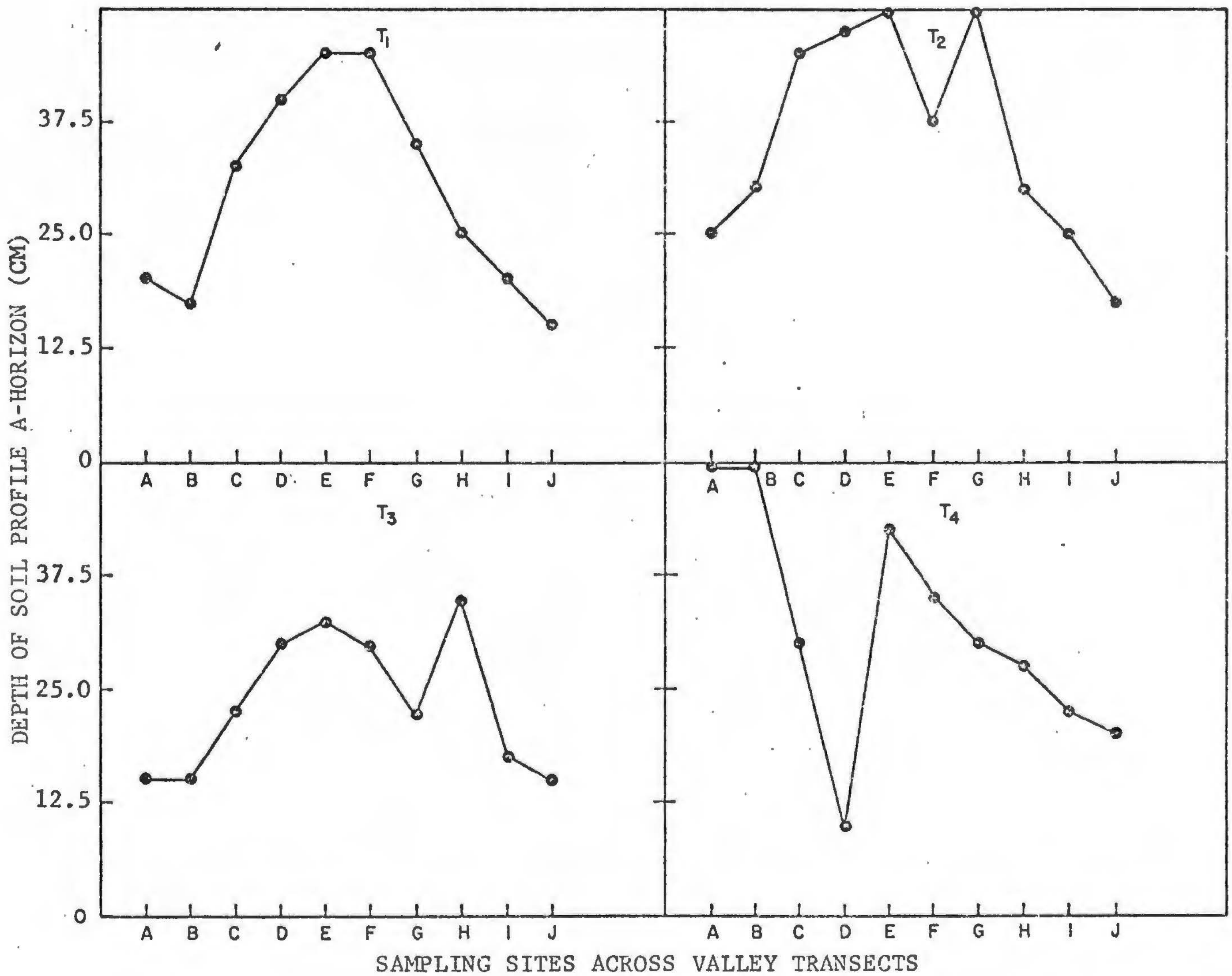

FIGURE 26. GRADIENTS OF DEPTH OF SOIL A-HORIZON ALONG FOUR VALLEY TRANSECTS. 'A' IS AT THE TOP OF THE SOUTH-FACING SLOPE AND 'J' IS AT THE TOP OF THE NORTH-FACING SLOPE.

Topography

The percent slope at each of the forty sampling sites ranged from 0 to 75% along the transect (vertical slope), to 60% at right angles to the transects (horizontal slope). Along all four transects the south-facing, vertical slope was steeper than that on the north-facing slope, the former averaging 56% and the latter 42% (Table 5). This slope difference did not influence the soil moisture regime of either slope. As was seen in the discussion on soil surface temperatures, the slope aspect influenced angle, duration and intensity of the sun's rays and other factors such as humidity and the cooling effect of wind. Even though there was evident species distribution patterns within a particular slope, there was no evident differences in species composition between slopes of different aspects.

Drip Ring Ash Leachate

It is evident from the data represented in Figures 27 through 32 that there was much variation in the nutrients leached from the ashed samples of the brush species studied. For each species, successive 2.5 cm increments of the leachate were analyzed separately for potassium, magnesium and calcium. From the data it is evident that the majority of each particular nutrient element is leached from the ash in the first 2.5 cm-equivalent of rainfall.

In the case of potassium, all species except melastoma showed greater than 1000 ppm K in the total of all increments of the leachate, with lantana, guava and Java plum having the highest values. Nearly 80% of the total water extractable potassium of the melastoma ash was removed by the first 2.5 cm of water, but only 50% in the case of the other species.

TABLE 5. HORIZONTAL AND VERTICAL SLOPE FACTORS AT SAMPLING SITES ALONG FOUR VALLEY TRANSECTS

	Slope Factors (%)																			
	A		B		C		D		E		F		G		H		I		J	
	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.	Ver.	Hor.
T1	50	0	61	1	75	0	45	0	32	12	10	0	60	55	40	60	0	50	0	2
T2	0	0	55	50	70	34	75	5	60	3	1	5	45	4	46	0	52	0	1	0
T3	20	35	65	15	45	10	50	0	25	0	50	2	35	10	32	5	30	2	0	0
T4	65	0	55	0	60	0	35	0	30	5	15	0	35	0	30	30	30	10	10	0

A = Top of south-facing slope

J = Top of north-facing slope

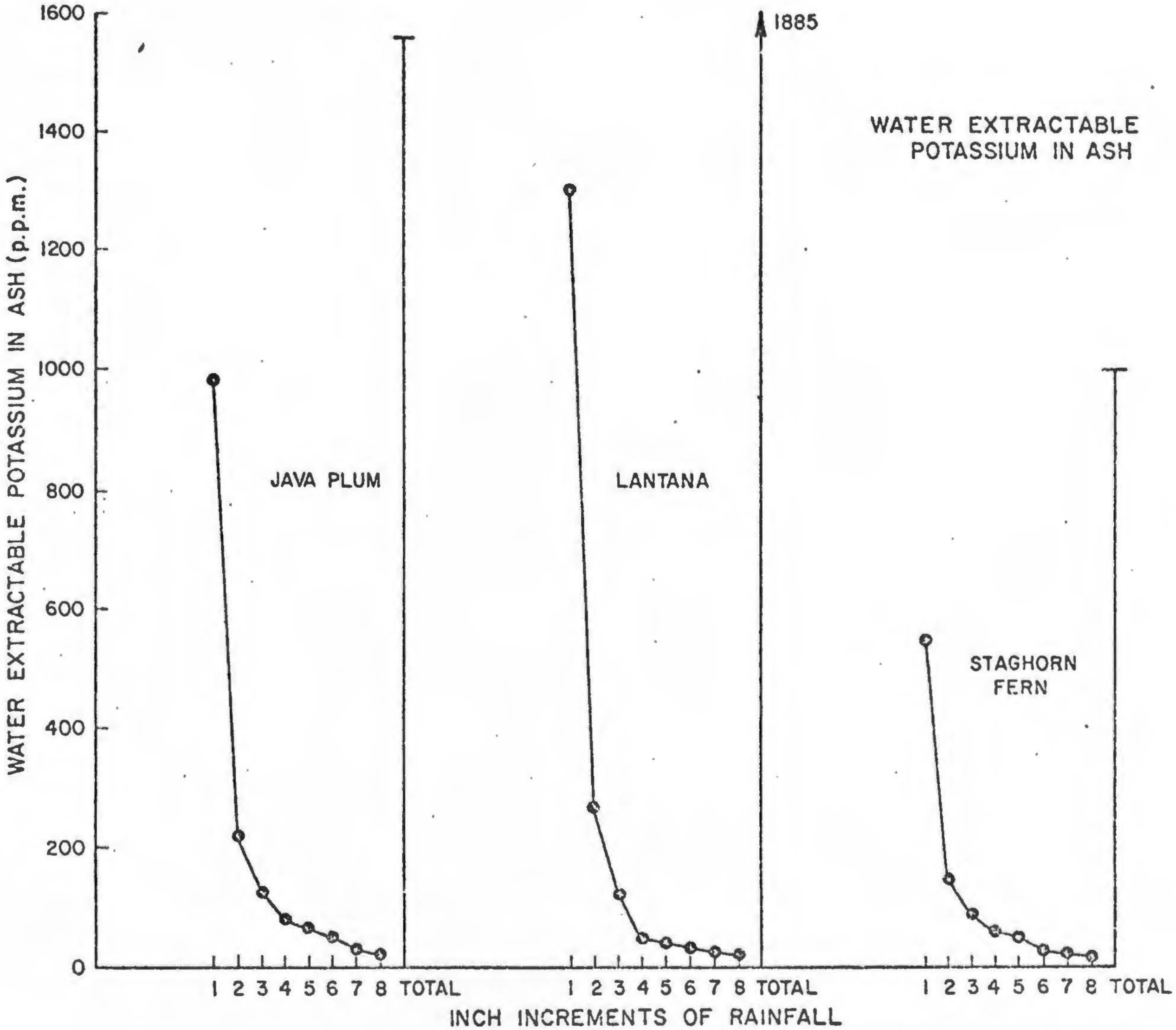

FIGURE 27. WATER EXTRACTABLE POTASSIUM FROM ASH RESIDUE OF JAVA PLUM, LANTANA AND STAGHORN FERN, WITH EACH 2.5 CM INCREMENT OF SIMULATED RAINFALL.

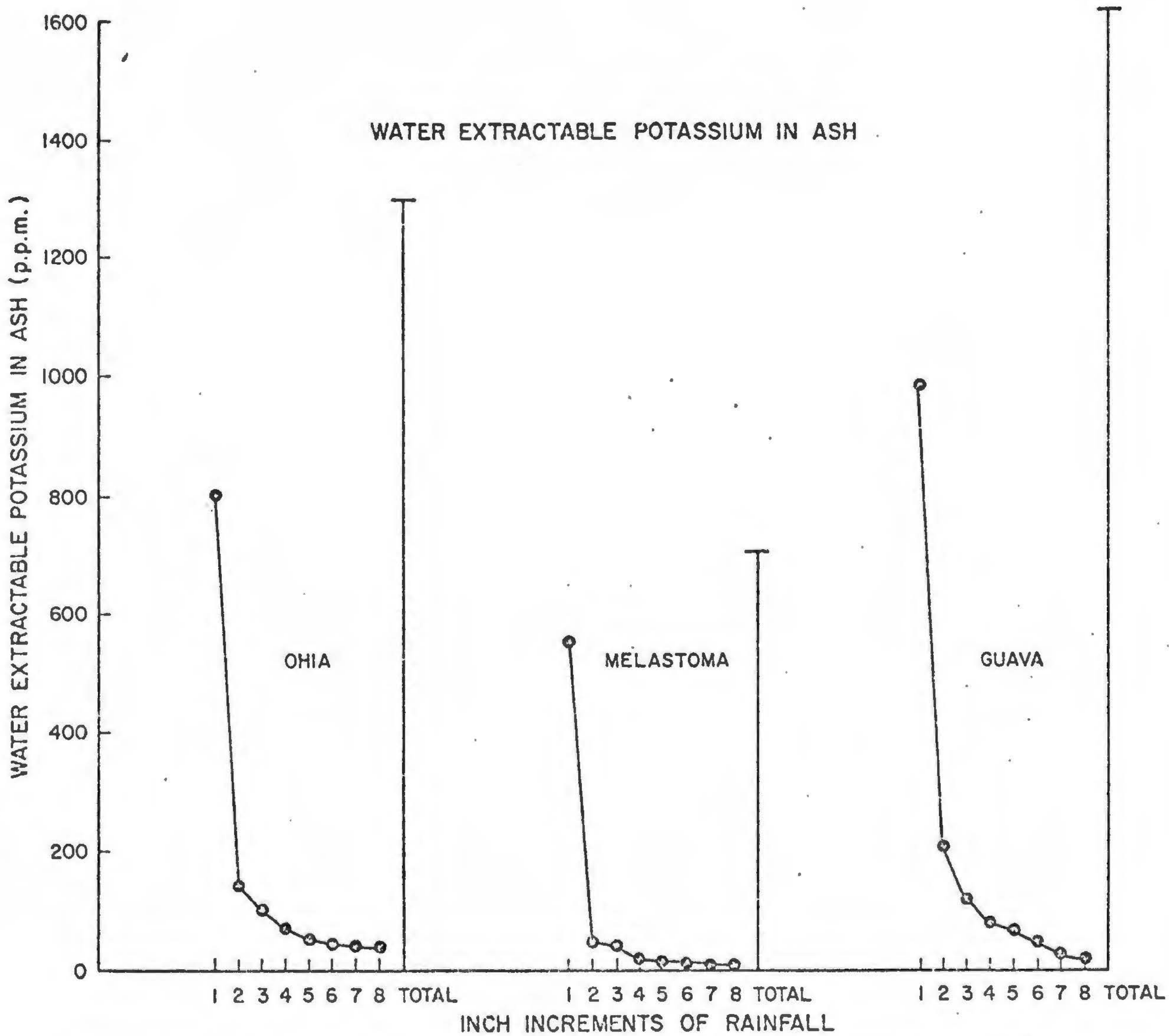

FIGURE 28. WATER EXTRACTABLE POTASSIUM FROM ASH RESIDUE OF OHIA, BANKS MELASTOMA AND GUAVA, WITH EACH 2.5 CM INCREMENT OF SIMULATED RAINFALL.

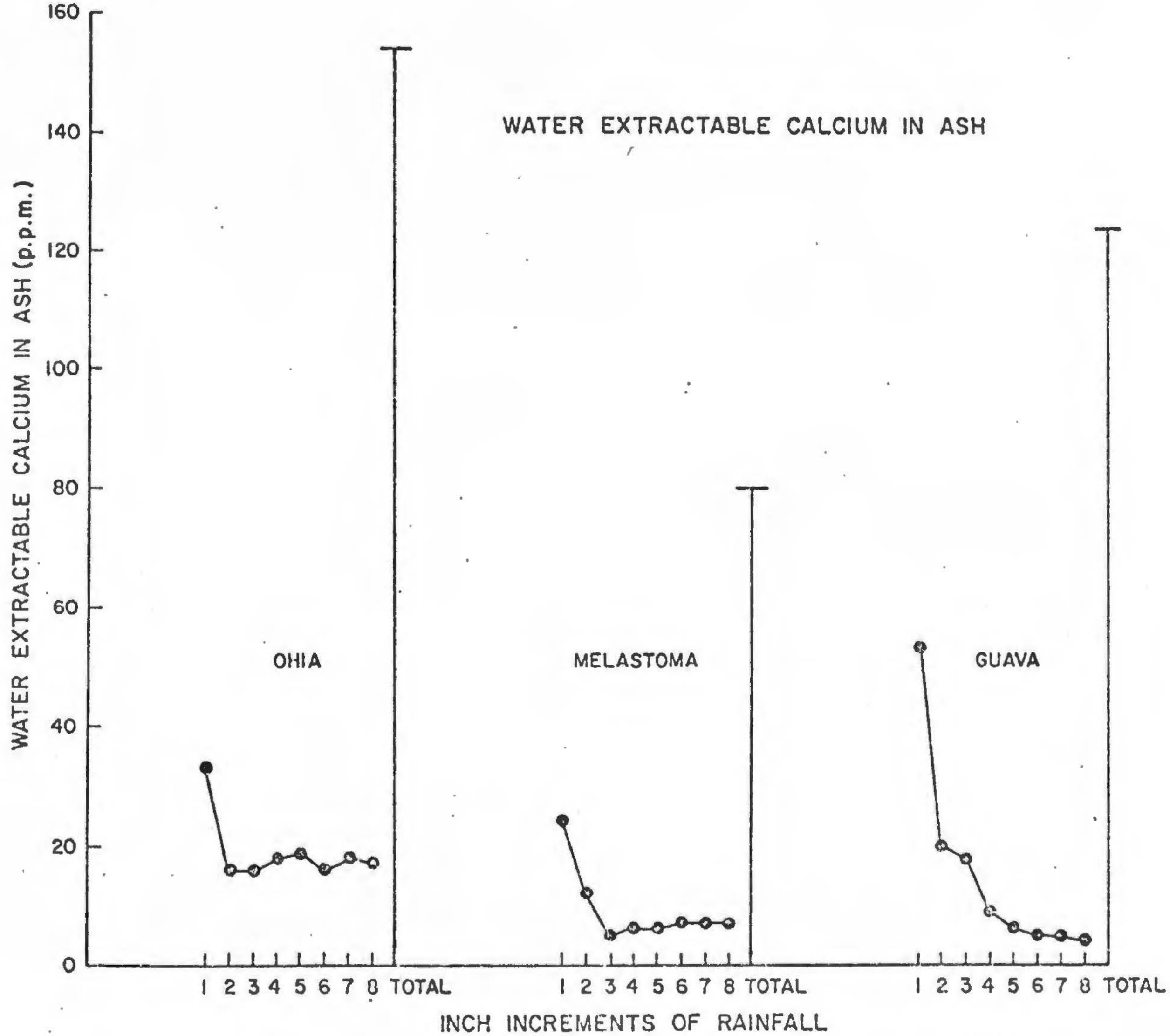

FIGURE 29. WATER EXTRACTABLE CALCIUM FROM ASH RESIDUE OF OHIA, BANKS MELASTOMA AND GUAVA, WITH EACH 2.5 CM INCREMENT OF SIMULATED RAINFALL.

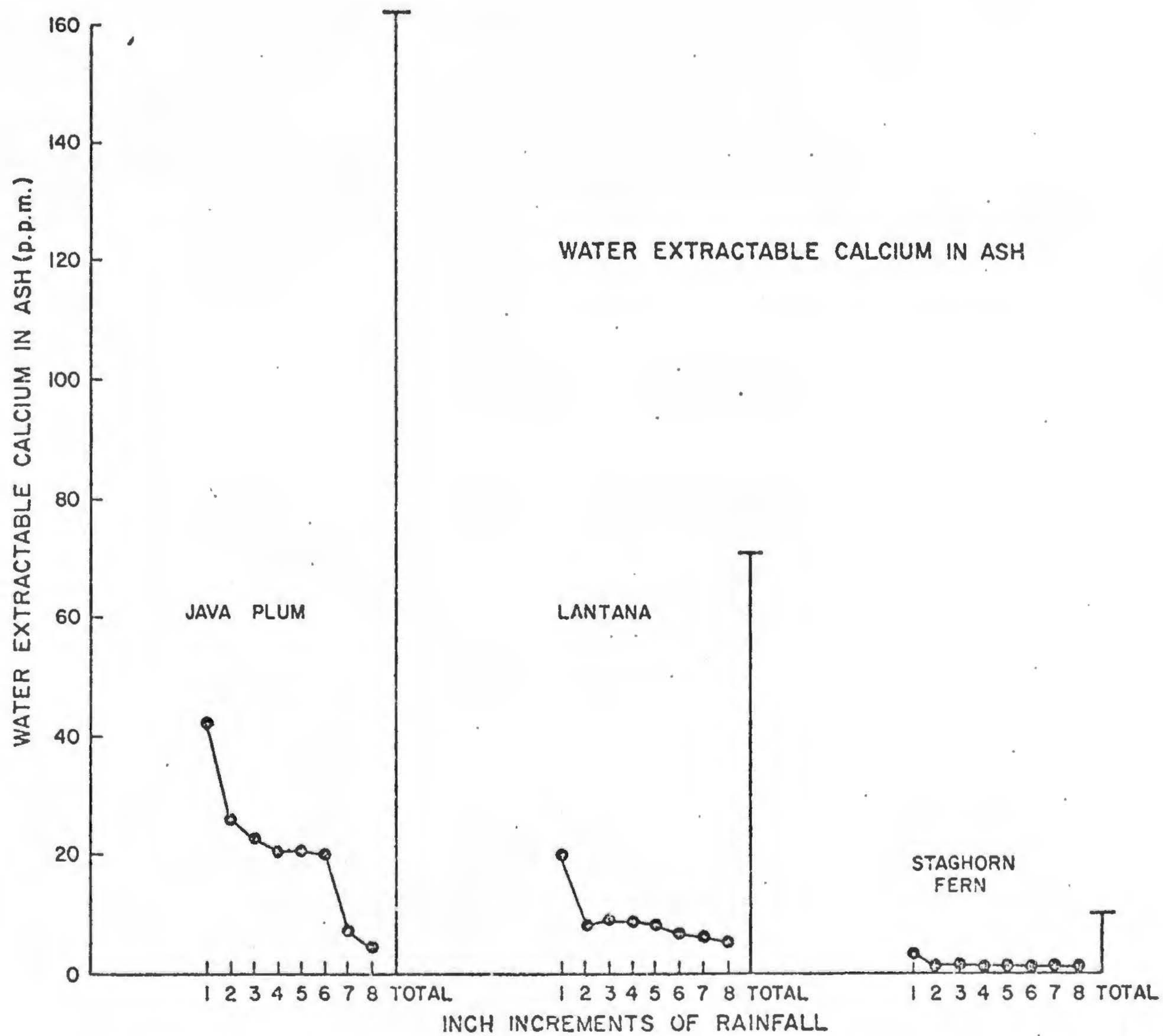

FIGURE 30. WATER EXTRACTABLE CALCIUM FROM ASH RESIDUE OF JAVA PLUM, LANTANA AND STAGHORN FERN, WITH EACH 2.5 CM INCREMENT OF SIMULATED RAINFALL.

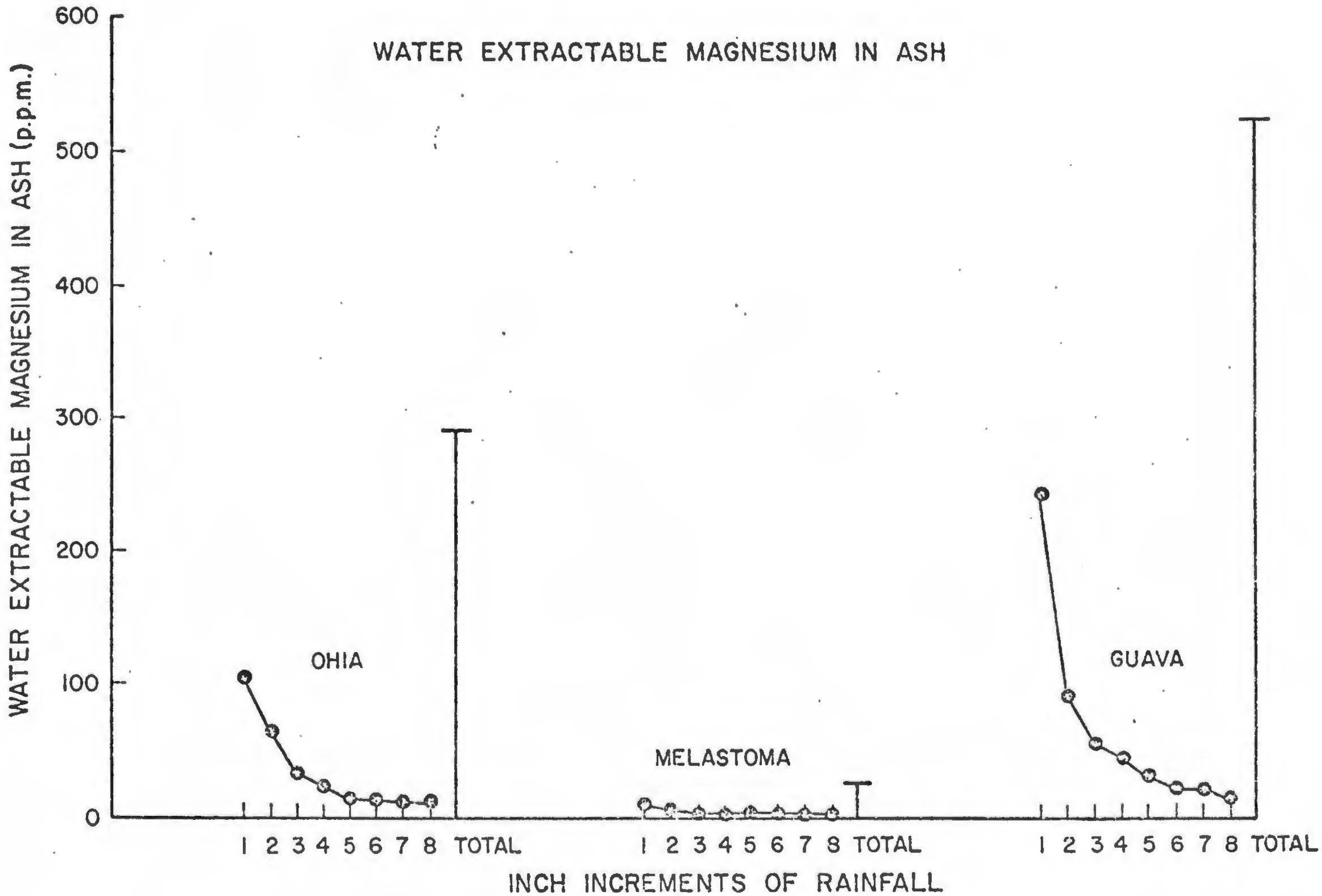

FIGURE 31. WATER EXTRACTABLE MAGNESIUM FROM ASH RESIDUE OF OHIA, BANKS MELASTOMA AND GUAVA, WITH EACH 2.5 CM INCREMENT OF SIMULATED RAINFALL.

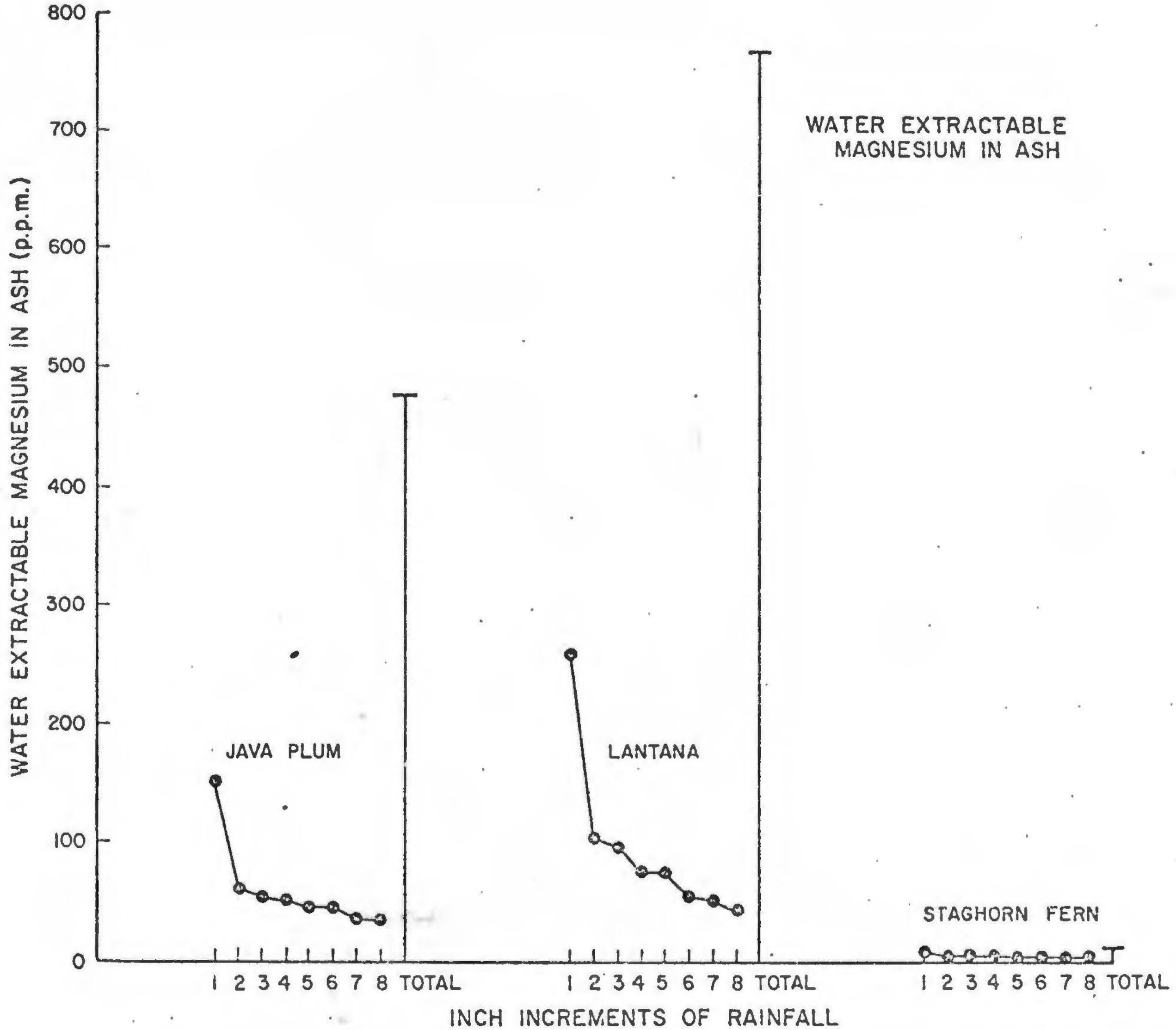

FIGURE 32. WATER EXTRACTABLE MAGNESIUM FROM ASH RESIDUE OF JAVA PLUM, LANTANA AND STAGHORN FERN, WITH EACH 2.5 CM INCREMENT OF SIMULATED RAINFALL.

FIGURE 33. AN EXPOSED STAGHORN FERN THICKET, SHOWING ITS DEPTH AND DENSITY.

Calcium in the ash was much lower than potassium, with the highest total value being 165 ppm for java plum. Ohia and guava were the other species with high calcium contents in the ash. Staghorn fern exhibited an extremely low value of 10 ppm calcium in the total leachate. Only a trace was extracted in each increment after the initial removal of 3 ppm.

Lantana and guava had the greatest amount of water-extractable magnesium in the ash (768 ppm and 523 ppm respectively). Once again staghorn fern and melastoma were the poorest accumulators of magnesium.

From the high values of these nutrient elements extracted from ash gathered from such brush species as lantana, guava, Java plum and ohia, it is not surprising to see an accumulation of legumes in the drip ring of these species after burning and reseeding. The low nutrient contents of staghorn fern ash may also help to explain why, firstly very little seedling growth of either improved or weed species occurs on freshly burnt staghorn fern thickets and secondly, why this species forms dense pure stands (Figure 33). The full explanation of these observations, however, will only be gained by more detailed work on the nature of root exudates and organic components of this plant.

SUMMARY AND CONCLUSION

In this study, where the experimental site provided north and south slopes, environmental parameters were measured along valley transects running at right angles to the main patterns of species distribution. In this way methods were later set up to relate gradients of environmental parameters to gradients of species occurrence.

Of the environmental parameters measured along the transects, as one approached the valley bottom, there was a marked increase in: soil moisture, depth of the soil profile, total soil nitrogen, exchangeable soil calcium, magnesium and manganese, soil pH (measured in 1N KCl and 1N K_2SO_4 solutions) and the daily maximum and afternoon temperatures at the ground surface. The factors showing a decrease in value towards the valley bottom were: soil pH (measured in water) and the morning temperature at the ground surface. It was evident from these data why conditions towards the valley bottom were more favorable for more vigorous growth of improved forage species. The lower fertility-requiring and less aggressive of these species were forced from this sward to locations where another set of conditions, less conducive to vigorous growth, offered them a competitive advantage.

As well as studying parameters along these valley transects, soil nutrient data was also collected within tree drip rings. To support such data as a possible explanation for enhanced plant growth in these drip rings, nutrient analysis of the water extractable portion of the ash gathered after burning brush species was carried out.

The soil nutrient regime was more favorable within the tree drip ring. Of the soil nutrient factors studied, total soil nitrogen, extractable soil phosphorus, exchangeable soil potassium, calcium, magnesium and water extractable silicon showed a marked increase toward the center of the drip ring.

From the analysis of ash leachate of burned brush species, it was evident that the ash of most species was high in water extractable potassium, calcium and magnesium. These factors along with the natural recycling of plant nutrients in the form of leaf drop can explain why soil nutrient conditions are more favorable in tree drip rings.

CHAPTER VI. RELATIONSHIP BETWEEN SPECIES DISTRIBUTION AND ENVIRONMENTAL FACTORS

In defining aspects of plant/environment relationships we must first collect detailed and reliable data on as many cause and effect components as is practically possible. Environmental parameters (causes) combine to influence a particular plant species or species association (effects). Next, it is essential that details of such relationships be extracted and defined from the data.

Several attempts at relating these variables have been made using simple univariate regression analyses. However, environmental factors exhibit much inter-dependence and interaction, rendering such techniques of analysis useless. If environmental parameters are to be classified in order of importance in influencing certain vegetation patterns, some form of multivariate analysis must be used. Norris (1970) has summarized several forms of multivariate analysis of which the canonical analysis of Horton, et al., (1968), Little, et al., (1968), Cooley and Lohnes (1962), Morrison (1967), Austin (1968), and Barkham and Norris (1970); the path analysis of Scott (1966), Tukey (1954), Turner and Stevens (1959) and Scott and Billings (1964); and the ordination analysis of Seal (1964) and Anderson (1958) are the more important.

The objective of this phase of the ecological approach to pasture research was to identify the more important environmental factors and to estimate the magnitude of their influence on the distribution patterns of particular species or species associations. The strong interdependence of many environmental parameters makes meaningful extraction very difficult.

MATERIALS AND METHODS

The techniques used to collect both the plant and environmental data have been outlined in General Materials and Methods. In an attempt to identify relationships between species distribution patterns and selected micro-environmental parameters, correlation and regression analyses were used.

The correlation analysis revealed the degree of relationship between individual species and environmental factors, as well as the interrelationships within each of these cause and effect classes. Since simple regression analyses do not take into account this factor of intercorrelation, it was decided to use multiple regression techniques to rank environmental parameters in order of their importance in influencing species distribution patterns.

This process employed a step-wise multiple regression analysis which developed a series of regression equations for the dependent (species) variable with an increasing number of independent (environmental) variables (Dixon, 1968). An explanation of the procedures within such a program may help interpretation of the data in Tables 6 to 21 and Figures 34 to 41.

If one considers each plant species or species association separately, the first independent variable appearing in the regression equation is selected on the basis of the highest simple correlation coefficient (Table 6). From this point on others are selected on the basis of their partial correlation coefficient with the dependent variable. The independent variable with the highest partial correlation coefficient which has a significant partial 'F' value is selected to enter the equation next. This process is repeated in each step with all the independent variables being re-evaluated each time and continues until all independent variables have entered the equation or until remaining variables have non-significant partial 'F' values. The change in the value R^2, (where R is the regression coefficient) on the inclusion of each independent variable is the proportion of the total variation which can be explained by the factor just included in combination with the factors already in the multiple regression equation.

RESULTS AND DISCUSSION

Study of the correlation matrices in Table 6 and 7 revealed that there was much interdependence within and between the two groups of variables. The correlation coefficients in Table 6 were the basis for selecting the specific multiple regression analyses used to rank environmental factors in order of their importance in influencing a particular vegetation pattern. Also, the correlation matrix for plant species classes (Table 7), were used to identify species which occurred together in association.

Environmental factors are listed in Tables 8 through 15 in order of importance in affecting the distribution pattern of individual species or species association. Multiple regression coefficients (R) and the change in R^2 values are also presented in these tables. The coefficient of determination (R^2 x 100) is a measure of the variation in the dependent variable accounted for by variables in the regression equation.

TABLE 6. CORRELATION COEFFICIENTS (r) OF PLANT SPECIES AND ENVIRONMENTAL FACTORS

df = 38, r = 0.310 (5%), r = 0.405 (1%)

	Soil H_2O	p^H H_2O	p^H KCl	p^H K_2SO_4	Soil N	Soil P	Soil K	Soil Ca	Soil Mg	Soil Na	Soil Si	Vert. slope	Hor. slope	Soil depth
Stylosanthes (St.)	$\overline{.437}$	.585	$\overline{.056}$	$\overline{.079}$	$\overline{.441}$	$\overline{.303}$	.199	$\overline{.353}$	$\overline{.385}$	$\overline{.579}$	$\overline{.072}$	$\overline{.293}$	.362	$\overline{.697}$
Desmodium (Des.)	.431	$\overline{.405}$	$\overline{.229}$	$\overline{.153}$	.659	.330	$\overline{.009}$	.432	.422	.556	$\overline{.119}$	.196	.001	.491
Green panic (GP)	.529	$\overline{.531}$	$\overline{.163}$	$\overline{.143}$	.544	.307	.057	.386	.462	.545	$\overline{.142}$	.215	$\overline{.023}$	.398
Paspalum/foxtail (p/f)	$\overline{.508}$	.603	.039	$\overline{.034}$	$\overline{.503}$	$\overline{.371}$	.047	$\overline{.397}$	$\overline{.392}$	$\overline{.598}$	.167	$\overline{.414}$	.054	$\overline{.709}$
Lantana	.073	.106	.344	.338	$\overline{.338}$	$\overline{.183}$	.035	$\overline{.149}$	.295	$\overline{.146}$	.361	$\overline{.192}$	$\overline{.039}$	$\overline{.332}$
Melastoma	.307	.375	.145	.143	$\overline{.305}$	$\overline{.285}$	$\overline{.215}$	$\overline{.208}$	$\overline{.271}$	$\overline{.418}$	.435	$\overline{.475}$	.001	$\overline{.396}$
Elephantopus	$\overline{.338}$	.582	$\overline{.012}$	.078	$\overline{.406}$	$\overline{.325}$	$\overline{.001}$	$\overline{.309}$	$\overline{.235}$	$\overline{.442}$	.169	$\overline{.531}$	$\overline{.079}$	$\overline{.409}$
Sword fern (Fs)	$\overline{.123}$	.097	.185	.012	$\overline{.178}$	$\overline{.231}$	.131	$\overline{.199}$	.098	$\overline{.063}$	.031	.073	$\overline{.240}$	$\overline{.076}$
Bracken fern (Fb)	$\overline{.250}$	.349	.063	.062	$\overline{.127}$	$\overline{.100}$	.096	.076	$\overline{.011}$	$\overline{.054}$	$\overline{.013}$	$\overline{.039}$	.327	$\overline{.283}$
Commelina (Comm.)	.609	$\overline{.749}$	.179	.060	.490	.378	$\overline{.153}$	.226	.346	.495	$\overline{.043}$	.092	$\overline{.298}$	.411
Fireweed (FW)	.250	$\overline{.139}$	$\overline{.192}$	$\overline{.109}$	.211	$\overline{.131}$	$\overline{.055}$	.429	.326	.305	$\overline{.009}$	$\overline{.240}$	$\overline{.149}$	.181
Stachytarpheta	$\overline{.301}$	.464	.199	.131	$\overline{.351}$	$\overline{.081}$	.074	$\overline{.026}$	$\overline{.309}$	$\overline{.265}$	.269	$\overline{.146}$	.435	$\overline{.322}$
St./GP	$\overline{.104}$	.311	$\overline{.218}$	$\overline{.171}$	$\overline{.051}$	$\overline{.075}$	.344	.079	.018	$\overline{.126}$	$\overline{.083}$	.179	.351	$\overline{.159}$
St./p/f.	$\overline{.437}$	.565	.019	.036	$\overline{.404}$	$\overline{.302}$	.177	$\overline{.270}$	$\overline{.468}$	$\overline{.528}$	.020	$\overline{.429}$	.323	$\overline{.597}$
St./weed	$\overline{.373}$	.606	$\overline{.076}$	$\overline{.056}$	$\overline{.356}$	$\overline{.309}$	.252	$\overline{.192}$	$\overline{.331}$	$\overline{.479}$	$\overline{.002}$	$\overline{.251}$	.469	$\overline{.594}$
Des./GP	.481	$\overline{.559}$	$\overline{.194}$	$\overline{.123}$	.573	.397	$\overline{.139}$	.410	.404	.521	$\overline{.089}$	.165	$\overline{.117}$	.452
Des./p/f.	$\overline{.308}$	.309	$\overline{.061}$	$\overline{.077}$	$\overline{.148}$	$\overline{.117}$	.269	$\overline{.058}$	$\overline{.212}$	$\overline{.284}$	$\overline{.094}$	.020	.192	$\overline{.311}$
Des./weed	.475	$\overline{.526}$	$\overline{.090}$	$\overline{.027}$	.498	.312	$\overline{.055}$	.404	.399	.457	$\overline{.109}$	.167	$\overline{.076}$	.340
Des./GP/comm.	.612	$\overline{.791}$	.171	.097	.443	.301	$\overline{.131}$	.158	.334	.448	$\overline{.103}$	.089	$\overline{.335}$	.369
St./Des.	$\overline{.250}$	.371	$\overline{.215}$	$\overline{.118}$	$\overline{.101}$	$\overline{.043}$	.305	$\overline{.023}$	$\overline{.190}$	$\overline{.278}$	$\overline{.144}$	.240	.444	$\overline{.224}$
GP/p/f.	$\overline{.244}$	.351	$\overline{.272}$	$\overline{.221}$	$\overline{.065}$	$\overline{.096}$	.279	$\overline{.006}$	$\overline{.156}$	$\overline{.239}$	$\overline{.053}$	$\overline{.065}$	.050	$\overline{.112}$

	Feb. - April				May - July				Aug. - Oct.				Nov. - Jan.			
	am Temp.	pm Temp.	max. Temp.	min. Temp.	am Temp.	pm Temp.	max. Temp.	min. Temp.	am Temp.	pm Temp.	max. Temp.	min. Temp.	am Temp.	pm Temp.	max. Temp.	min. Temp.
Stylosanthes (St.)	.505	$\overline{.569}$	$\overline{.554}$	.399	.539	$\overline{.371}$	$\overline{.613}$	.471	.468	$\overline{.389}$	$\overline{.435}$	$\overline{.041}$	.652	$\overline{.207}$	$\overline{.225}$	.252
Desmodium (Des.)	$\overline{.573}$	.792	.608	$\overline{.593}$	$\overline{.630}$	.327	.729	$\overline{.549}$	$\overline{.629}$	.390	.386	$\overline{.045}$	$\overline{.704}$	.102	.211	$\overline{.155}$
Green panic (GP)	$\overline{.547}$	.693	.623	$\overline{.461}$	$\overline{.575}$	.355	.635	$\overline{.509}$	$\overline{.531}$	.440	.444	.025	$\overline{.739}$	.172	.269	$\overline{.208}$
Paspalum/foxtail (p/f)	.679	$\overline{.693}$	.745	.372	.689	$\overline{.489}$	$\overline{.742}$	.639	.627	$\overline{.530}$	$\overline{.578}$	$\overline{.232}$	.796	$\overline{.349}$	$\overline{.429}$	.318
Lantana	.181	$\overline{.091}$	$\overline{.186}$	.074	.191	$\overline{.171}$	$\overline{.232}$	.225	.129	$\overline{.078}$	$\overline{.187}$	$\overline{.181}$	.176	$\overline{.171}$	$\overline{.160}$	.113
Melastoma	.649	$\overline{.431}$	$\overline{.649}$	.079	.636	$\overline{.522}$	$\overline{.626}$	.639	.616	$\overline{.513}$	$\overline{.561}$	$\overline{.471}$	.550	$\overline{.487}$	$\overline{.532}$	.395
Elephantopus	.602	$\overline{.567}$	$\overline{.595}$	.285	.615	$\overline{.406}$	$\overline{.661}$	.562	.620	$\overline{.416}$	$\overline{.439}$	$\overline{.245}$	.628	$\overline{.502}$	$\overline{.366}$	.257
Sword fern (Fs)	.032	$\overline{.235}$	.081	.361	.018	.147	$\overline{.136}$	$\overline{.023}$	.059	.181	.169	.300	.136	.257	.237	$\overline{.181}$
Bracken fern (Fb)	.021	$\overline{.229}$	.028	.272	.035	$\overline{.014}$	$\overline{.069}$	$\overline{.000}$	.022	$\overline{.062}$	.001	.300	.151	.120	.075	.024
Commelina (Comm.)	$\overline{.610}$	.617	.579	$\overline{.428}$	$\overline{.660}$	.576	.700	$\overline{.632}$	$\overline{.551}$	.503	.580	.091	$\overline{.649}$	.349	.428	$\overline{.492}$
Fireweed (FW)	.004	.433	.051	$\overline{.649}$	$\overline{.073}$	$\overline{.226}$	.281	$\overline{.102}$	$\overline{.116}$	$\overline{.158}$	$\overline{.172}$	$\overline{.412}$	$\overline{.339}$	$\overline{.369}$	$\overline{.327}$	.319
Stachytarpheta	.375	$\overline{.408}$	$\overline{.307}$	.291	.367	$\overline{.285}$	$\overline{.308}$	.306	.338	$\overline{.359}$	$\overline{.307}$	.074	.478	$\overline{.173}$	.201	.236
St./GP	.031	$\overline{.067}$	$\overline{.011}$	.179	.059	$\overline{.097}$	$\overline{.106}$	.053	$\overline{.014}$	.001	$\overline{.059}$	.104	.077	$\overline{.021}$	.021	.098
St./p/f.	.622	$\overline{.557}$	$\overline{.669}$	.249	.623	$\overline{.478}$	$\overline{.647}$	.572	.571	$\overline{.519}$	$\overline{.545}$	$\overline{.246}$	.669	$\overline{.364}$	$\overline{.439}$	.346
St./weed	.459	$\overline{.457}$	$\overline{.501}$	.308	.475	$\overline{.391}$	$\overline{.531}$	.418	.374	$\overline{.366}$	$\overline{.432}$	$\overline{.089}$	.564	$\overline{.249}$	$\overline{.311}$	.280
Des./GP	$\overline{.527}$	.683	.574	$\overline{.529}$	$\overline{.577}$	.331	.603	$\overline{.499}$	$\overline{.528}$	.352	.395	$\overline{.017}$	$\overline{.734}$	.135	.223	$\overline{.171}$
Des./p/f.	.156	$\overline{.087}$	$\overline{.174}$	.105	.179	$\overline{.232}$	$\overline{.213}$	.233	.064	$\overline{.147}$	$\overline{.256}$	$\overline{.056}$	.165	$\overline{.164}$	.178	.242
Des./weed	$\overline{.549}$	.608	.594	$\overline{.478}$	$\overline{.587}$	.332	.662	$\overline{.493}$	$\overline{.571}$	.389	.391	.031	$\overline{.725}$	.156	.245	$\overline{.102}$
Des./GP/comm.	$\overline{.596}$	.590	.599	$\overline{.432}$	$\overline{.644}$	.559	.703	$\overline{.598}$	$\overline{.511}$	.469	.574	.104	$\overline{.671}$	.381	.418	$\overline{.449}$
St./Des.	$\overline{.008}$	$\overline{.104}$	.017	.297	.047	$\overline{.071}$	$\overline{.139}$	.088	$\overline{.054}$	.043	$\overline{.057}$	.220	.097	.059	.043	$\overline{.057}$
GP/p/f.	.319	$\overline{.006}$	$\overline{.283}$	$\overline{.033}$	.311	$\overline{.381}$	$\overline{.291}$	.384	.237	.276	$\overline{.367}$	$\overline{.321}$	.167	$\overline{.372}$	$\overline{.371}$	.366

TABLE 7. CORRELATION COEFFICIENTS (r) OF PLANT SPECIES AND SPECIES ASSOCIATIONS

df = 38, r = 0.310 (5%), r = 0.405 (1%)

	Stylosanthes (St)	Desmodium (Des.)	Green panic (GP)	Paspalum/foxtail (p/f)	Lantana	Melastoma	Elephantopus	Sword fern (Fs)	Bracken fern (Fb)	Commelina (Comm.)	Fireweed (FW)	Stachytarpheta	St./GP	St./p/f.	St./weed	Des./GP	Des./p/f.	Des./weed	Des./GP/comm.	St./Des.	GP/p/f.
Stylosanthes (St.)																					
Desmodium (Des.)	$\overline{.537}$																				
Green Panic (G.P.)	$\overline{.576}$	.802																			
Paspelum/foxtail (p/f)	.777	$\overline{.755}$	.812																		
Lantana	.120	$\overline{.379}$	$\overline{.268}$	.409																	
Melastoma	.232	$\overline{.535}$	$\overline{.531}$	.626	.539																
Elephantopus	.429	$\overline{.641}$	$\overline{.546}$	.673	.555	.679															
Sword fern (Fs)	.012	$\overline{.332}$	$\overline{.262}$	.249	.476	.139	.364														
Bracken fern (Fb)	.300	.010	$\overline{.102}$	.162	$\overline{.136}$	$\overline{.118}$	$\overline{.044}$	.155													
Commelina (Comm.)	$\overline{.628}$	.606	.556	$\overline{.507}$	$\overline{.301}$	$\overline{.320}$	$\overline{.452}$	$\overline{.112}$	$\overline{.177}$												
Fireweed (FW)	$\overline{.333}$	.601	.577	$\overline{.441}$	$\overline{.319}$	$\overline{.266}$	$\overline{.309}$	$\overline{.370}$	$\overline{.043}$	.230											
Stachytarpheta	.418	$\overline{.489}$	$\overline{.469}$	.449	.193	.320	.303	.318	.427	$\overline{.455}$	$\overline{.381}$										
St./GP	.421	.026	.174	.091	.109	$\overline{.207}$	.019	.008	$\overline{.194}$	$\overline{.451}$	$\overline{.016}$	.182									
St./p/f.	.854	$\overline{.519}$	$\overline{.669}$	.774	$\overline{.019}$	.388	.447	$\overline{.115}$	.329	$\overline{.452}$	$\overline{.271}$	.352	.033								
St./weed	.914	$\overline{.427}$	$\overline{.520}$	.706	.084	.226	.396	$\overline{.043}$	.398	$\overline{.623}$	$\overline{.259}$	.446	.538	.804							
Des./GP	$\overline{.662}$	.859	.919	$\overline{.825}$	$\overline{.320}$	$\overline{.487}$	$\overline{.536}$	$\overline{.366}$	$\overline{.194}$	.588	.612	$\overline{.463}$	.041	$\overline{.700}$	$\overline{.585}$						
Des./p/f.	.497	.084	$\overline{.163}$	.304	$\overline{.002}$	$\overline{.084}$	$\overline{.023}$	$\overline{.035}$	.422	$\overline{.302}$	$\overline{.016}$	$\overline{.019}$	.248	.430	.421	$\overline{.244}$					
Des./weed	$\overline{.524}$	.900	.837	$\overline{.742}$	$\overline{.282}$	$\overline{.502}$	$\overline{.562}$	$\overline{.342}$	$\overline{.007}$	.559	.567	$\overline{.478}$	.046	$\overline{.563}$	$\overline{.438}$	.898	.076				
Des./GP/comm.	$\overline{.664}$	.602	.638	$\overline{.672}$	$\overline{.330}$	$\overline{.355}$	$\overline{.493}$	$\overline{.204}$	$\overline{.269}$	.914	.328	$\overline{.493}$	$\overline{.469}$	$\overline{.517}$	$\overline{.693}$	.696	$\overline{.320}$	.652			
St./Des.	.555	.110	$\overline{.022}$	.162	$\overline{.013}$	$\overline{.217}$	$\overline{.021}$	$\overline{.054}$	.432	$\overline{.450}$	$\overline{.105}$	.137	.724	.269	.597	$\overline{.071}$	.701	.158	$\overline{.457}$		
GP/p/f.	.249	$\overline{.053}$	.167	.156	.048	$\overline{.026}$	.065	$\overline{.099}$	$\overline{.090}$	$\overline{.309}$	.175	$\overline{.112}$	.424	.171	.198	$\overline{.039}$	.364	$\overline{.076}$	$\overline{.347}$	.236	

Stylosanthes guyanensis

It is evident from Table 8 that soil depth and soil pH were the most influential factors in describing the distribution pattern of stylo. The higher soil pH and shallower soil profile combined to describe the conditions on the ridge tops where stylo was predominantly found. Figure 34 illustrates these relationships. With an increase in soil depth and a more favorable nutrient situation going down the slope, there was a corresponding decrease in stylo as a sward component. This is explained by the fact that conditions further down the slope were more favorable for plant growth and the more vigorous, fertility-responsive species provided too much competition for the less vigorous stylo. However, on the ridge tops these more vigorous species could not thrive in the poorer conditions. Stylo, with its ability to utilize soil nutrients and soil moisture more efficiently, was able to survive and produce in these locations.

Soil depth alone explained 49% of the total variation in the distribution of stylo. Apart from soil pH, other factors entering into the multiple regression equation such as slope, soil surface temperature, water extractable silicon, soil potassium and soil water have little effect on the fit of the equation.

Desmodium intortum

From the multiple regression analysis illustrated in Table 9 and Figure 35, the environmental factors which appeared to have the most influence on the distribution pattern of intortum were soil surface temperature during the February-April period, total soil nitrogen, exchangeable soil calcium and manganese.

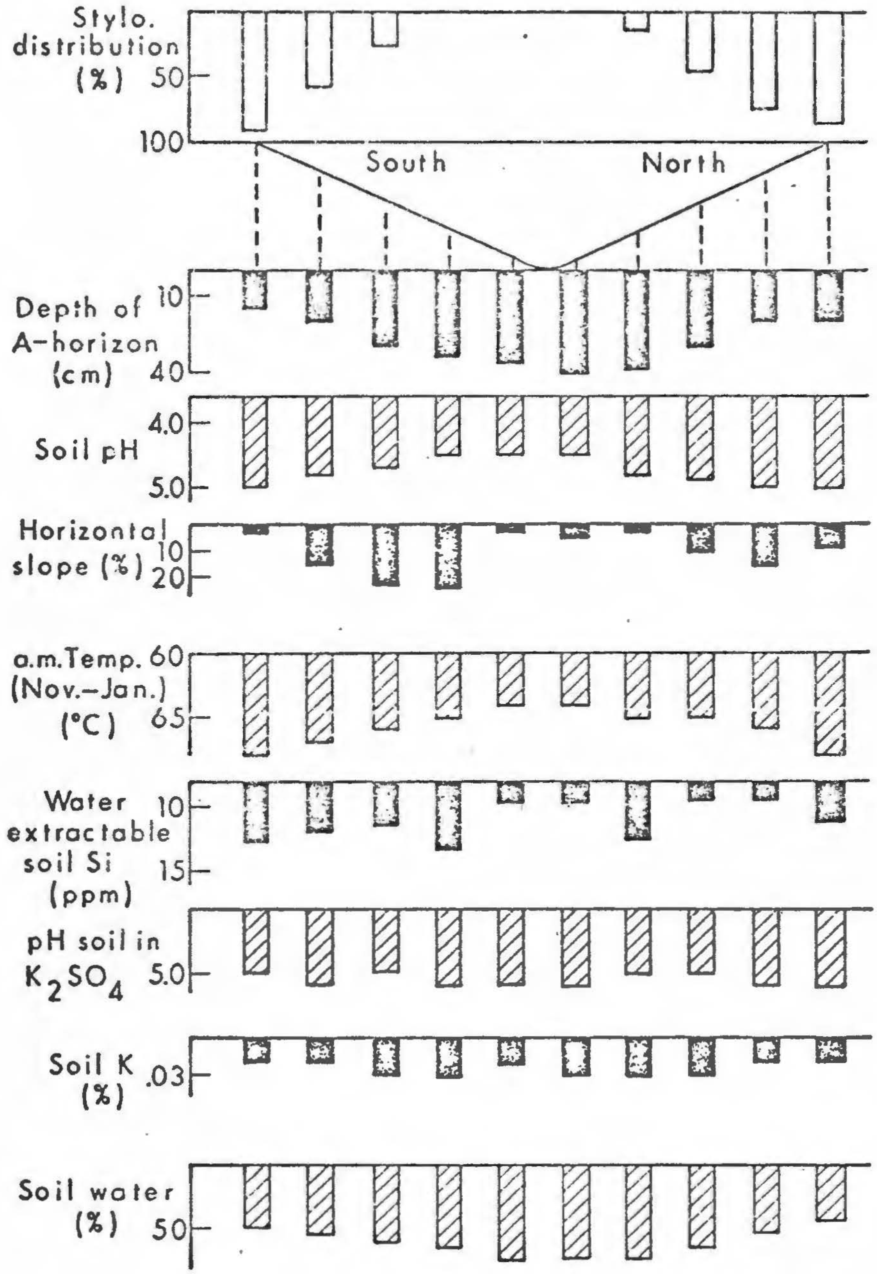

FIGURE 34. THE DISTRIBUTION OF *Stylosanthes guyanensis* AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 8. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stylosanthes guyanensis*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stylosanthes guyanensis*	R	Inc. in R^2
Soil Depth (x_1)	$Y = 115.1 - 6.1x_1$	0.697**	0.486
Soil pH (x_2)	$Y = -306.7 - 4.9x_1 + 83.9x_2$	0 783**	0.127
Hor. Slope (x_3)	$Y = -234.3 - 4.9x_1 + 68.0x_2 + 0.5x_3$	0.808**	0.039
Nov.-Jan. a.m. Temp. (x_4)	$Y = -352.6 - 4.0x_1 + 22.9x_2 + 0.7x_3 + 0.07x_4$	0.837**	0.047
Soil Silicon (x_5)	$Y = -296.4 - 4.3x_1 \quad + 0.7x_3 + 0.09x_4 - 3.5x_5$	0.865**	0.054
pH K_2SO_4 (x_6)	$Y = -48.8 - 4.5x_1 \quad + 0.8x_3 + 0.09x_4 - 3.4x_5 - 45.2x_6$	0.883**	0.031
Soil Potassium (x_7)	$Y = -52.5 - 4.4x_1 \quad + 0.8x_3 + 0.09x_4 - 3.4x_5 - 48.3x_6 + 358.6x_7$	0.888**	0.009
Soil Water (x_8)	$Y = -118.4 - 4.1x_1 \quad + 0.8x_3 + 0.1x_4 - 3.6x_5 - 64.1x_6 + 433.7x_7 + 0.4x_8$	0.892**	0.008

R = Regression coefficient

** = Significance at the 1% level

Referring to Appendix Table 9 it is evident that there was a high correlation between the afternoon temperature at the ground surface in the February to April period and soil water. This leads to the possibility that one of the main causes of the increased amount of intortum toward the valley bottom could have been soil moisture. In an attempt to verify this the analysis was rerun with all soil surface temperature factors excluded from the list of independent variables. Under these conditions soil moisture, soil nitrogen, soil calcium and soil manganese were selected as the three most important factors influencing the distribution of intortum.

However when these three variables were forced into the analysis ahead of all remaining environmental parameters, including soil surface temperature, the afternoon temperature at the ground surface during the February to April period once again contributed to a slightly greater proportion of the total variation than soil moisture (Table 10). This leads to the conclusion that temperature and moisture effects both influenced the distribution of intortum, but other influential factors were soil nitrogen and soil calcium.

The reason why there was such a strong positive correlation between afternoon temperature and soil moisture may have been because there was very little cooling influence of the tradewinds in the valley bottoms, which were coincidentally wetter.

Intortum, an improved, vigorous legume with high moisture and fertility requirements, was found predominantly on the lower slopes and valley bottoms. Its superior competitive ability at these locations forced stylo out of the sward. However, isolated intortum plants found on the ridge tops and higher up the slopes were very weak and unproductive.

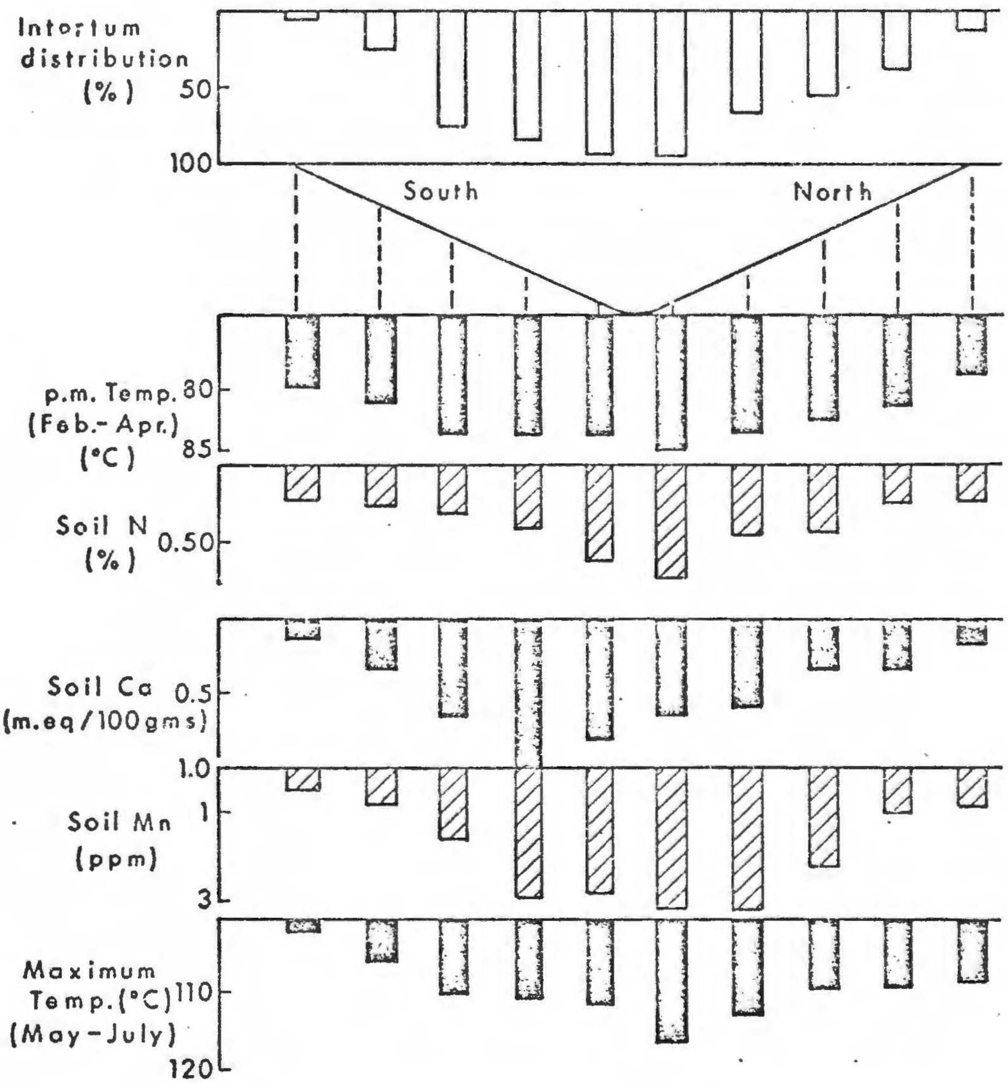

FIGURE 35. THE DISTRIBUTION OF Desmodium introtum AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 9. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Desmodium intortum*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Desmodium intortum*	R	Inc. in R^2
Feb.-April p.m. Temp. (x_1)	$Y = -1593.6+20.1x_1$	0.792**	0.627
Soil Nitrogen (x_2)	$Y = -1247.7+15.6x_1+54.2x_2$	0.837**	0.073
Soil Calcium (x_3)	$Y = -1041.2+13.0x_1+61.6x_2+13.0x_3$	0.851**	0.024
Soil Manganese (x_4)	$Y = -1159.9+14.5x_1+70.7x_2+20.6x_3-5.6x_4$	0.859**	0.014
May-July Max. Temp. (x_5)	$Y = -1113.2+11.2x_1+66.2x_2+22.5x_3-7.2x_4+2.1x_5$	0.867**	0.014

R = Regression coefficient

** = Significance at the 1% level

TABLE 10. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Desmodium intortum*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Desmodium intortum*	R	INCREASE IN R^2
Soil nitrogen (x_1)	$Y = 10.6+110.6x_1$	0.659**	0.43
Soil calcium (x_2)	$Y = -2.7+106.1x_1+28.4x_2$	0.765**	0.15
Soil water (x_3)	$Y = -39.5+101.1x_1+23.7x_2+0.7x_3$	0.801**	0.06
pm Temp. (Feb.-Apr.) (x_4)	$Y = -1054.9+61.2x_1+12.9x_2-0.02x_3+13.1x_4$	0.851**	0.08
Soil manganese (x_5)	$Y = -1132.3+71.8x_1+20.8x_2+0.05x_3+14.1x_4-5.7x_5$	0.859**	0.01
Max. Temp. (May-July) (x_6)	$Y = -1129.7+65.5x_1+22.3x_2-0.03x_3+11.3x_4-7.1x_5+2.1x_6$	0.867**	0.01
Soil pH in KCl (x_7)	$Y = -1059.9+47.4x_1+22.8x_2+0.27x_3+10.2x_4-6.9x_5+2.4x_6-5.0x_7$	0.872**	0.01

R = Regression coefficient

** = Significance at the 1% level

The conditions at these locations swung thecompetitive balance in favor of stylo.

Panicum maximum (var. trichoglume)

As the results appear in Table 11 and Figure 36, the distribution of green panic was more closely associated with the morning temperature at the ground surface during the winter months. This was an inverse relationship, with an increase in green panic going down the slope. However on referring to Appendix Table 9, morning temperature at the soil surface was also strongly correlated with soil moisture. This high negative correlation may be caused by the lower morning temperature in the wetter valley bottoms.

Once again to remove the masking effect of temperature, these factors were omitted from the list of independent variables and the analysis was repeated. This resulted in such factors as soil manganese, soil nitrogen and soil moisture being extracted as the most important factors influencing the distribution of green panic.

When these three factors were forced into the equation ahead of all other environmental parameters, including the soil surface temperatures, the fit of the equation was improved only slightly by the addition of the morning temperature at the ground surface (Table 12). In this case it was obvious that the high correlation between the temperature at the soil surface and other environmental factors resulted in a masking of the true contribution of these other factors.

Like intortum, green panic is a vigorous, improved forage species which responds to increased soil fertility and moisture. With this in mind, of the remaining factors extracted by the analysis it was felt

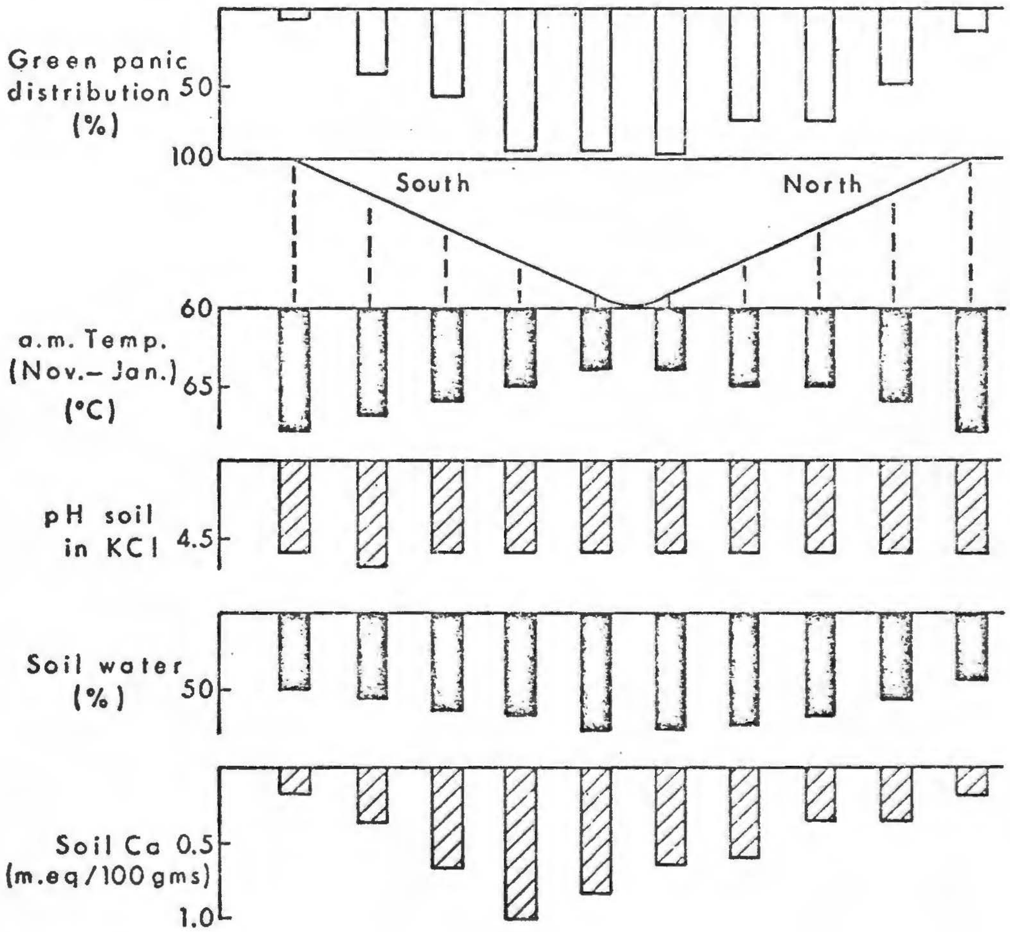

FIGURE 36. THE DISTRIBUTION OF Panicum maximum (var. trichoglume) AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 11. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Panicum maximum* (var. *trichoglume*)

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Panicum maximum* (var. *trichoglume*)	R	Inc. in R^2
Nov.-Jan. a.m. Temp. (x_1)	$Y = 1453.4-21.2x_1$	0.739**	0.546
pH KCl (x_2)	$Y = 1476.3-21.2x_1-5.2x_2$	0.758**	0.029
Soil Water (x_3)	$Y = 906.9-13.3x_1-11.8x_2+1.2x_3$	0.793**	0.054
Soil Calcium (x_4)	$Y = 720.3-10.6x_1-13.1x_2+1.3x_3+13.4x_4$	0.809**	0.025

R = Regression coefficient

** = Significance at the 1% level

TABLE 12. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Panicum maximum* var. *trichoglume*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Panicum maximum* var. *trichoglume*	R	INCREASE IN R^2
Soil manganese (x_1)	$Y = 29.9+15.7x_1$	0.545**	0.29
Soil nitrogen (x_2)	$Y = 13.3+10.8x_1+64.9x_2$	0.637**	0.11
Soil water (x_3)	$Y = -44.3+5.7x_1+68.4x_2+1.1x_3$	0.723**	0.12
Soil pH in KCl (x_4)	$Y = -17.6+6.3x_1+15.9x_2+1.8x_3-13.8x_4$	0.766**	0.06
am Temp. (Nov.-Jan.) (x_5)	$Y = 847.3+2.6x_1-10.7x_2+1.2x_3-13.1x_4-12.3x_5$	0.796**	0.05
Soil calcium (x_6)	$Y = 762.1-2.1x_1+3.5x_2+1.3x_3-12.9x_4-11.2x_5+16.2x_6$	0.809**	0.02

R = Regression coefficient

** = Significance at the 1% level

that soil moisture, soil nitrogen and soil manganese conditions more reliably explained the pattern of green panic occurrence.

Providing management conditions were favorable, the combination of green panic and intortum provided a competitive barrier to the invasion of less vigorous species such as stylo and weeds. This balance only occurred at locations lower down the slopes where conditions for vigorous growth were more favorable to these improved species.

Paspalum-Foxtail Association

From observation this association has been considered as the most reliable indicator of shallow soils of poor fertility. However, in an effort to interpret the masses of data collected, the method of analysis used once again extracted the soil surface temperature factors as being more closely associated with the distribution pattern of this particular species.

To remove the masking effect of the high correlation between this temperature factor and soil moisture, the analysis was performed omitting the surface soil temperatures from the list of independent variables. When this was done soil moisture contributed 15% of the variation and soil depth contributed 50%.

On forcing these two factors into a separate analysis which included the soil surface temperature components, the morning temperature at the ground surface during the winter period again appeared to be relatively important (Table 14). However, as compared to the results of the original analysis the contribution of this temperature factor was minimal most of the variation being explained by previously masked environmental parameters such as soil depth and soil moisture.

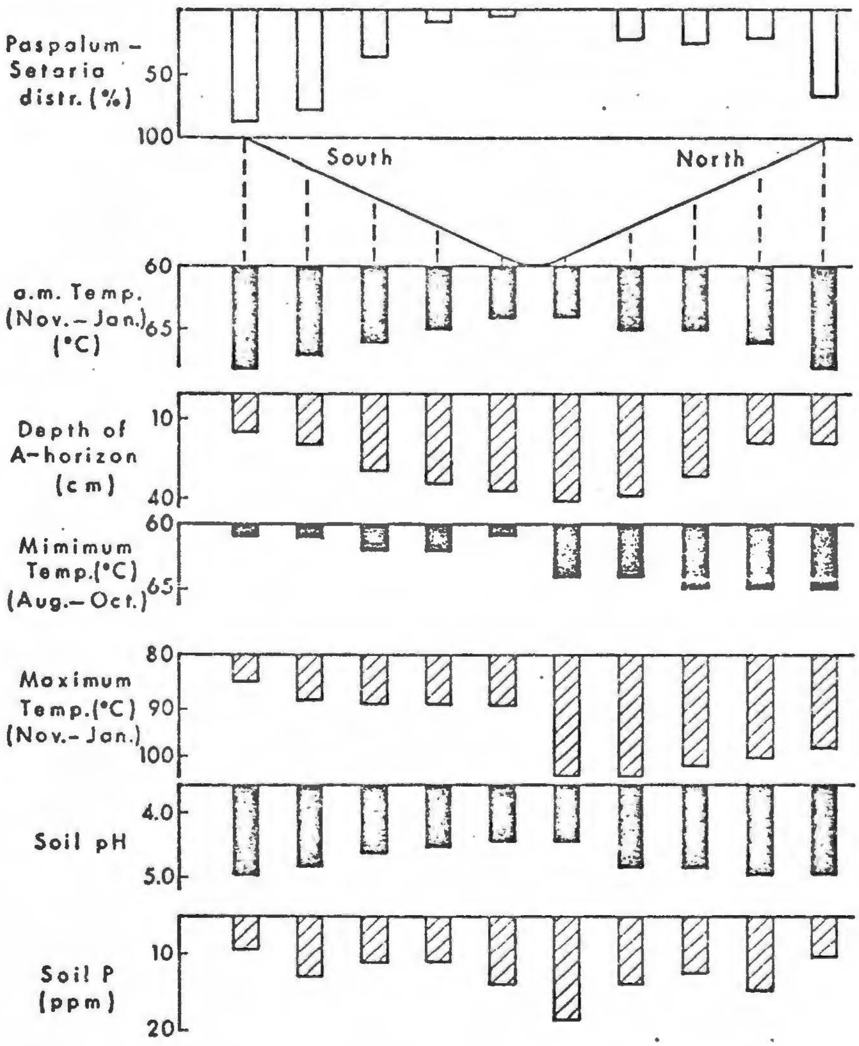

FIGURE 37. THE DISTRIBUTION OF THE Paspalum/Setaria ASSOCIATION AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 13. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Paspalum*/*Setaria* ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE *Paspalum*/*Setaria* ASSOCIATION	R	Inc. in R^2
(Nov.-Jan. a.m. Temp.)^2 (x_1	$Y = -627.6+0.2x_1$	0.796**	0.634
Soil Depth (x_2)	$Y = -415.0+0.1x_1-3.0x_2$	0.866**	0.116
Aug.-Oct.min. Temp. (x_3)	$Y = -276.4+0.1x_1-2.9x_2-2.3x_3$	0.872**	0.011
Nov.-Jan. max. Temp (x_4)	$Y = -95.8+0.1x_1-2.8x_2-11.3x_3+2.5x_4$	0.885**	0.023
Soil pH (x_5)	$Y = -137.7+0.1x_1-2.7x_2-15.3x_3+3.7x_4+46.0x_5$	0.899**	0.026
Soil phosphorus (x_6)	$Y = -113.7+0.1x_1-2.7x_2-15.7x_3+3.9x_4+46.7x_5-0.8x_6$	0.904**	0.008

R = Regression coefficient

** = Significance at the 1% level

TABLE 14. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE *Paspalum*/*Setaria* ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE *Paspalum*/*Setaria* ASSOCIATION	R	INCREASE IN R^2
Soil depth (x_1)	$Y = 99.4-5.4x_1$	0.709**	0.50
Soil water (x_2)	$Y = 153.9-4.8x_1-0.9x_2$	0.809**	0.15
am Temp. (Nov.-Jan.) (x_3)	$Y = -753.0-3.2x_1-0.3x_2+12.8x_3$	0.868**	0.09
Min. Temp. (Aug.-Oct.) (x_4)	$Y = -577.2-3.1x_1-0.3x_2+12.5x_3-2.5x_4$	0.876**	0.01
Max. Temp. (Nov.-Jan.) (x_5)	$Y = -494.9-3.0x_1-0.4x_2+17.1x_3-12.6x_4+2.7x_5$	0.892**	0.03
Soil Phosphorus (x_6)	$Y = -583.6-2.8x_1-0.2x_2+16.8x_3-15.8x_4+3.9x_5+39.9x_6$	0.901**	0.02
Soil pH (x_7)	$Y = -623.4-2.8x_1-0.2x_2+17.1x_3-15.4x_4+3.7x_5+39.9x_6-0.9x_7$	0.905**	0.01

R = Regression coefficient

** = Significance at the 1% level

Of the soil factors, soil depth and soil moisture seemed to be more closely associated with the distribution pattern of this community. Shallower soils, coupled with lower soil moisture and less available nutrients at locations on the ridge tops, were more favorable for survival of these less vigorous grassy weeds. If soil nutrients and moisture were higher, the more fertility-responsive and vigorous forage species would dominate. This was the situation further down the slopes, resulting in the distribution pattern of the Paspalum-Foxtail association shown in Figure 37.

Stylosanthes/Paspalum/Foxtail Association

As can be seen from the correlation matrix for species in Table 7, there was a strong relationship between stylo and the weedy grass association. Considering the environmental factors most closely associated with the distribution pattern of this ridge-top community, Table 15 indicates that the morning temperature at the soil surface during the November to January period was most influential.

By removing this temperature component from the analysis, soil depth and soil magnesium appeared to be the most influential factors. These parameters were then forced into an equation in an analysis which included all soil surface temperature components. Under these conditions the morning temperature at the ground surface during the November to January period was replaced by the daily maximum temperature during the February to April period (Table 16). The contribution of this factor is not considered important.

It is felt that of the environmental factors considered, those most influencing the distribution of this plant association were soil depth, soil magnesium and soil slope.

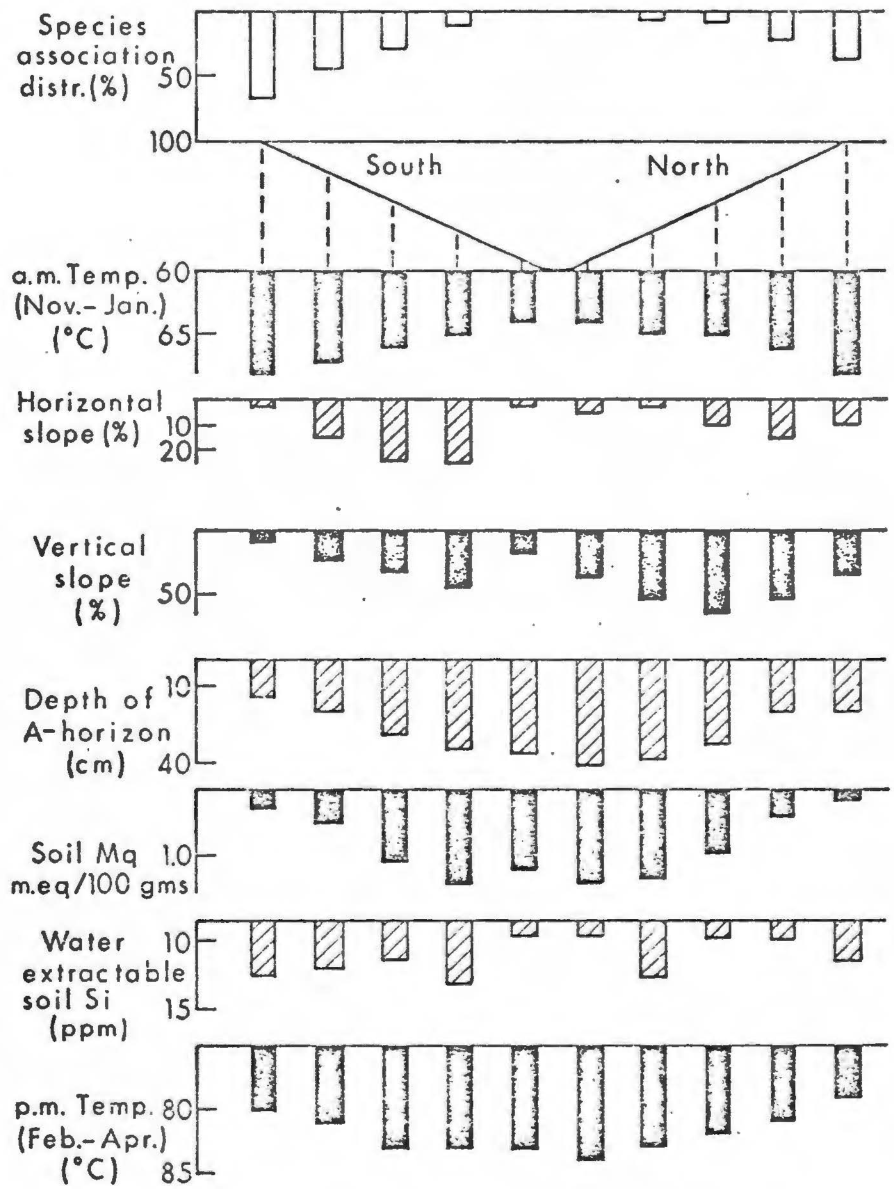

FIGURE 38. THE DISTRIBUTION OF THE Stylosanthes/Paspalum/Setaria ASSOCIATION AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 15. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stylosanthes*/*Paspalum*/*Setaria* ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stylosanthes*/*Paspalum*/*Setaria* ASSOCIATION	R	Inc. in R^2
(Nov.-Jan. a.m. Temp)^2 (x_1)	$Y = -452.5+0.1x_1$	0.670**	0.449
Hor. Slope (x_2)	$Y = -454.3+0.1x_1+0.6x_2$	0.738**	0.096
Vert. Slope (x_3)	$Y = -381.9+0.1x_1+0.6x_2-0.4x_3$	0.783**	0.068
Soil Depth (x_4)	$Y = -289.2+0.1x_1+0.5x_2-0.3x_3-1.5x_4$	0.807**	0.038
Soil Magnesium (x_5)	$Y = -163.5+0.05x_1+0.5x_2-0.3x_3-1.8x_4-9.2x_5$	0.822**	0.026
Soil Silicon (x_6)	$Y = -161.1+0.05x_1+0.5x_2-0.3x_3-1.9x_4-9.0x_5-1.4x_6$	0.831**	0.015
Feb.-April p.m. Temp. (x_7)	$Y = -989.4+0.1x_1+0.4x_2-0.3x_3-2.0x_4-11.9x_5-1.9x_6+7.6x_7$	0.842**	0.018

R = Regression coefficient

** = Significance at the 1% level

TABLE 16. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE *Stylosanthes*/*Paspalum*/*Setaria* ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STFP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE *Stylosanthes*/*Paspalum*/*Setaria* ASSOCIATION	R	INCREASE IN R^2
Soil depth (x_1)	$Y = 69.1-3.9x_1$	0.597**	0.36
Soil magnesium (x_2)	$Y = 80.9-3.5x_1-17.2x_2$	0.713**	0.15
Max. Temp. (Feb.-Apr.) (x_3)	$Y = 377.2-2.5x_1-10.7x_2-2.8x_3$	0.766**	0.08
Horizontal Slope (x_4)	$Y = 376.4-2.3x_1-9.5x_2-2.9x_3+4.3x_4$	0.804**	0.06
Soil silicon (x_5)	$Y = 433.7-2.4x_1-9.1x_2-3.2x_3+0.4x_4-1.8x_5$	0.819**	0.03
pm Temp. (Aug.-Oct.) (x_6)	$Y = 368.9-2.1x_1-7.6x_2-5.7x_3+0.5x_4-1.9x_5+3.9x_6$	0.829**	0.02
Vertical slope (x_7)	$Y = 236.6-1.9x_1-9.9x_2-5.5x_3+0.5x_4-1.7x_5+5.3x_6-1.9x_7$	0.845**	0.03

R = Regression coefficient

** = Significance at the 1% level

Stylo and the shallow-rooted weedy grasses were dominant in areas of steeper slope and shallower soil profiles. In these situations conditions were not favorable for growth of the more vigorous, improved forage species. Other soil factors apparently closely associated with the distribution pattern of this group of species were soil magnesium and water extractable soil silicon.

Stylosanthes/weed species Association

The weed species considered in this association were: *Lantana camara*, *Melastoma malabathricum*, *Elephantopus mollis* and *Stachytarpheta urticaefolia*. Generally, their individual distribution patterns followed that of stylo, that is, towards the tops of the slopes and ridges.

As could be expected on ridge-tops, the environmental factors influencing plant growth included soil depth, soil pH and soil moisture. This is illustrated in Table 17 and Figure 39. Ridge-tops, with a high proportion of bare ground and lack of vigorous, competitive forage species, provided ideal conditions for invasion by weeds. Further down the slope conditions were more favorable for vigorous growth of forage species, thus providing too much competition for the survival of such weeds. Relationships between distribution patterns of individual weed species and environmental factors have been discussed previously (Nicholls and Plucknett, 1973) and are tabulated and illustrated in Appendix III.

Desmodium intortum/*Panicum maximum* var. *trichoglume* Association

It is evident from Table 7 that these species were closely associated. Conditions for their growth were much more favorable at

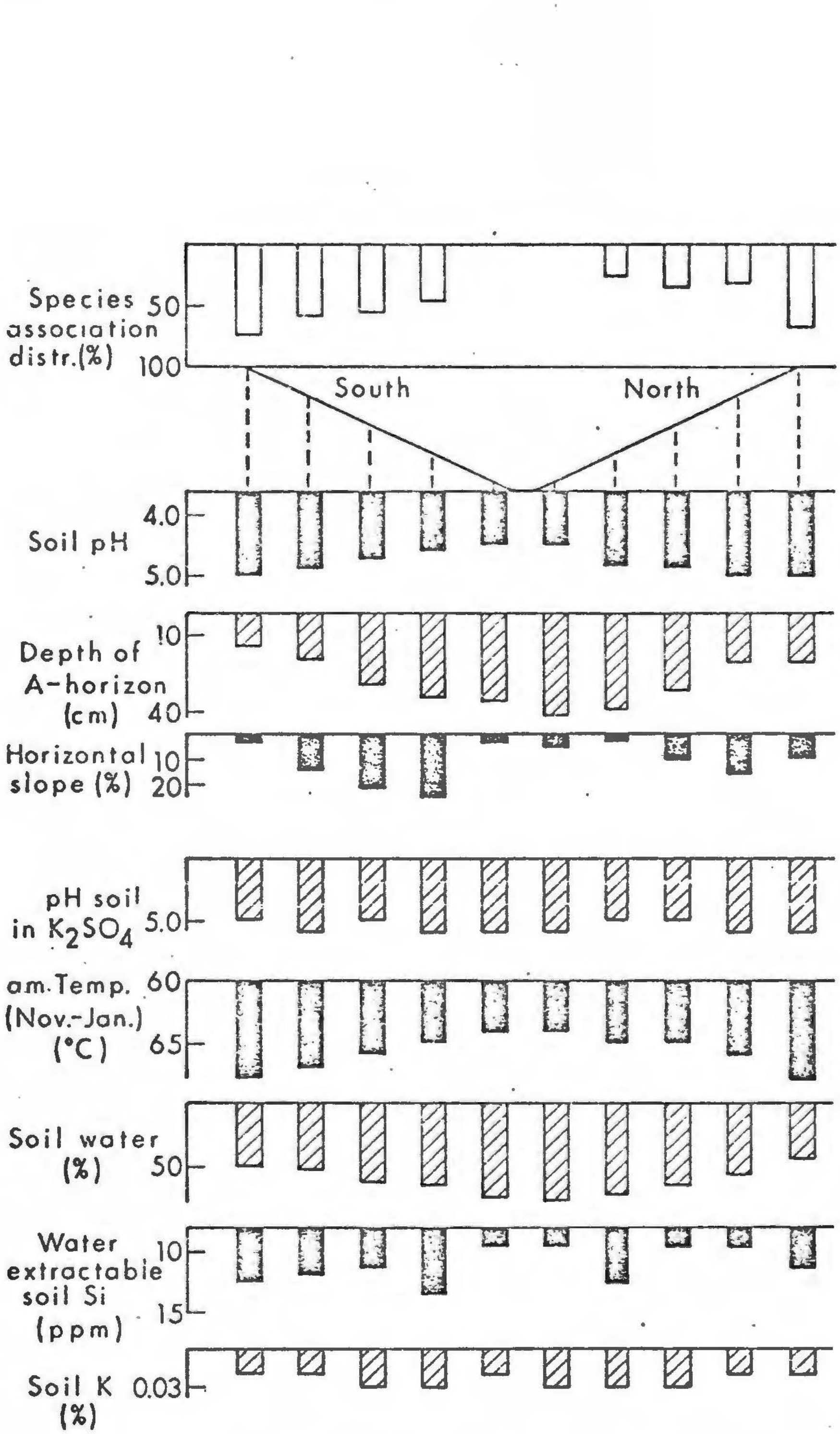

FIGURE 39. THE DISTRIBUTION OF THE Stylosanthes/ WEED SPECIES ASSOCIATION AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 17. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stylosanthes*/WEED SPECIES ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE *Stylosanthes*/WEED SPECIES ASSOCIATION	R	Inc. in R^2
Soil pH (x_1)	$Y = -556.7+123.0x_1$	0.606**	0.368
Soil Depth (x_2)	$Y = -366.2+92.3x_1-3.4x_2$	0.721**	0.153
Hor. Slopr (x_3)	$Y = -264.9+70.1x_1-3.5x_2+0.7x_3$	0.781**	0.089
pH K_2SO_4 (x_4)	$Y = -29.2+67.2x_1-3.7x_2+0.8x_3-43.8x_4$	0.803**	0.034
(Nov.-Jan. a.m. Temp)^2(x_5)	$Y = -113.4+39.6x_1-3.1x_2+0.9x_3-41.7x_4+0.05x_5$	0.816**	0.021
Soil Water (x_6)	$Y = -283.0+64.9x_1-2.6x_2+0.9x_3-69.8x_4+0.08x_5+0.8x_6$	0.832**	0.026
Soil Silicon (x_7)	$Y = -289.1+62.2x_1-2.6x_2+0.9x_3-71.7x_4+0.08x_5+0.9x_6-1.8x_7$	0.841**	0.016
Soil Potassium (x_8)	$Y = -293.5+56.1x_1-2.5x_2+0.9x_3-78.3x_4+0.09x_5+1.0x_6-1.9x_7+444.0x_8$	0.849**	0.014

R = Regression coefficient

** = Significance at the 1% level

locations towards the valley bottom. Again the winter morning temperature at the ground surface appeared to be the most influential environmental factor (Table 18).

As was the case for each component of this association, high correlation between soil moisture and temperature at the soil surface masked the effects of soil moisture. By removing temperature factors from the analysis, it was evident that the distribution pattern of this particular species association was more closely related to soil fertility factors such as soil moisture, soil nitrogen and soil calcium.

By forcing soil moisture into an analysis which included soil surface temperatures, the morning temperature at the ground surface during winter again appeared to have some influence on the association distribution. As was seen earlier, this particular temperature component had masked the effect of other soil fertility factors. In this case the contribution of this temperature factor to the total variation was small compared to that of soil nitrogen and soil moisture (Table 19).

Commelina diffusa

As can be seen in Figure 41 this weed species was found at locations on the lower slopes and in the valley bottoms. In such locations the vigorous green panic and intortum dominated; however, spreading dayflower was also found, especially during wet periods and after heavy grazing.

According to the analysis shown in Table 20, distribution of this weed species was most closely related to the variation in soil pH. Other environmental factors closely associated with its growth patterns were the maximum temperature at the ground surface during May to July, slope, soil phosphorus and total soil nitrogen.

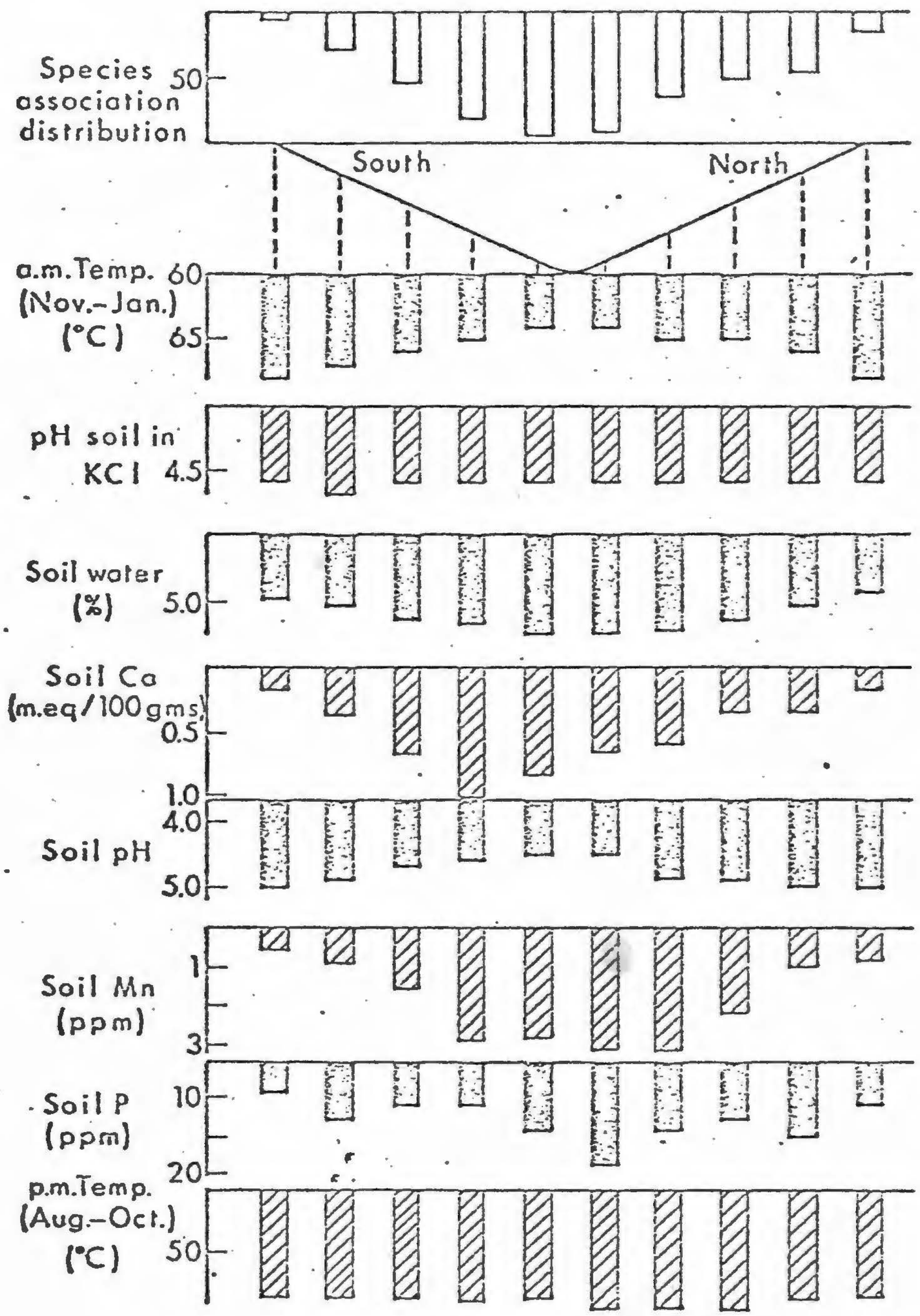

FIGURE 40. THE DISTRIBUTION OF THE *Desmodium intortum*/*Panicum maximum* (var. *trichoglume*) ASSOCIATION, AS INFLUENCED BY ENVIRONMENTAL FACTORS

TABLE 18. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Desmodium intortum*/*Panicum maximum* ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Desmodium intortum*/*Panicum maximum* ASSOCIATION	R	Inc. in R^2
Nov.-Jan. a.m. Temp. (x_1)	$Y = 1422.4-20.8x_1$	0.734**	0.538
pH KCl (x_2)	$Y = 1449.2-20.9x_1-6.1x_2$	0.760**	0.040
Soil Water (x_3)	$Y = 1017.2-14.8x_1-11.1x_2+0.9x_3$	0.781**	0.032
Soil Calcium (x_4)	$Y = 801.4-11.7x_1-12.6x_2+1.0x_3+15.5x_4$	0.803**	0.034
Soil pH (x_5)	$Y = 835.3-8.2x_1-12.9x_2+0.8x_3+19.3x_4-51.3x_5$	0.819**	0.026
Soil Manganese (x_6)	$Y = 1116.2-10.7x_1-13.9x_2+0.7x_3+31.6x_4-71.5x_5-8.6x_6$	0.835**	0.027
Soil Phosphorus (x_7)	$Y = 1039.4-10.2x_1-13.5x_2+0.7x_3+31.5x_4-67.5x_3-9.5x_6+1.5x_7$	0.847**	0.019
Aug.-Oct. p.m. Temp. (x_8)	$Y = 1556.6-13.4x_1-12.6x_2+0.6x_3+25.9x_4-75.2x_5-7.7x_6+1.6x_7-3.0x_8$	0.856**	0.015
Soil Magnesium (x_9)	$Y = 1576.4-11.9x_1-13.2x_2+0.3x_3+28.3x_4-94.8x_5-10.9x_6+1.9x_7-3.2x_8+11.0x_9$	0.863**	0.013

R = Regression coefficient

** = Significance at the 1% level

TABLE 19. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE <u>Desmodium/Panicum maximum</u> ASSOCIATION

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR THE Desmodium/Panicum maximum ASSOCIATION	R	INCREASE IN R^2
Soil nitrogen (x_1)	$Y = 13.0+99.1x_1$	0.573**	0.33
Soil water (x_2)	$Y = -51.1+88.1x_1+1.1x_2$	0.695**	0.16
am Temp. (Nov.-Jan.) (x_3)	$Y = 1001.0+41.7x_1+0.3x_2-14.9x_3$	0.754**	0.09
Soil pH in KCl (x_4)	$Y = 1003.0+2.3x_1+0.9x_2-14.6x_3-10.8x_4$	0.781**	0.04
Soil calcium (x_5)	$Y = 718.7+12.2x_1+0.9x_2-10.6x_3-11.3x_4+16.0x_5$	0.804**	0.04
Soil pH in water (x_6)	$Y = 862.3-3.8x_1+0.8x_2-8.5x_3-13.3x_4+19.2x_5-52.5x_6$	0.819**	0.02
Soil phosphorus (x_7)	$Y = 1080.4+5.9x_1+0.7x_2-10.4x_3-13.3x_4+31.9x_5-70.0x_6+1.5x_7$	0.835**	0.03

R = Regression coefficient

** = Significance at the 1% level

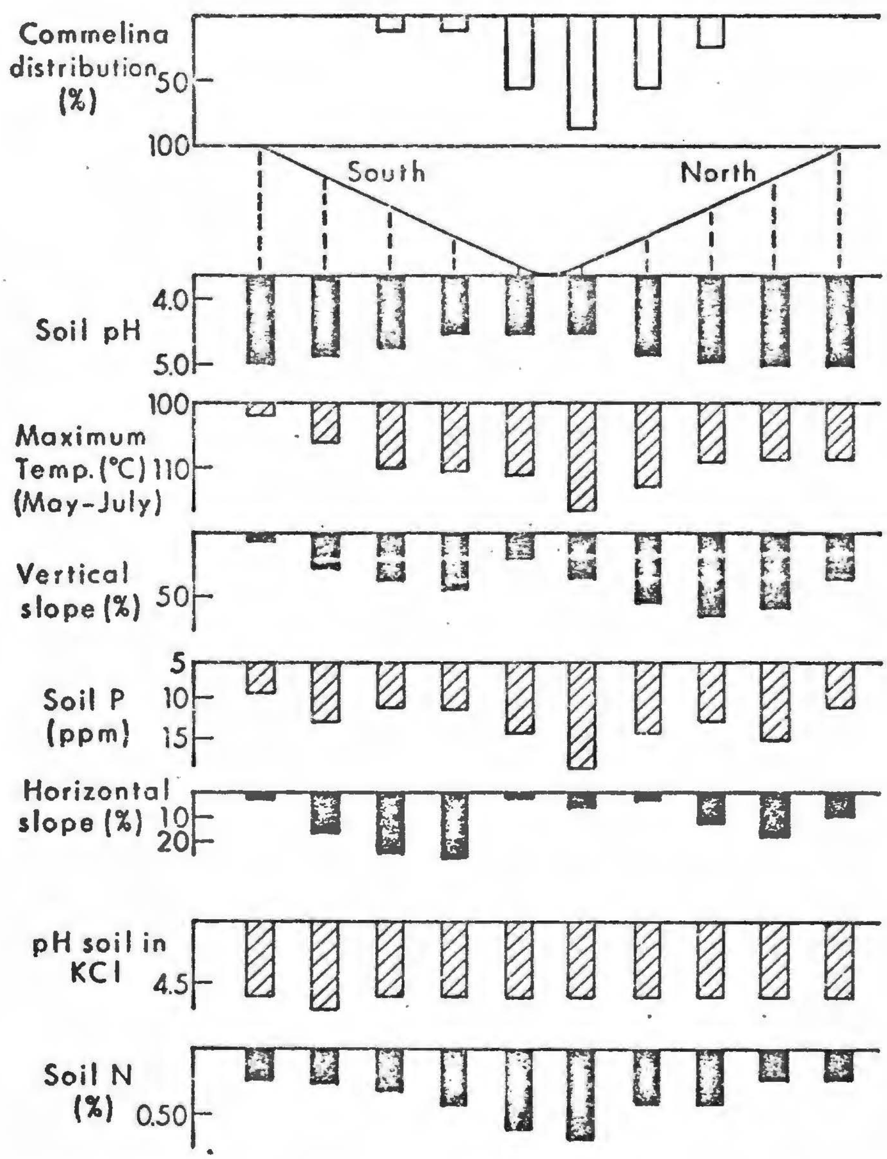

FIGURE 41. THE DISTRIBUTION OF *Commelina diffusa* AS INFLUENCED BY ENVIRONMENTAL FACTORS.

TABLE 20. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Commelina diffusa*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Commelina diffusa*	R	Inc. in R^2
Soil pH (x_1)	$Y = 727.1-144.8x_1$	0.749**	0.561
(May-July Max.)^2 (x_2)	$Y = 297.9-96.4x_1+0.02x_2$	0.802**	0.081
Vert. Slope (x_3)	$Y = 303.3-99.3x_1+0.02x_2-0.3x_3$	0.815**	0.023
Soil Phosphorus (x_4)	$Y = 314.0-99.4x_1+0.02x_2-0.3x_3+1.2x_4$	0.824**	0.016
Hor. Slope (x_5)	$Y = 233.1-86.1x_1+0.02x_2-0.3x_3+1.2x_4-0.3x_5$	0.832**	0.013
pH KCl (x_6)	$Y = 164.4-76.9x_1+0.02x_2-0.2x_3+1.3x_4-0.3x_5+2.9x_6$	0.838**	0.009
Soil Total Nitrogen (x_7)	$Y = 82.5-57.5x_1+0.01x_2-0.2x_3+0.9x_4-0.3x_5+7.8x_6+44.0x_7$	0.850**	0.021

R = Regression coefficient

** = Significance at the 1% level

TABLE 21. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Commelina diffusa*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION FOR *Commelina diffusa*	R	INCREASE IN R^2
Soil pH in water (x_1)	$Y = 727.1-144.8x_1$	0.749**	0.56
Soil phosphorus (x_2)	$Y = 656.3-133.9x_1+1.7x_2$	0.771**	0.04
Soil water (x_3)	$Y = 493.9-101.2x_1+1.7x_2+0.5x_3$	0.787**	0.02
Max. Temp. (May-July) (x_4)	$Y = 108.2-84.7x_1+1.1x_2+0.3x_3+2.7x_4$	0.811**	0.04
Vertical slope (x_5)	$Y = 107.7-90.3x_1+1.3x_2+0.3x_3+3.0x_4-0.3x_5$	0.826**	0.02
Horizontal slope (x_6)	$Y = -9.7-73.9x_1+1.3x_2+0.3x_3+3.3x_4-0.2x_5-0.3x_1$	0.835**	0.02

Because of the relatively high positive correlation between soil moisture and temperature at the soil surface during May to July, the true effect of soil moisture was once again masked. When the temperature factors were excluded from the analysis the resulting equation showed a close relationship between soil water and the distribution of spreading dayflower. This was also evident by observation since this particular weed species was an excellent indicator of wet or waterlogged soil conditions. It also became more dominant during the wet season. Other factors that are considered important in determining the distribution of this species are soil pH and soil phosphorus.

SUMMARY AND CONCLUSION

The aim of this phase of such an ecological approach to pasture research was to identify the environmental factors that most strongly influenced the distribution of particular plant species or species associations. The step-wise multiple regression analysis used enabled the sorting of complex data on environmental and vegetation components.

The ridge top community was composed of *Stylosanthes guyanensis* and the weedy grass association. Here higher soil pH and a shallower soil profile combined to most aptly describe the plant distribution at these locations.

The dominant legume on the more fertile lower slopes and valley bottoms was *Desmodium intortum*. Its distribution pattern was closely related to the variation in soil nitrogen and soil calcium.

The dominant grass of the more fertile locations was *Panicum maximum* (var. *trichoglume*). Its distribution was related to variations in soil moisture, soil nitrogen and exchangeable soil manganese.

When management conditions were favorable, the combination of green panic and intortum provided a competitive barrier to less vigorous species such as stylo and weeds. This balance only seems possible at locations lower down the slopes where conditions for vigorous growth are more favorable to these improved forage species.

Of the more dominant weed species studied, the Paspalum conjugatum - Setaria geniculata association showed a very marked adaptation to the tops of the slopes. This corresponded closely with the gradient of soil depth and soil moisture going down the slope. The distribution of Commelina diffusa, located toward the valley bottom, was closely related to soil moisture. The other annual weed, Erechtites hieracifolia, exhibited a more varied distribution pattern which was related closely to total soil nitrogen and soil moisture. The more woody perennials, Lantana camara, Melastoma malabathricum, Stachytarpheta urticaefolia and Elephantopus mollis, all showed distribution patterns closely related to water extractable soil silica, among other environmental parameters.

The need for such a multiple regression analysis to extract meaningful conclusions from such a mass of data was evident. However the inclusion of so many interrelated environmental factors lead to conclusions which over-emphasized individual components at the expense of other highly correlated parameters. By logically manipulating the environmental parameters their actual influence on a certain plant species or species association can be better evaluated. Even though it was impossible to study the influence of all factors of the environment, we were able to extract groups of factors which explained a significant portion of the variation in distribution of particular species or species community response.

It is felt that the more important environmental factors that should be studied in more detail in the future include: soil nutrient and moisture components, soil pH, soil profile characteristics, position on the slope and slope aspect. The importance of such factors as the temperature at the ground surface will only be clarified after a much more detailed collection of data over a longer period of time and examination of intercorrelations with other factors.

CHAPTER VII. SWARD DYNAMICS AND PRODUCTIVITY

Literature on the study of dynamics of sward components and seasonal fluctuations in productivity of tropical forage species is scarce. Conditions of high temperature and moisture in the tropics favor vigorous invasion of species once the existing vegetation has been removed, or some other aspect of the environment gradually swings in favor of another species. Such a trend will not be so rapid in regions where conditions for perennial plant growth are not as conducive as those in the tropics. This is especially so in improved pastures. If a pasture is overgrazed or heavily trampled, exposing bare ground, and soil fertility is allowed to decline, weed species will quickly spread. In an effort to evaluate improved species and to recognize species retrogression, periodic measurement of the individual contribution of each of the dominant species is necessary. To remove the time consumed by destructive sampling and to increase the number of samples to be considered, 't Mannetje and Haydock (1963) constructed indices for tropical forage species to provide reliable estimates of dry matter percent contribution of each component to the overall production of the sward. This procedure is based on the rank method of de Vries (1933).

The main objective of this phase of such an ecological study was to identify seasonal trends in species dominance and productivity. In doing so it was hoped that particular species would emerge as reliable indicators of sward condition under the influence of normal grazing, overgrazing, undergrazing, and a natural decline in soil fertility. Destructive sampling of vegetation and photography at selected sites enabled better verification and interpretation of the data collected on seasonal productivity and dominance of both improved and weed species.

MATERIALS AND METHODS

Dry Matter Percent Estimate

This method of estimation removes the necessity to cut and hand-separate large numbers of samples in an effort to determine the contribution of each species to the total dry matter yield of a sward. In each quadrat along the transect the first three species were ranked in order of estimated dry matter production. By using the multiplying indices set out by 't Mannetje and Haydock (1963), the percent contribution of each species to the total dry matter of the community can be determined (Table 22).

Table 22. Indices used by 't Mannetje and Haydock (1963)

Rank	Multiplying Index
1	70.2
2	21.1
3	8.7

Taking species A, for example. If the proportion of the total number of quadrates in which A is ranked first is given value 'x', second the value 'y' and third the value 'z', then the estimated percent of the total dry matter yield attributed to species A is:

$$\% A = (x \times 70.2) + (y \times 21.1) + (z \times 8.7)$$

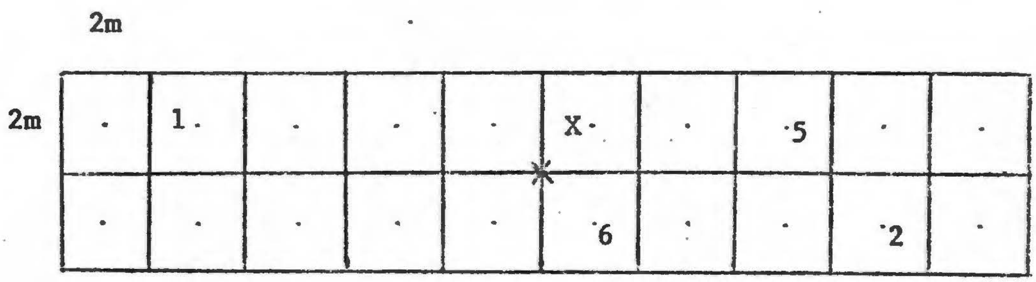

FIGURE 42. THE GRID SAMPLING DESIGN FOR VEGETATION ANALYSIS AT SITE 'X'.

With practice at estimating by rank the first three species in a quadrat on the basis of dry matter, verified by destructive sampling, drying and weighing, it was possible to reduce sampling time and to increase the number of quadrats sampled.

Dry Matter Yields

Destructive sampling of vegetation took place before and after each grazing period. In the vicinity of each of the forty sampling sites described in 'General Materials and Methods', twenty points were located on a two meter square grid (see Figure 42). Each square was randomly allocated a number and two of these were taken at each sampling in order; for example, at the first harvest material from a one meter quadrat centered in blocks 1 and 2 was sampled. At the third harvest, that vegetation in the meter quadrats centered in blocks 5 and 6 was sampled, and so on. The two samples from each site were bulked at each harvest, sorted into species, sub-sampled if necessary, oven dried at 120^{o} F and weighed.

The lack of sufficient variation at each sampling site and the size of the sampling unit did not warrant more than two samples to be taken per site at each harvest date. The initial randomization of sampling blocks was such that no one site was destructively sampled twice during the experimental period.

Both destructive sampling and dry matter percentage estimates took place before and after each grazing period. In Figures 43 through 51, Roman numerals I through VIII were used to designate the sampling dates. Samplings I, III, V and VII were taken before grazing and samplings II, IV, VI and VIII after grazing. The corresponding dates for samplings I through VIII were as follows: March 1970, July 1970, September 1970, January 1971, April 1971, July 1971, December 1971 and July 1972.

Photography

Black and white photographs of each sampling site were taken before and after each grazing (corresponding with the plant sampling procedure). Such a photographic record illustrated selective grazing patterns, trampling damage and the degree of grazing pressure. This enabled more accurate interpretation of data collected on each species under the influence of the grazing animal. Sward condition and weed invasion was better illustrated using photography of this kind.

Plant Analysis

As an addendum to this phase of the ecological study, seasonal fluctuations in crude protein and nutrient contents of the forage species were studied.

The species were sampled according to their growth habit. The grasses were 'pluck' sampled, simulating that portion selected by the grazing animal. In the case of the legumes, the portion of the shoot containing the last nine fully expanded trifoliate leaves was taken.

After drying each sample and grinding through a 20 mesh sieve in a Wiley mill, the samples were analyzed as explained in Appendix I. Graphical representation of the results appear in Appendix IV. The forage species analyzed were: Panicum maximum (var. trichoglume) (green panic), Digitaria decumbens (pangola grass), Paspalum conjugatum/ Setaria geniculata association, Desmodium intortum (intortum), Stylosanthes guyanensis (Stylo) and Centrosema pubescens (centro).

RESULTS AND DISCUSSION

By superimposing the influence of the grazing animal and a decline in soil fertility over the natural seasonal fluctuations in productivity and competitive characteristics of certain species, one can detect rapid successional trends within a sward. Figures 43 through 47 illustrate the variation in relative contribution of the forage species to the total seasonal dry matter production. In the case of the weed species studied, Figures 48 through 51 represent the fluctuations in dominance of the more important components.

Forage Species

Panicum maximum (var. trichoglume) - green panic. At each sampling period this species provided the highest proportion of the total dry matter of any of the improved forage species. Before the controlled grazing commenced in 1969, green panic was yielding over 8000 kg of dry material per hectare per grazing period. At the time of the March 1970 sampling, after the cattle were removed, the available dry matter provided by green panic was down to 700 kg/ha, which was about 30% of the total forage yield at this time.

As can be seen from Figure 43, in all but transect T3, there was a general decline in yield of green panic after sampling III. This was mainly due to the cessation of the annual fertilizer application after June 1970 and the corresponding increased grazing pressure. The influence of this increased grazing pressure is best seen at sampling VII. Because of the inadequate water supply for the cattle in adjacent areas, the sampling areas were grazed continuously from July 1971 through the dry summer until late November. As also will be seen

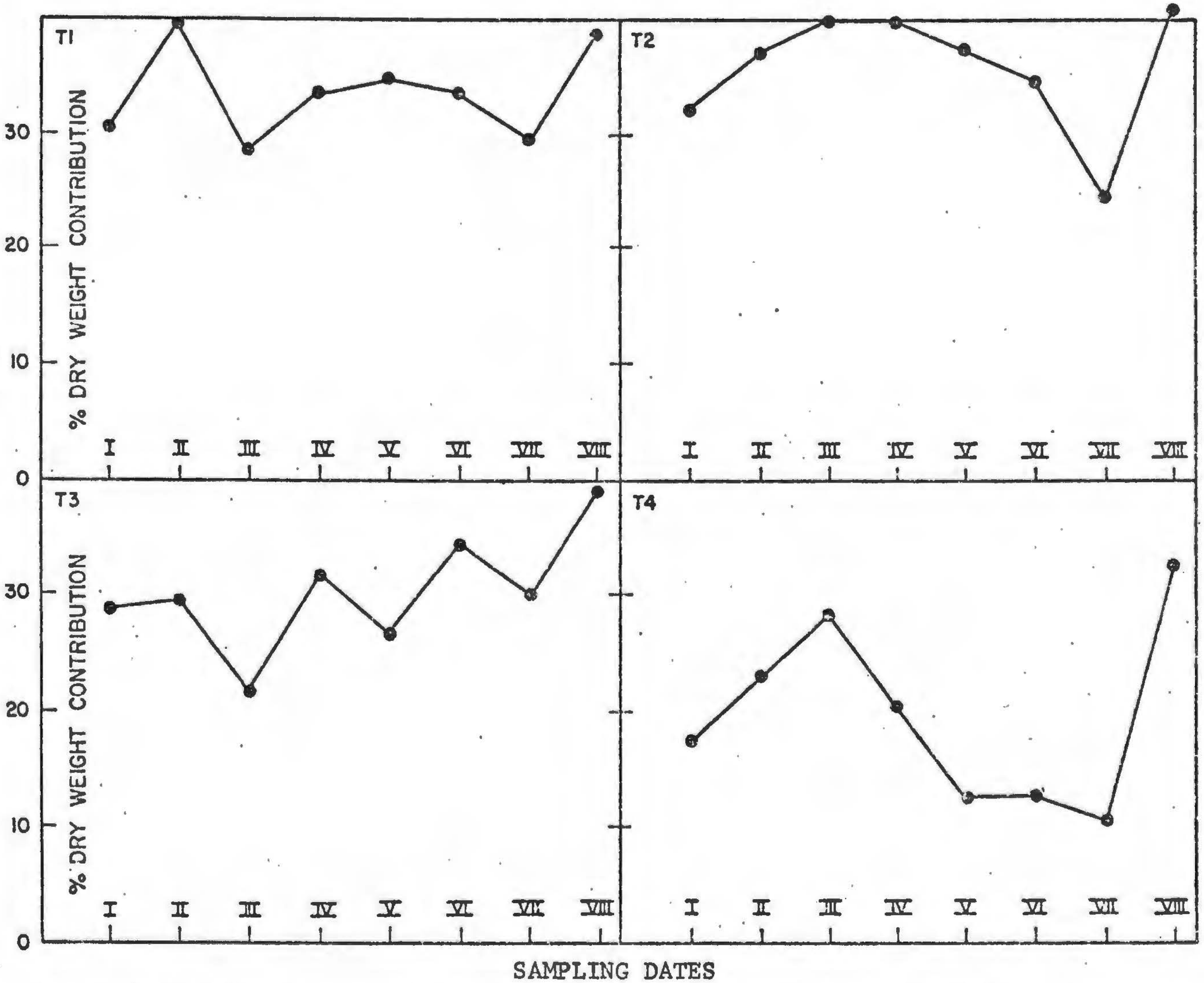

FIGURE 43. THE VARIATION IN PERCENT DRY WEIGHT CONTRIBUTION OF Panicum maximum (var. trichoglume) BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

later with the other improved forage species, the contribution of green panic to the total yield dropped conspicuously and that of the weeds increased rapidly.

There was evidence of nutrient deficiencies in some of the improved species. Intortum exhibited the same potassium deficiency symptom which was visible before the 1970 application of fertilizer. In the areas of more acute deficiency symptoms, green panic showed nitrogen deficiency due to the decreased efficiency of nitrogen fixation and transfer by the associated legumes. However, even though the soil fertility level was not maintained, a six month rest period brought the contribution of green panic back to and above the 30% level at sampling VIII, at the expense of the weeds.

Over the whole experimental period, green panic in combination with mainly intortum yielded up to 12,000 kg/ha/year of dry material, with a mean of around 7,000 kg/ha/year.

<u>Desmodium intortum</u> (intortum). Before grazing commenced in 1969, intortum was providing over 1000 kg/ha of dry material per grazing period. At sampling I, after grazing, 5-600 kg/ha of dry material remained; this was about 15-20% of the total dry matter remaining (Figure 44). After the normal six to eight week regrowth period, dry matter yields of intortum depended on the severity of the previous grazing. At sampling II it produced around 900 kg/ha, dropped to 200 kg/ha after grazing, then dropped to a low of 75 kg/ha following the next severe grazing at sampling V. An even lower yield of 50 kg/ha was reached after the long summer to fall grazing of 1971. However, once again even though the soil fertility level was decreasing, the long rest period through the winter of 1971-72 allowed intortum to

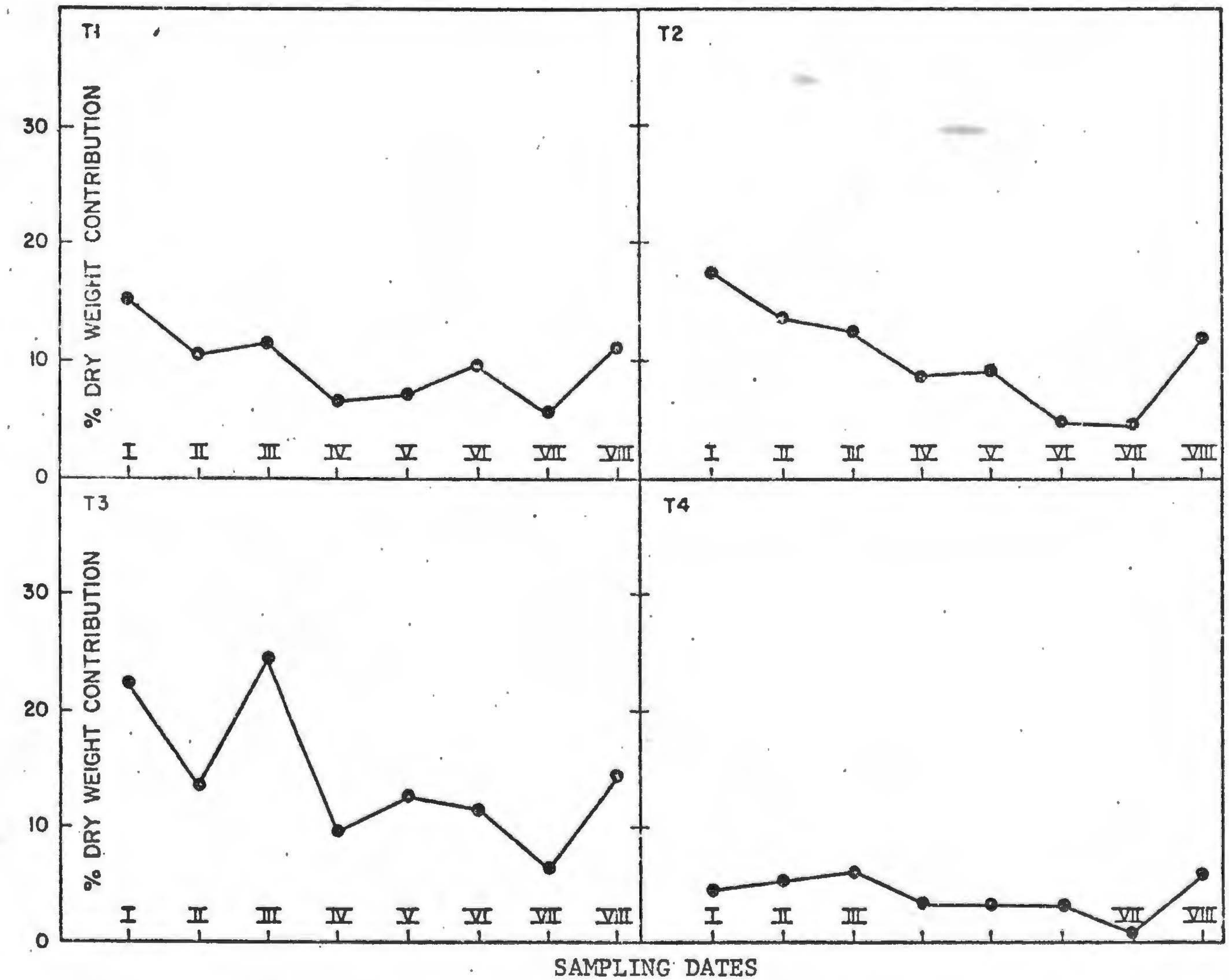

FIGURE 44. THE VARIATION IN PERCENT DRY WEIGHT CONTRIBUTION OF <u>Desmodium intortum</u> BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

FIGURE 52 (a) SWARD CONDITION AFTER HEAVY GRAZING SHOWING ABSENCE OF IMPROVED FORAGE SPECIES.

FIGURE 52 (b) SWARD CONDITION AFTER REST PERIOD SHOWING VIGOROUS REGROWTH OF IMPROVED FORAGE SPECIES.

increase in yield to 1200 kg/ha, 10-15% of the total dry matter produced by the sward. This recovery after severe grazing is illustrated by the photographs in Figure 52. Plate (a) shows the sward condition after heavy grazing, with nearly all the improved forage species removed and only the weed, Commelina diffusa, remaining. Plate (b) shows the sward after the long rest period, with green panic and intortum in a good combination. Weeds are not visible.

As was mentioned earlier, in 1970 intortum began to exhibit typical potassium deficiency symptoms. This resulted from the absence of potassium in the annual fertilizer mix since planting in 1967. The addition of 224 kg/ha of 7-30-20 alleviated this problem, but it became evident again during the wet 1971-72 winter period.

In combination with green panic, intortum produced up to 3000 kg/ha/year of dry material. The annual productivity of the green panic/intortum sward was in the order of 15,000 kg/ha under these conditions.

Stylosanthes guyanensis (stylo). As was seen in Chapter 4, stylo was generally confined to the poorer, shallower soils of the upper slopes and ridge tops. It was found in association with brush and grass weeds. During the earlier grazing periods when plenty of forage was available, the cattle made little use of stylo. However during the periods of forced, heavier grazing in 1971, stylo was utilized more fully by the cattle. This can be illustrated by the fact that the dry matter availability of stylo never fluctuated outside the limits of 2000-3000 kg/ha, except after the prolonged summer grazing of 1971 when the dry matter level was reduced to below 1000 kg/ha.

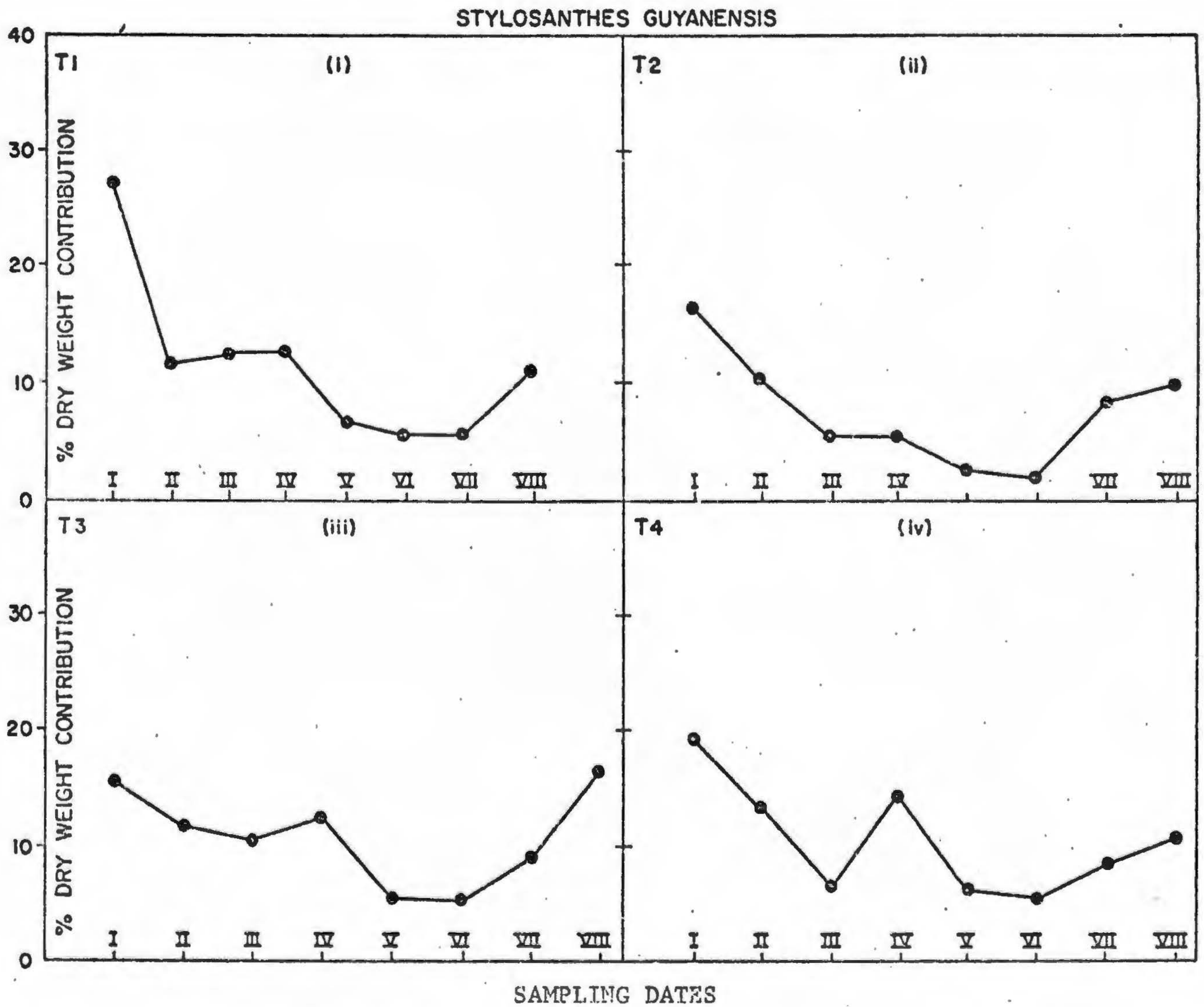

FIGURE 45. THE VARIATION IN PERCENT DRY WEIGHT CONTRIBUTION OF <u>Stylosanthes guyanensis</u> BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

This may have been due to a combination of: increased grazing pressure, adequate time for the animal to become acquainted with the species, and the increased palatability with 'haying-off' after the spring seeding period.

At the first sampling period, the contribution of stylo to the total dry matter yield was 15-20%. This level was high considering its limited distribution throughout the valley, especially along the sampling transects. This high contribution by stylo can be explained simply by the fact that the animals did not graze it as readily as they did the other improved species. The greater utilization of stylo up to sampling VI is illustrated in Figure 45. The general increase in the contribution by stylo at sampling VIII indicates that even though all species were heavily grazed during the summer period, stylo was grazed less severely and responded well to the rest.

Digitaria decumbens (pangola grass). Even though pangola grass only occurred along transects T1 and T4, at the top of the south-facing slope, there was an interesting trend shown by its gradual movement down the slope. The isolated areas of pangola were not grazed readily by the cattle. Later in this discussion it will be seen that the plant analysis data for mature stands of pangola grass showed relatively low levels of phosphorus and crude protein. These factors alone may have lead to the lower acceptability of such material. Because of the low utilization of pangola by the cattle, the fluctuation of dry matter production from samplings before and after grazing was small, remaining within the limits of 5-6000 kg/ha of available dry material. The increase in contribution to the total yield provided by pangola grass at sampling VII is explained by the fact that all other

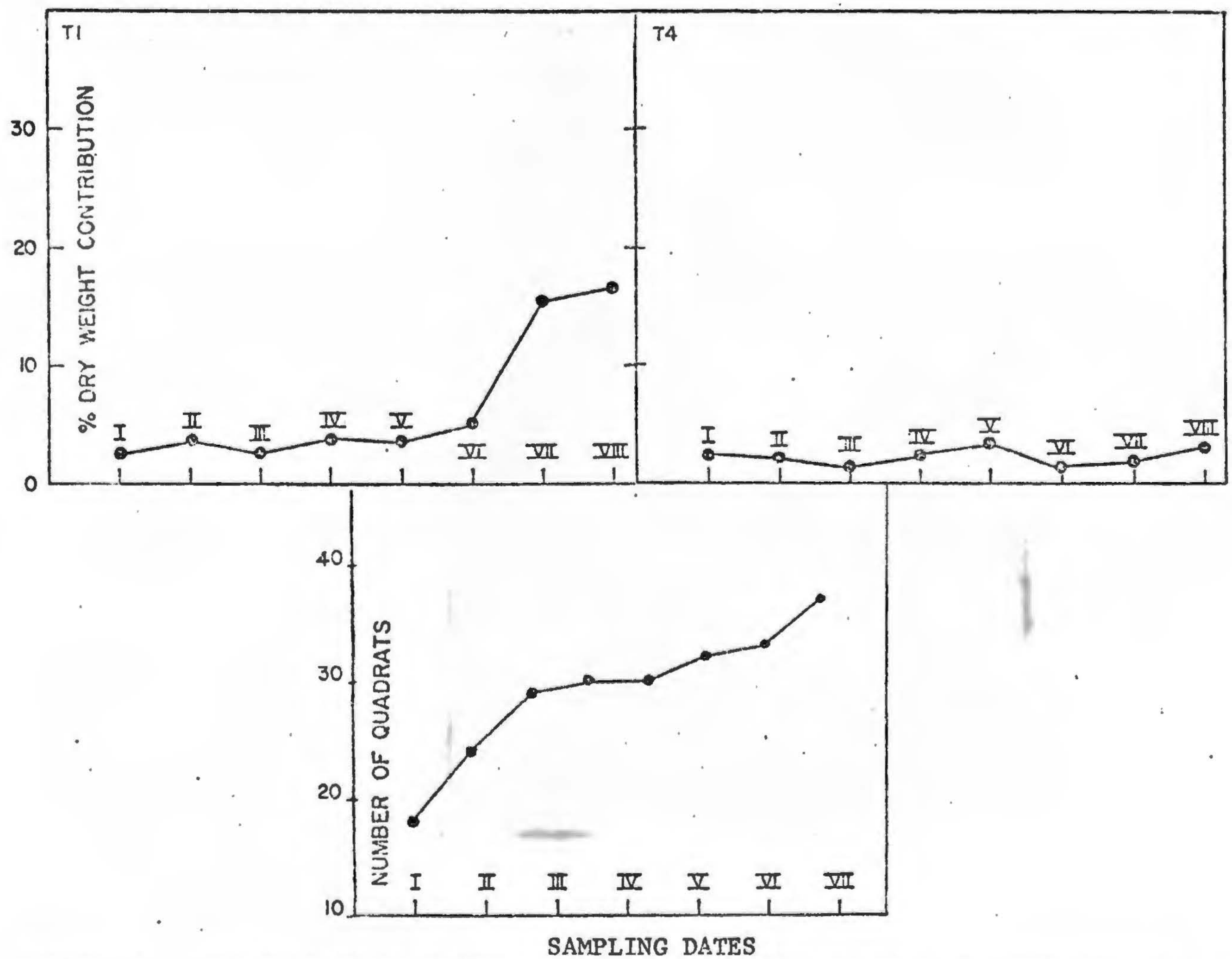

FIGURE 46. THE VARIATION IN PERCENT DRY WEIGHT CONTRIBUTION AND DOMINANCE OF Digitaria decumbens BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

FIGURE 53. THE DOWNWARD MOVEMENT OF Digitaria decumbens (UPPER LEFT) INTO THE Panicum maximum SWARD (LOWER RIGHT).

improved species were utilized more fully during the severe summer grazing period. Following the long winter rest period, pangola was able to encroach into damaged brush thickets and into heavily grazed green panic areas (Figure 53).

Paspalum conjugatum/Setaria geniculata association. Even though these grasses are generally considered to be weeds, they can still be important forage for the grazing animal, especially under range conditions.

As can be seen from Figure 47 there was a general increase in contribution by this association up until sampling VII. With increased grazing pressure and with decreasing soil fertility, this association contributed more to the total yield of the sward (10-15% and up to 30%). However, after the 1971-72 winter rest period the improved species, especially green panic and intortum, responded better to the more favorable growth conditions. Figure 47 shows the rapid decline in contribution by this weedy grass association at sampling VIII, explained simply by the fact that the rest period allowed the improved forage species to regain vigor and forced the less vigorous weed species out of the sward.

Weed Species

Under a regime of good soil fertility and grazing management, improved forage species remain vigorous and competitive. However, if over-grazing and a natural decline in soil fertility is allowed, weed species of lower fertility requirements and of less acceptability to the grazing animal are favored in the ecological shift of dominant species. Unless control measures are taken, the dominant components of a community will change rapidly. The recognition of this replacement of one type of plant cover by another is a necessary requirement in

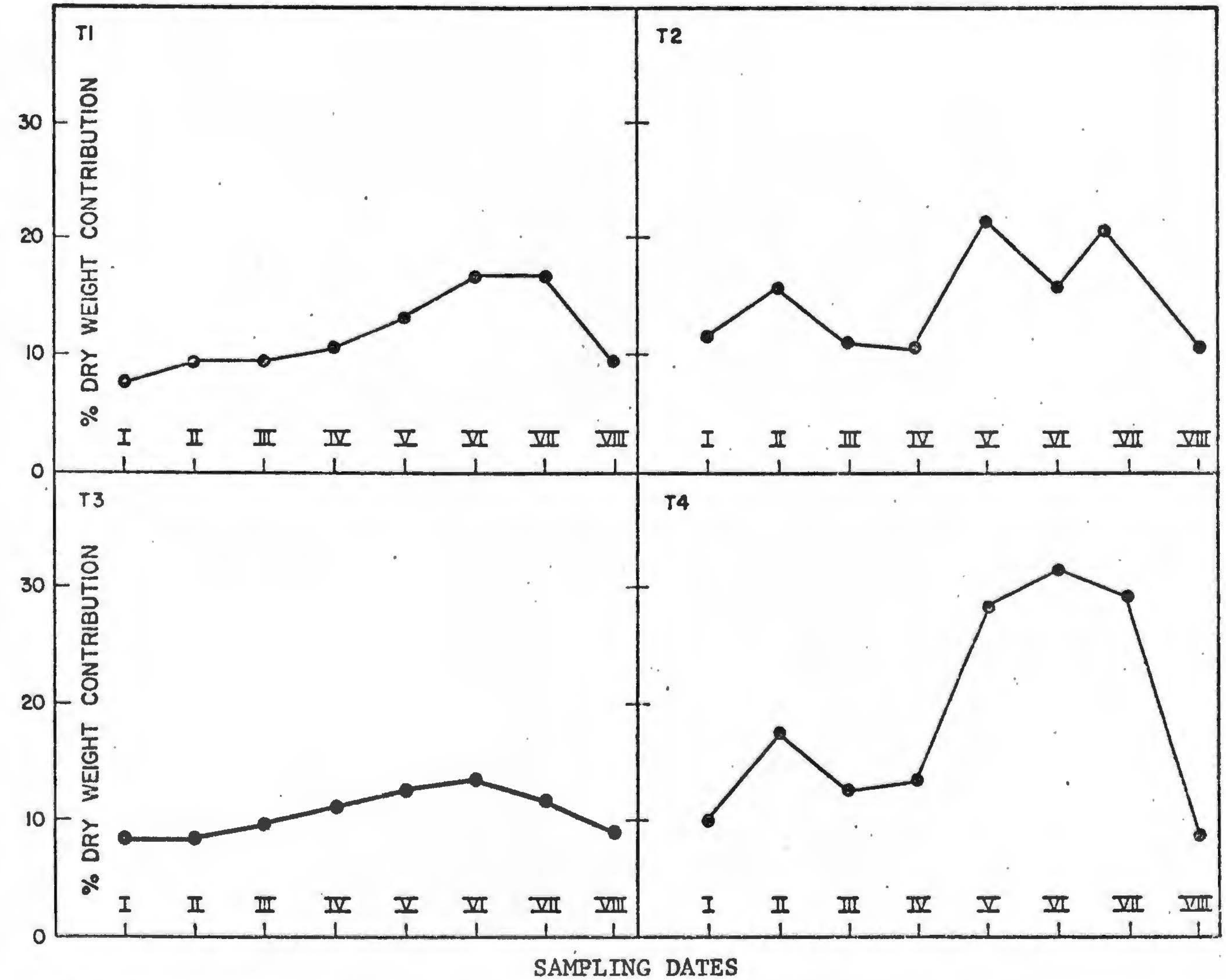

FIGURE 47. THE VARIATION IN PERCENT DRY WEIGHT CONTRIBUTION OF THE Paspalum/Setaria ASSOCIATION BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

good range and pasture management.

Since the actual dry matter production of these weed species is not as important as the area covered by such sward components, the evaluation of their spread is measured here by the total number of quadrats studied in which these species are recorded. Figures 48 through 51 illustrate the population trend from one sampling period to the next of the following weed species: Lantana camara L. (lantana), Psidium gujava L. (guava), Melastoma malabathricum L. (Banks melastoma), Elephantopus mollis L. (Hawaiian elephantsfoot), Mimosa pudica L. (sensitive plant), Passiflora foetida L. (redfruit passionflower), Ageratum conyzoides L. (tropic ageratum), Nephrolepis exultata (L.) Schott (Boston fern), Commelina diffusa Burm. f. (spreading dayflower), Erechtites hieracifolia (L.) Raf. (American burnweed), Stachytarpheta urticaefolia Dalz. and Gibs. (nettleleaf vervain), Cuphea carthagenensis (Jacq.) Macbr. (tarweed cuphea), Stenoloma chinensis L. (lace fern), and Pteridium aquilinum (L.) Kuhn (bracken fern).

Lantana camara. Lantana is one of the more important brush species in these humid wetlands. The graph in Figure 48 shows the gradual increase in spread of lantana thickets and the number of lantana seedlings under the grazing regime. There was a rapid spread of lantana following the severe summer grazing of 1971-72 which reduced competition and provided more bare ground for subsequent invasion and spread by lantana and other undesirable weeds. However with the increased vigor of the improved species as a result of the wet season rest, there was an obvious drop in the distribution of lantana. Also cattle were forced to push down and trample lantana thickets in order to browse the climbing legumes such as Centrosema pubescens, Phaseolus atropurpureus and Glycine wightii (Figure 54). During the rest period, the more vigorous improved species, especially intortum and pangola grass, rapidly spread over these cleared areas and subsequently smothered many brush thickets and seedlings (Figure 55).

Psidium gujava. As can be seen in Figure 48, there was considerable variation in presence of guava seedlings and the extent of guava thickets. Of the invading brush species, guava is the most vigorous and hardest to control. It must be realized that the invasion of guava is a result of over-grazing or excessive grazing pressure in the wet periods. The cattle are readily attracted to the fruit of this species and dung pats are impregnated with dozens of scarified, easily-terminated seeds. With such a system of dispersal any bare areas, especially camp sites, are susceptible to invasion of many small guava seedlings. However if the pasture is rested sufficiently and fertility is maintained, the natural vigor of the improved species can suppress such potential invaders, as can be seen by the periodic fluctuations in the graph in Figure 48. There was an increase in guava after grazing, since reduced competition from the forage species allowed emergence of guava seedlings. The decrease in guava population recorded at the before-grazing samplings, was due to the competitive advantage the improved forage species had over the weed seedlings at this stage.

Melastoma malabathricum (Banks melastoma). The fluctuation shown in the graph for this species in Figure 48 can be explained by competition among improved and weed species. The initial high point at sampling I was a result of weedy conditions encouraged by the lack of subdivisional fencing and uncontrolled grazing. As a result of rotational grazing there was a drop in the population at sampling II.

The low point at sampling V, which took place after the severe wet season grazing, can best be explained by the fact that the strong influx of Paspalum conjugatum on the upper slopes and shallow soils of the rides and spur tops reduced the competitive ability of the melastoma seedlings.

Elephantopus mollis (Hawaiian elephantsfoot). It is evident from Figure 48 that the population of elephantsfoot increased up to sampling VII. From one sampling to the next this species was a good indication of the sward condition. However, as was seen earlier, this species generally only appeared on the upper slopes and other areas of poorer soil on the north-facing slope. The ability to produce and disperse large volumes of viable seed makes its invasion a reflection on incidence of bare ground and reduced competition from other species. Being a winter seeding species, heavy grazing during the wet season will lead to rapid invasion by its seedlings. This seedling release is exhibited by the high point at sampling VI and VII following the previous heavy winter grazing. The response of this species to sward conditions is clear if one considers the data collected at sampling VIII. At this stage there was a rapid drop in the population following the wet season rest period during which the more competitive, improved forage species were able to subdue the invasion of this weed.

Commelina diffusa (spreading dayflower). As was seen earlier, this weed was only found in the wetter, lower slopes in association with green panic and intortum. Up until sampling II the grazing pressure was lenient, but the wet season grazing in late 1970 caused a rapid increase in this weed (Figure 49). The rest period following the 1971 wet season grazing was sufficient to strengthen green panic

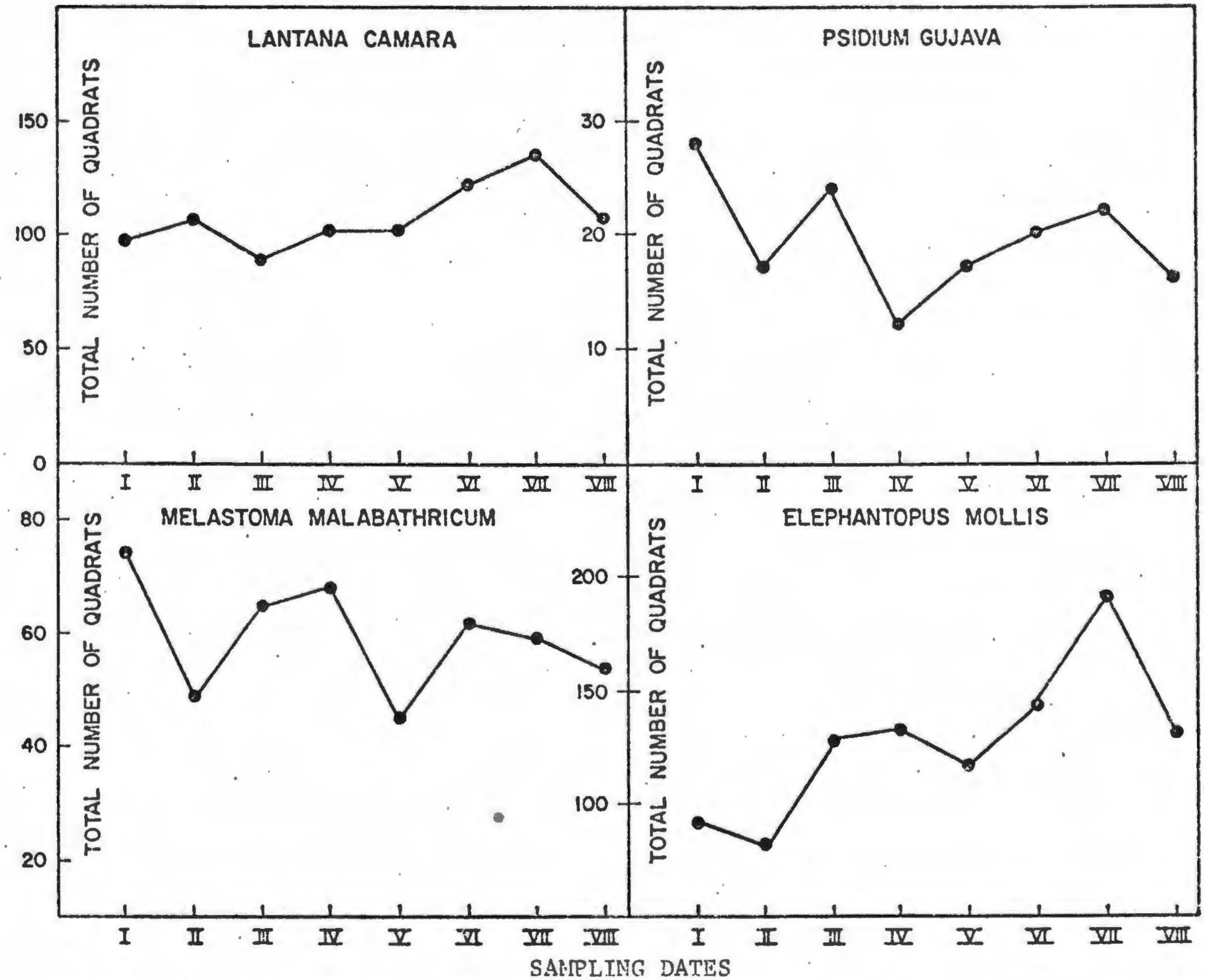

FIGURE 48. THE VARIATION IN FREQUENCY OF OCCURRENCE OF Lantana camara, Melastoma malabathricum, Elephantopus mollis and Psidium gujava BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

and intortum at the expense of spreading dayflower, thus the drop in the graph at sampling VI. The prolonged grazing of the 1971 summer - fall period, along with the favorable conditions of the oncoming wet season, led to the marked increase in spread of the weed at sampling VII, only to see the influence of another rest period at sampling VIII.

Erechtites hieracifolia (American burnweed). This winter annual is noted for its ability to spread even under medium grazing pressures. Where soil moisture conditions are favorable and some bare ground is available this species will thrive through the winter months and up to the latter parts of July. From the graph in Figure 49 there was an apparent increase of the species after the winter grazing of 1970, followed by a sharp decrease during the summer period. There was a gradual increase in burnweed during the winter of 1971 through to sampling VII. Even though there was a severe grazing pressure in winter of 1971 the weed was suppressed by trampling and grazing pressures during this period. This very succulent weak annual is no great threat to the productivity of a pasture but can be used as a useful indicator of pasture condition during the wetter months. It was observed in the establishment of this pasture that fireweed acted as a physical lattice for the climbing legumes which were then able to compete for light with the taller grasses. Once the annual nature of this weed caused its eventual removal from the sward, the legume species were in a more favorable competitive position than would otherwise have been possible.

Stachytarpheta urticaefolia. It is evident from Figure 49 that the nettleleaf vervain population remained fairly constant throughout the three year observation period. This species was found on the less fertile ridge tops and spurs in association with other woody weed species, stylo and the grass weed association. The only evident drop in dominance of the species in these locations was after the prolonged wet season rest period of 1971 - 72 when stylo was able to compete more effectively with the nettleleaf vervain seedlings.

Cuphea carthagenensis (tarweed cuphea). It is evident from the graph in Figure 49 that cuphea is also another species which gives a good indication of the condition and vigor of the pasture sward. The early drop in its population strength at sampling II was a direct result of the increased competitive vigor of the improved forage species after a rest period following the light 1969 grazing. From this sampling period through to late 1971, sampling VII, there was a steady increase in cuphea. The value of the wet season rest period before sampling VIII is evident in the rapid drop in the number of quadrats in which this weed was recorded. Even though cuphea does not provide great competition to improved species its presence in a sward is a good indication of the condition and management of the pasture.

Mimosa pudica (Sensitive plant). Even though its distribution throughout the pasture was not extensive, sensitive plant gradually disappeared from the areas where it was initially found (Figure 50). Being a legume itself, high in protein, the cattle did select it as a part of their diet. Due to the competitive advantage of its habit, the only explanation for its removal was grazing pressure. Even though the dark green, patchy appearance of sensitive plant throughout a pasture removes some aesthetic value, its classification as a weed is questionable.

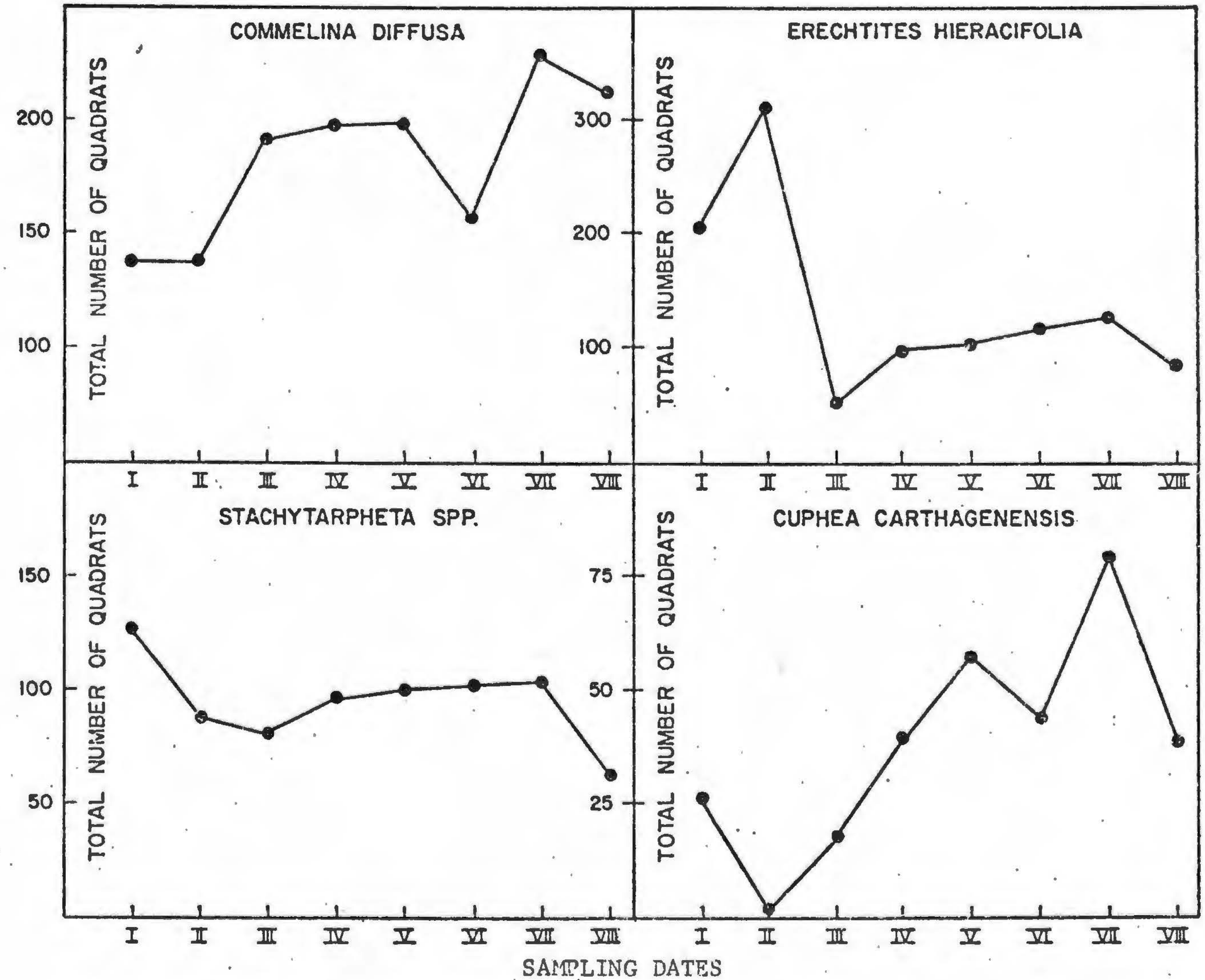

FIGURE 49. THE VARIATION IN FREQUENCY OF OCCURRENCE OF Commelina diffusa, Erechtites hieracifolia, Stachytarpheta urticafolia and Cuphea carthagenensis BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

Ageratum conyzoides (tropic ageratum). It is evident from Figure 50 that tropic ageratum is a good indicator of sward condition. After the initial low numbers of this species there was a conspicuous increase in its spread following the first intensive grazing period. However with the occurrence of the very severe grazing pressure during 1971 much of the ageratum was removed. However the bare ground and more favorable conditions brought about by this prolonged summer - fall grazing resulted in a rapid increase in ageratum. As with the other weed species, the long rest period through the wet winter of 1971 - 72 resulted in a conspicuous drop in the ageratum stand as the more vigorous, improved species took over once again.

Nephrolepis exultata (Boston fern). As can be seen from the graph in Figure 50, this species did not show any significant movement in or out of the pasture sward. It was evident however that where it occurred with pangola grass and stylo that competition favored the improved species. Its low vigor makes this species a less serious threat to the pastures productivity and it can be controlled by encouraging the growth of improved forage species.

Stenoloma chinensis (lace fern) and Pteridium aquilinum (bracken fern) exhibited similar trends in their populations (Figure 51). It is evident that initially these less vigorous unpalatable ferns were one of the important weed components of the sward, but as grazing pressure was increased, mechanical or competitive removal of both species occurred. At sampling VIII the previous influence of trampling and increased vigor of the improved species over the long rest period resulted in a further reduction in these ferns.

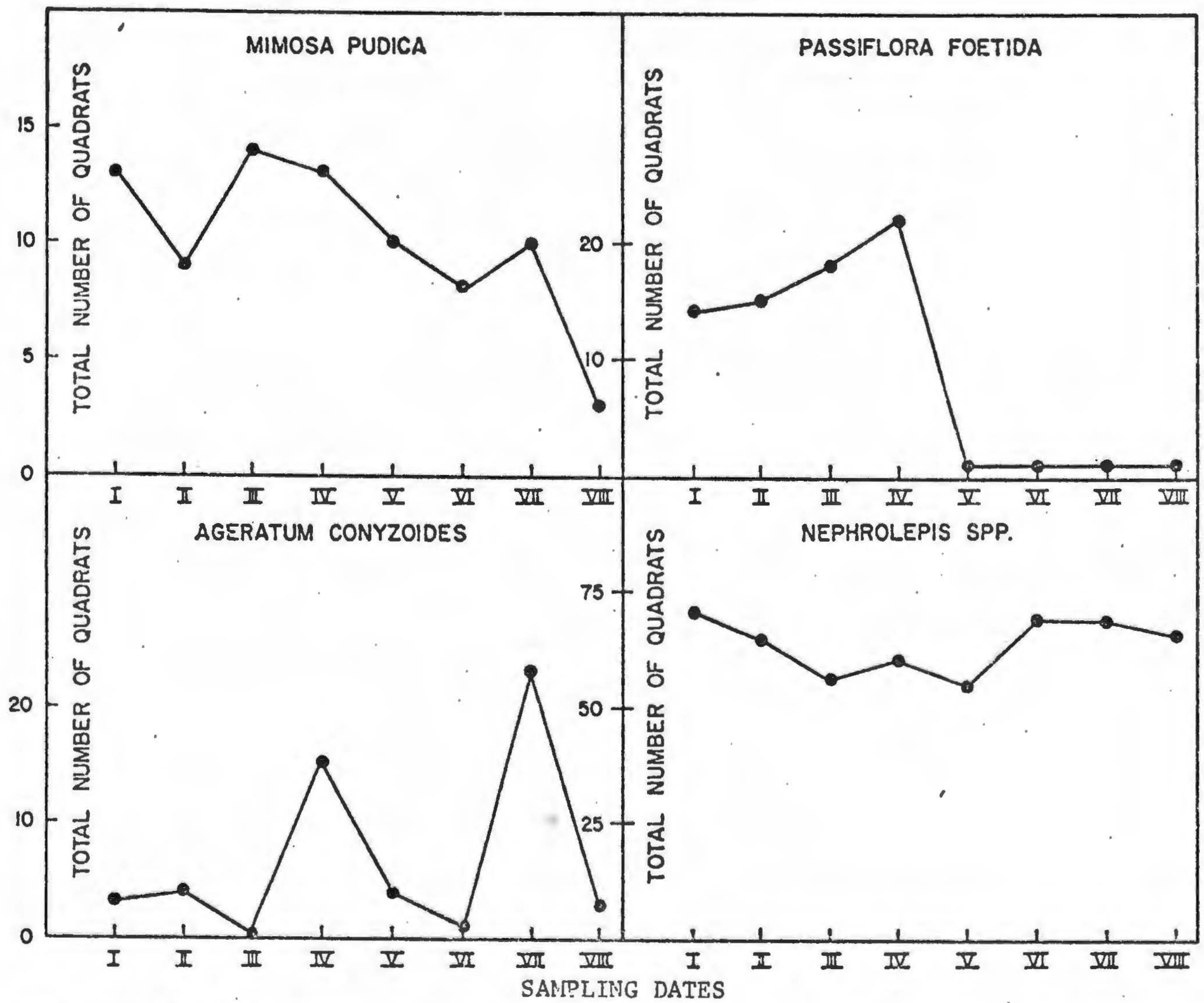

FIGURE 50. THE VARIATION IN FREQUENCY OF OCCURRENCE OF *Mimosa pudica*, *Passiflora foetida*, *Ageratum conyzoides* and *Nephrolepis exultata* BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

Passiflora foetida. From Figure 50 there is an evident initial increase in this weed up to sampling IV but, with increased grazing pressure this vine was damaged and drastically reduced as a constituent of the pasture.

As an addendum to this phase of the research program, data were collected on the seasonal variations in liveweight production by the cattle grazing the experimental area.

It is evident from Figure 56 that there was no precise pattern of liveweight gains, even though there were general peaks at the beginning and at the end of the dry season and low points during the wet season and in the stress periods of the dry season. From results of plant analyses, presented graphically in Appendix IV, there was no evident wet season deficiency of crude protein or minerals in the available forage material. With this in mind, the only explanations for the drop in wet season liveweight gains were the high moisture content of the forage and the psychological effect of the cool, wet, overcast conditions. This may help to explain why animals standing in knee-deep forage are actually losing weight. The effective grazing time and intake of digestible nutrients by the animal are obviously reduced under such adverse conditions.

In order to clarify the actual effect of the environment on the productivity of both animal and forage species, there is a need to continue such seasonal liveweight gain studies. The average daily liveweight gain of 0.4 kg/head would have increased to over 0.5 kg/head if higher quality animals had been used and if the fertilizer program had been maintained. The average annual liveweight production per hectare of 125 kg make these results comparable to those in areas of

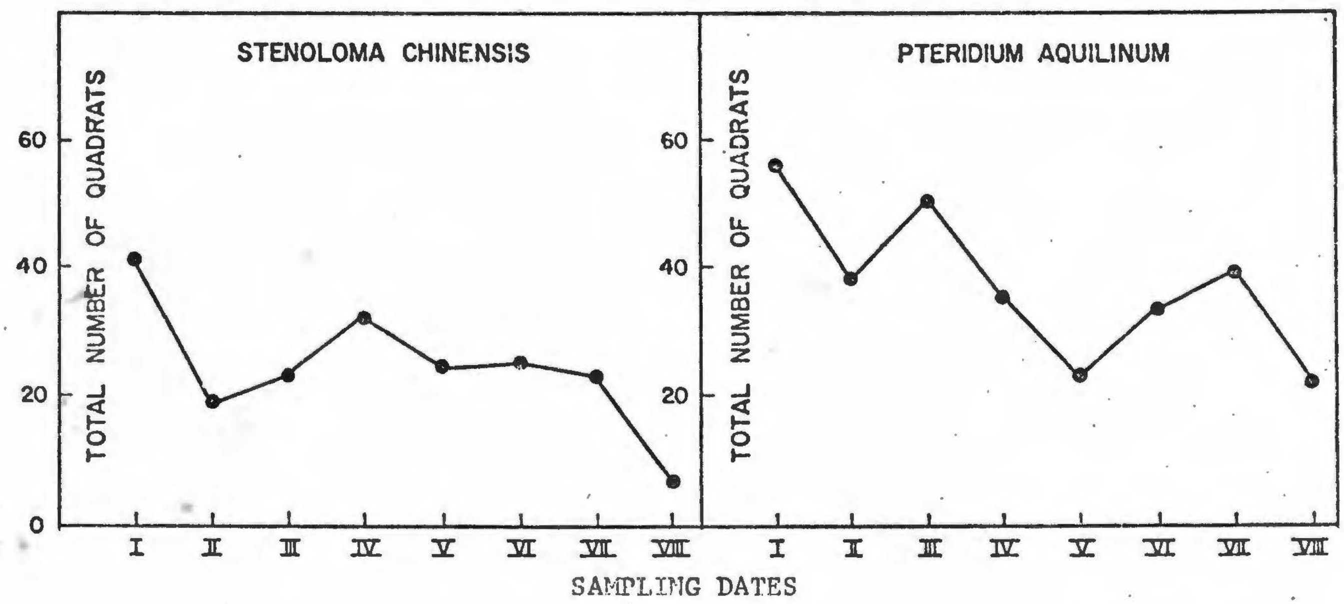

FIGURE 51. THE VARIATION IN FREQUENCY OF OCCURRENCE OF Stenoloma chinensis AND Pteridium aquilinum BEFORE AND AFTER EACH GRAZING PERIOD. SAMPLING I IS BEFORE GRAZING.

FIGURE 54. (a) *Glycine wightii* COVERING DENSE *Lantana camara* THICKET.

FIGURE 54. (b) AFTER AN EXTENDED GRAZING PERIOD THE *Lantana camara* THICKET OPENED UP BY THE GRAZING ANIMAL.

FIGURE 55. Lantana camara THICKETS BEING COVERED BY Desmodium intortum, Glycine wightii and Centrosema pubescens.

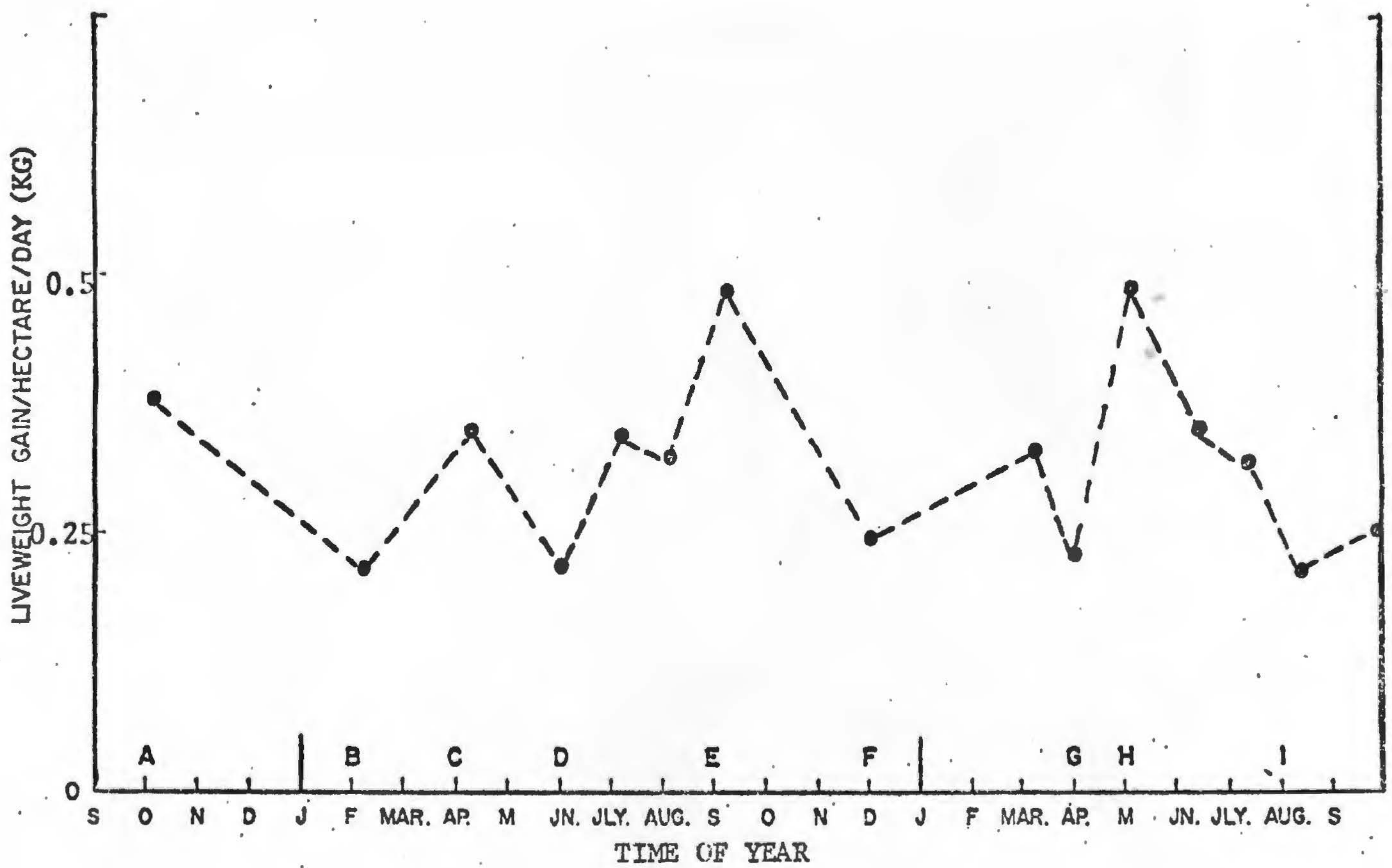

FIGURE 56. THE SEASONAL VARIATION IN LIVEWEIGHT GAIN PER HECTARE PER DAY.

more productive and manageable terrain (Nuthall and Whiteman, 1972).

SUMMARY AND CONCLUSION

There is an obvious need in range and pasture research and management to evaluate improved forage species in terms of productivity and to recognize certain components as reliable indications of sward condition.

In this particular study, evaluations were made as to the influence the grazing animal and a natural decline in soil fertility had on seasonal productivity of improved forage species and dominance of weed components.

The most productive forage species studied was Panicum maximum (var. trichoglume) which produced up to 12,000 kgm/ha/year of dry material. Under conditions of good soil fertility and grazing management it contributed up to 30% of the total yield of the sward. With a natural decline in soil fertility and overgrazing, an invasion of weed species reduced its overall contribution to as low as 10%, only to recover to its original dominance after an extended rest period during the winter months.

A similar trend of productivity was shown by Desmodium intortum. Its available dry material fluctuated from 1000 kgm/ha to a low of 50 kgm/ha after a heavy grazing period. Once again after sufficient rest, this forage legume recovered and its annual production of dry matter approached 3000 kgm/ha or 15-20% of the total yield of the sward.

In the case of Stylosanthes guyanensis, the grazing animals did not readily utilize the forage material in the early periods. It was only during the heavy grazing periods that stylo was utilized. However, this is a useful property of this legume since being adapted to the poor, infertile ridge tops its unhindered spread improves soil fertility and thus productivity of these soils.

Digitaria decumbens (pangola grass), not included in the original seeding plan, spread quickly from cuttings, especially over areas where associated species were weakened by heavy grazing pressures.

The most reliable indicator of sward condition was the weedy grass association of Paspalum conjugatum and Setaria geniculata. After each heavy grazing period the contribution of this association increased, only to decrease after the rest period. With increased grazing pressure and with decreasing soil fertility, this association contributed up to 30% of the total forage yield of the sward, decreasing to less than 10% once the improved species recovered.

Under the environmental conditions of these humid wet-lands other weed species such as Lantana camara, Psidium gujava, Elephantopus mollis, Commelina diffusa, Erechtites hieracifolia, Cuphea carthagenensis and Ageratum conyzoides were also excellent indicators of environmental conditions favoring the decline in productivity of the improved forage species.

Even though there was no clear pattern of liveweight gains by the grazing animals, there was an evident drop in production during the wet season and during the stress periods of summer. High moisture content of forage as well as the psychological effect of the cool, wet, overcast conditions of winter contributed to the drop in liveweight during these months. The summer stresses, including high temperatures and low soil moisture, reduced the availability of nutritious green feed.

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APPENDIX I

METHODS OF ANALYSIS FOR PLANTS AND SOILS

Plants

I. Ashing for P, K, Ca, Mg, Mn, Fe, Cu, Zn - in plants

Reagents

1. Alcoholic-sulfuric acid - 50 mls of concentrated sulfuric acid (reagent grade) mixed with 950 mls of 95% ethyl alcohol.
2. 4N HCl - 1 part concentrated hydrochloric acid (reagent grade) added to 2 parts of distilled water.
3. Filter paper No. 589
4. Porcelain crucibles - Coors No. 0 or No. 1

Procedure

1. Weigh 0.5 gm dry, ground sample into porcelain crucible.
2. Cover sample with alcoholic-sulfuric acid mixture.
3. Ignite sample with bunsen burner in a hood. (Do not use match or splinter directly over samples to avoid contamination.)
4. Put samples in the muffle furnace and ash overnight at 500 - 550^{o} C.
5. After ashing, allow samples to cool then add a few drops of distilled water. Add 10 mls of 4N HCl and warm for 20-30 minutes on a hot plate to dissolve the ash.
6. Filter into 100 ml volumetric flasks and make to volume. This plant extract can be stored and used for analysis of P, K, Ca, Mg, Fe, Zn, Fu, Mn, etc. on the atomic absorption spectroscope.

II. Total N in plants

Reagents

1. Sulfuric-salicylic acid solution. Dissolve 67 gm of salicylic acid in 2 liters of concentrated sulfuric acid.

2. 50% or 1:1 NaOH. Dissolve 25 lb of sodium hydroxide flakes in 11.4 liters of water. Allow solution to cool to room temperature before use.
3. Sodium sulfate crystals.
4. Sodium thiosulfate crystals.
5. Mossy zinc, large pieces.
6. Copper sulfate crystals.
7. Glass beads, 5 mm in diameter.
8. 4% boric acid. Dissolve 40 gm of boric acid in 1 liter of distilled water.
9. Standard H_2SO_4 - 0.0714 N sulfuric acid, standardized with sodium carbonate.
10. Mixed indicator. Dissolve 0.20 gm methyl red in 50 mls of 95% ethyl alcohol (grind in a fine mortar if necessary). Dissolve 0.1 gm of methylene blue in 50 mls of 95% ethyl alcohol. Mix both solutions for use.

Procedure

1. Weigh 0.5 gm of dried, ground plant sample into 800 ml Kjeldahl flask.
2. Add 10 gms of sodium sulfate crystals (about 1 teaspoon) into the samples.
3. Add 1.0 gm of copper sulfate crystals.
4. Add 2-3 glass beads and 35 mls of concentrated sulfuric acid-salicylic acid mixture. Whirl the flask to mix the acid and samples. Let stand for 15-30 minutes.
5. Add 5-10 gms of sodium thiosulfate crystals (about 1 teaspoon) and immediately put flask into digestion manifold. Turn on

heat until samples begin to froth. Turn heat off and rotate flasks to prevent excessive frothing. Cool for about 15 minutes, then turn heat on and digest for 1 hour. Digested plant material should be a clear, greenish blue.

6. After digestion turn off heat, cool flasks and add about 250 mls water.
7. After the digest solution has cooled to room temperature proceed with the distillation.
8. Into 500 ml Erlenmeyer flasks, put 50 mls of 4% boric acid. Add 4-5 drops of mixed indicator and set in the receiving end of the condensers with the condenser tube touching the boric acid solution.
9. Into the digest material add 70-80 mls of 50% sodium hydroxide solution, 2-3 pieces of mossy zinc and quickly connect the flask to the condenser.
10. Shake flask and contents and start distillation with a low heat or flame. After about one-half of the solution has been distilled, increase the heat or flame as long as there is no more danger of the samples boiling over into the condenser trap and tube.
11. Distill about 250 mls of solution before lowering the flasks. Allow the distillation to proceed a few more minutes to drain the tubes before turning off the heat.
12. Titrate the distillate with standard sulfuric acid to a light pink or purple end-point.

Soils

I. Total N in soils

Same procedure as for total N in plants but 5-10 gms of air dried soil are used.

In step 5 excess frothing may occur. Rotation of flasks and low heat at the start are therefore necessary until danger of overflowing is over. Also cutting down on the amount of soil and zinc used will help. The use of paraffin wax will also reduce frothing during distillation.

II. Cation exchange capacity of soils

Reagents

1. 1N ammonium acetate. Add 57 mls of glacial acetic acid into about 800 mls of distilled water. Slowly add 67 mls of concentrated ammonium hydroxide, stir and adjust the pH to 7.0 then dilute to a final volume of 1 liter. For large numbers of determinations, 18-20 liters of the solution may be prepared at a time.
2. Methyl alcohol.
3. 4% KCl. Dissolve 4 gms potassium chloride in 100 mls of distilled water.

Procedure

1. Weigh out 25 gms of air-dried (20 mesh) soil and place in a 500 ml Erlenmeyer flask. Add 200 mls of 1N ammonium acetate solution and shake well. Stopper flasks tightly and shake in an automatic shaker for 1 hour (or let stand for 24 hours with occasional shaking). Filter through a Buchner funnel using a Whatman No. 5 filter paper. Wash with another 200 mls of

ammonium acetate solution using about 50 ml portions at a time.

2. Save filtrate plus washings for determination of exchangeable K, Ca, Mg, Mn, etc. on the atomic absorption spectroscope (see procedure later).

3. Wash soil residue with 50 ml portions of methyl alcohol about four times. Discard the washings.

4. Transfer washed soil plus filter paper into the original flask (rinse flask with distilled water before transferring samples). Add 200 mls of 4% potassium chloride and shake for about 30 minutes. Filter on a Buchner funnel using Whatman No. 5 filter paper and wash three times with 50 ml portions of 4% potassium chloride.

5. Transfer filtrate into 800 ml Kjeldahl flasks and distill the ammonia as in the distillation process for total nitrogen (steps 8-12 for total N). Use 10 mls 50% NaOH only.

III. Extractable P in soils

Reagents

1. Extracting solution 0.02 N H_2SO_4 containing 3 gms ammonium sulfate, $(NH_2)_2\ SO_4$, per liter.

2. Ammonium aolybdate-sulfuric acid solution. Dissolve 25 gms ammonium milybdate in 200 mls of distilled water. Dilute 275 mls concentrated sulfuric acid to 750 mls. Allow to cool, add ammonium molybdate solution slowly and with stirring to the sulfuric acid solution. After combined solution has cooled, dilute with distilled water to one liter.

3. Stannous chloride solution. Dissolve 2.5 gms of stannous chloride, $SnCl_2\ 2H_2O$, in 10 mls of concentrated hydrochloric acid in Erlenmeyer flask, warming if necessary to dissolve. Dilute to 100 mls. This solution is prepared fresh each time. If longer use of a large amount of prepared solution is required, precautions must be taken to keep solution from going to the stannic form.

4. Standard P. Dissolve 0.2195 gm of recrystallized potassium dihydrogen phosphate, KH_2PO_4, and dilute to 1 liter. This solution contains 50 ppm P and a second stock solution containing 2 ppm P is prepared by diluting 20 mls of the base solution to 500 mls. Standards prepared were 0, 2, 4, 6, 8 and 10 ppm.

Procedure

1. Place 2 gms of 20-mesh soil in an Erlenmeyer flask and add 200 mls of the extracting solution. Place on a shaker and shake for 30 minutes.

2. Filter through a Whatman No. 40 filter paper, refiltering first portions if turbid.

3. Pipette a 10 ml aliquot from the filtrate into 50 ml volumetric flask.

4. Add 2 mls ammonium molybdate-sulfuric acid solution, make up to volume with the extracting solution and add 3 drops of stannous chloride solution, mix and read in the colorimeter with a 660 m filter. The reading must be done within solution. Calculate concentration of unknown solutions by interpolating the readings on a curve derived from the series of standards.

This method of phosphorus extraction is known as the modified Truog method.

IV. Water extractable Silicon in soils

1. Ammonium molybdate solution. Dissolve 7.5 gms of ammonium molybdate in 75 mls of distilled water. Add 10 mls of 18 N H_2SO_4 and dilute the solution to a volume of 100 mls with water. Store the solution in a plastic bottle.

2. Oxalic acid solution, 10% w/v. Dissolve 50 gms of oxalic acid in 450 mls of water and store the solution in a plastic bottle. Prepare a fresh solution when an appreciable amount of sediment forms.

3. Reducing solution. Dissolve 0.7 gm of sodium sulfite in 10 mls of water. Add 0.15 gm of 1- amino -2- naphthal -4- sulfonic acid, and stir the mixture until the salts dissolve. Dissolve 9 gms of sodium bisulfite in 90 mls of distilled water, and mix it with the solution above. Store the solution in a plastic bottle.

4. Standard silicon solution, 50 ppm of elemental Si. Digest clear quartz crystals in concentrated HCl for an hour. Rinse them with water, dry them, and then grind them to a fine powder in an agate morter. Transfer the quartz powder to a crucible, heat it to redness for a brief period, cool it, and transfer it to a screw cap vial. Fuse 0.1070 gm of quartz powder with sodium hydroxide in a nickel crucible. The crucible was grasped with nickel or platinum-tipped tongs and rotated so the melt spread over the sides of the lower half ot the crucible. Allow the melt to cool, add approximately 50 mls of

distilled water and transfer it to a one-liter volumetric flask. Add about 400 mls of water plus 20 mls of 6N HCl, and then add water to make 1 liter.

Procedure

1. To 10 gms of air-dried soil add 100 mls of distilled water.
2. Place on a shaker stand and shake for four hours.
3. After shaking add portion to centrifuge tubes and centrifuge at approximately 23,000 g.
4. Once the solution is clear, withdraw a 10 ml aliquot with a pipette and transfer it to a 100 ml volumetric flask. Treat a 10 ml aliquot of the reference blank solution in the same manner as the sample solution.
5. Add 1 ml of the ammonium molybdate reagent solution, swirling the contents of the flask during addition.
6. Mix the solutions well, and allow the flask to stand for 10 minutes.
7. Add 4 mls of oxalic acid solution while swirling contents of the flask and mix the solutions well.
8. Add 1 ml of reducing solution while swirling the contents of the flask, add distilled water to make to 100 mls, mix the contents well and allow the flask to stand at least 30 minutes.
9. Determine the percent transmission using a colorimeter at 660 m, setting the reference blank at 100. Calculate the concentration of Si from the standard curve.

APPENDIX II

DESCRIPTION AND REVIEW OF LESS DOMINANT WEED AND IMPROVED FORAGE SPECIES

Digitaria decumbens Stent (Pangola grass). Since its dissemination from its point of origin in South Africa this grass has become one of the most important forage species in the tropical and sub-tropical world. It has a strongly stoloniferous habit, glabrous leaves 14 - 30 cm long and 0.7 cm wide, with relatively thin, many-noded stems which are much branched and usually decumbent, rooting vigorously in contact with the soil. It flowers readily, the sterile inflorescence consiting of 6 - 10 thin racemes up to 13 cm long and arranged digitately (Davies and Hutton, 1970; Hodges, et al., 1967; Humphreys, 1969; Nestel and Creek, 1962).

Because of the extremely low viability of seed, this grass must be propagated vegetatively. Freshly cut stolon pieces or stem cuttings are spread over the prepared seed bed under favorable moisture conditions and then disced in. Nicholls and Plucknett (1971) introduced a new technique of propagating such species with the use of pre-rooted "packets" of vegetative material. This method reduces the amount of vegetative material needed as well as facilitating propagation on areas where the mechanical preparation of a seed bed is not feasible.

Pangola grass is adapted to a wide range of climatic conditions, but it is essentially a wet, coastal grass, flourishing in areas receiving more than 1,000 mm of annual rainfall. Its wide range of adaptability extends also to soil conditions. Good growth of pangola has been recorded at soil pH levels ranging from 4.2 - 8.5. It tolerates waterlogging, except in heavy clay soils where it requires good drainage and is of considerable importance as a soil stabilizer in erodable areas (Alleyne and Percy, 1966; Hodges, et al., 1967; Nestle and Creek, 1962).

Because of its low protein content, work with pangola grass has involved the use of high level of nitrogen fertilizer or the incorporation of legumes into mixtures with it. The cost of nitrogen fertilizer has resulted in an increased interest in the contribution of legumes (Kretschmer, 1966 and Nestle and Creek, 1962). Luh, et al. (1961), in Taiwan used a range of sub-tropical legumes in association with pangola grass, including Desmodium intortum, Centrosema pubescens and Glycine wightii. All combinations gave similar dry matter yields of approximately 14,500 kgm/ha/year, but the pangola/intortum combination was superior in crude protein production. Under Hawaiian conditions Younge, et al. (1964) recorded dry matter yields of 22,400 kgm/ha/year for adequately fertilized pangola/intortum pastures.

In general, studies on the digestibility of pangola grass show that crude protein content and digestibility decline progressively with age, and that a satisfactory yield of digestible protein and TDN may be obtained from pangola grass herbage only up to 6 weeks of age (Murphy, 1972).

Phaseolus atropurpureus Moq. & Sesse ex DC. (cv Siratro). Siratro is the result of a cross between two Mexican strains of P. atropurpureus and is now widely adapted to areas in Australia, New Guinea, Fiji, Philippines, Mexico, Southern Rhodesia, Florida and Brazil.

It is a strongly stoloniferous, perennial legume, having well developed taproots that reach to moderate depths. The characteristic stoloniferous habit results in greater persistence, stand density, and high yielding ability. These stolons root at the nodes once in contact with moist soil. The broad, lobed leaves are green on the upper surface and greyish-green on the pubescent lower surface (Murphy, 1972).

Being sensitive to low temperatures, severe frosting proving lethal, Siratro is best adapted to moist, warm, sub-tropical climates (Humphreys, 1969). Its best performance is obtained in areas receiving 750 - 1750 mm of annual rainfall but, because of its large, deep taproot, Siratro is very drought tolerant and can grow under lower rainfall.

Because of its climbing habit, introduction into grass swards results in plants of vine-like appearance whereas if established with the grass component into a prepared seed bed, it has a more prostrate habit. Rotar, *et al.* (1967) found inoculation with the more efficient strain of *Rhizobium* aided production. It has been grown successfully with a wide range of grasses including *Digitaria decumbens*, *Chloris gayana*, *Paspalum plicatulum* and *Setaria sphacelata*.

Lotononis bainesii Baker (Miles lotononis). Lotononis is a vigorous, fine-stemmed, prostrate, stoloniferous and perennial legume. It has a strong taproot and its leaves are digitate trifoliate leaves, and are borne in groups of 3 - 5 cm petioles less than 5 cm long at nodes 2 - 8 cm apart. It forms dense stands, varying from completely prostrate to 60 cm high, depending on grazing intensity. Stolons grow very rapidly but rooting at the nodes only occurs in sandy and self-mulching soils (Bryan, 1961; Kretschmer, 1963; and Humphreys, 1969).

Lotononis is adapted to a wide range of temperatures and day lengths and appears to be best suited to areas receiving more than 875 mm of annual precipitation with no prolonged dry spells, although it has some drought resistance. It is more frost tolerant than any of the other tropical pasture legumes (Murphy, 1972).

It is also adapted to a wide range of soils including those which are strongly acid with a pH of 5.1 (Bryan, 1961). Inoculation of the seed at planting with its specific, red Rhizobium strain is absolutely essential for successful establishment and production. Latononis combines well with a variety of pasture grasses including Paspalum commersonii, P. plicatulum, P. dilatatum, Chloris gayana and Digitaria decumbens, (Bryan, 1961). It appears to be an efficient fixer of atmospheric nitrogen.

As far as management is concerned, it is evident that heavier grazing is more beneficial to lotononis than lenient grazing (Wright, 1964; and Whiteman, 1969).

Centrosema pubescens Benth. (Centro). Centro is native to South America. It is a creeping, twining and perennial legume. It is slow to establish and yields are low in the first year (Thomas and Humphreys, 1970 and Douglas, 1958).

It is one of the more important perennial legumes for wet, tropical areas. It is very late flowering, so seed must be produced in areas free of frost and with a long growing season (Davies and Hutton, 1970). It is adapted to warm coastal areas with an annual rainfall of 1270 mm, growing on a variety of soils and rooting moderately at the nodes.

Centro's twining habit makes it readily compatible with tussock grass species such as Guinea grass, green panic, Pennisetum purpureum and has been found to do well with Brachiaria mutica and Melinis minutiflora (Douglas, 1959) and Cynodon plectostachyon (star grass).

In Australia and India centro has been found to be useful in suppressing Imperata cylindrica (Whyte, et al., 1953).

Melinis minutiflora Beauv. (Molasses grass). This grass is a freely branching, spreading perennial forming a thick but loose mat with a purple-tinged foliage, and with erect flowering stems supporting a panicle of purplish, bristled spikelets.

It is indigenous to Africa and is used extensively in Brazil and Australia as a pioneer species in well drained areas receiving in excess of 1000 mm rainfall annually. Its dense mat smothers other plant species and its leaves, covered with hairs exuding sticky secretions, have an odor of molasses.

It is widely used as pasture silage, hay or green soiling in South and Central America and in wetter parts of East Africa, Ceylon, the Philippines and Queensland, Australia.

Establishment is easy in prepared seed beds or into burned areas or cleared forests as the seed does not require covering. Uniform distribution of seed is facilitated by mixing it with sawdust or rice hulls. It has been found to combine well with wetland pasture legumes such as Pueraria phaseoloides, Stylosanthes guyanensis, Phaseolus lathyroides and Centrosema pubescens (Douglas, 1959). Rapid establishment and vigorous growth make it of particular value for weed-infested lands (Whyte, et al., 1965).

Molasses grass must be well established before subjected to grazing since it will not take close grazing. It is very sensitive to fire and supports combustion readily, leading to its usefulness in land clearing and pasture development programs.

Psidium guajava L. (guava). A member of the Myrtle family (Myrtaceae), guava is a small evergreen tree 2 - 8 m tall with wide-spreading branches and square, downy twigs. It is a native of tropical America. It is found in waste lands in Hawaii. Layers of smooth, reddish-brown bark scale off from the lighter inner bark giving a mottled pattern to the trunk. The oblong or oval, blunt leaves are prominently feather-veined, more or less hairy beneath, 8 - 14 cm long. The flowers have a bell-shaped calyx, splitting, irregularly, and the corolla is composed of 4 - 6 white petals with numerous white stamens with yellow anthers. The lemon-like yellow fruit is made up of a solid pink or cream colored, acid pulp, within which is a juicier pulp full of small, hard, kidney-shaped seeds (Neal, 1948). These seeds are spread readily by birds and cattle. This leads to a problem on grazing lands in the wetter tropics. Incorrect management will lead to an invasion of guava seedlings.

Rhodomyrtus tomentosa (Ait.) Hassk. (downy rosemyrtle). This plant is another shrubby member of the Myrtaceae and is native to South eastern Asia, Malaysia and the Philippines. It has downy twigs, oblong or oval, short-stemmed leaves, 3-veined, commonly blunt, somewhat white-woolly on the under surface. Flowers are solitary or 2 or 3 together, not fragrant, with five sepals, five pink petals, many pink stamens with yellow anthers. Fruits are 1 cm long, green to purple, pubescent, and have several seeds embedded in sweet, edible, purple pulp (Neal, 1948).

Metrosideros collina (Forst.) Gray subsp. polymorpha (Gaud.) Rock. A member of the Myrtaceae, 'ohia' is more commonly found at higher elevations in Hawaii where it is native tree. It is very variable, especially in size and leaf shape, pointedness and texture. Young ohia leaves are more or less reddish, the older ones, dull or shiny green. Flowers are bright red, (stamen color) and are 1 - 3 cm long forming tufts at branch ends. Rarely are the flowers salmon, pink, yellow or white (Neal, 1948).

Melastoma malabathricum L. (Banks melastoma). Melastoma is a member of the Melastomaceae, and was originally introduced as an ornamental from India. It is a rapidly spreading shrub about 2 - 3 m tall, with narrow, oval, pointed leaves 4 - 12 cm long with three to five veins from the base, both surfaces covered with stiff, flat-lying hairs. Branchlets, leaf and flower stems, and calyx are covered with narrow, pointed, commonly toothed, light-colored scales. Pink to purple flowers are 3 - 8 cm in diameter, 5 - 7 parted and clustered on short stems at branch tips (Neal, 1948).

Lantana camara L. Lantana is a member of the Verbenaceae. It is a native of tropical America and has been introduced to many subtropical countries originally as an ornamental shrub but has spread to become a pest on waste, range and pasture lands. Plants grow to a height of 0.3 - 1 m and are smooth or somewhat prickly. In the wild plants can grow to heights of 7 m. The leaves are ovate, thick, fine-toothed, opposite or whorled and produce a pungent odor. They are 3 - 13 cm long, rough on top and downy beneath. At the base of these leaves develop dense, flat-topped flower heads, 3 - 6 cm in diameter, borne on strong stems (Neal, 1948). The flowers seem variegated since they open yellow or orange, change to pink or red in the wild, or orange changing to red in the cultivated form. The black berry-like fruit is ovoid, about 1 cm long and consists of many tiny, juicy, two-seeded drupes (Neal, 1948).

Stachytarpheta urticaefolia (Salisb.) Sims. Also a member of the Verbenaceae, it is an erect, woody, freely branching plant 0.5 - 2 m tall. Leaves are opposite or alternate, wrinkled, 5 - 7 cm long, ovate, hairy on both surfaces, margin toothed, sharply contracted at the base. Flowering stalks 27 - 33 cm long, hairy, and terminal. Only 4 - 6 flowers appear at one time. Flowers are dark blue-violet to lavender.

Dicranoptoris linearis (Burm.) Underw. (False staghorn fern). A member the Gleicheniaceae it is a dense terrestrial fern with creeping underground rhizomes and wiry frond stems up to a meter in length; fronds divide repeatedly and at the end of each is a pair of pinnae cut into many small lobes.

Burnt mulch of staghorn fern limits growth of all vegetation for several years, indicating the possibility that it contains water-extractable, growth-regulating compounds.

Pteridium aquilinum (L.) Kuhn (Bracken fern). This species is a member of the common fern family Polypodiaceae and is terrestrial with creeping underground rhizomes and 0.5 - 1 m long frond stems; fronds are triangular in shape, much divided, dull green and leathery. It is found as scattered tufts in open areas, usually mixed with other ferns.

Pandanus odoratissimus L. f. (Pandanus, or hala in Hawaii). Pandanus is a member of the screw pine family, Pandanaceae. It is a wide-branched native tree 6 m or more tall with a few to many conspicuous aerial roots; leaves 1 m or more in length, narrow, smooth, with sharp toothed margins, arranged spirally on branches. Male and female trees occur. The male flowering spike is about a foot long, and is surrounded by white, narrow, pointed, fragrant, edible bracts. The fruit on the female tree consists of 50 angular, wedge-shaped, yellow to red drupes about 2.5 cm by 4 cm each with 4 to 12 one-seeded or empty cells.

Ageratum conyzoides L. Tropic ageratum is a member of the Eupatorium tribe of the aster family Asteraceae (formerly Compositae). It is a branching, hairy, rather weak-stemmed and unpleasant smelling, tropical American annual, 0.3 - 0.5 m tall. Stems are cylindrical and hairy. Flower heads are blue (rarely white) packed in broad, flat-topped clusters. The blue flowered form is probably A. houstonianum Mill. The two weeds are often confused.

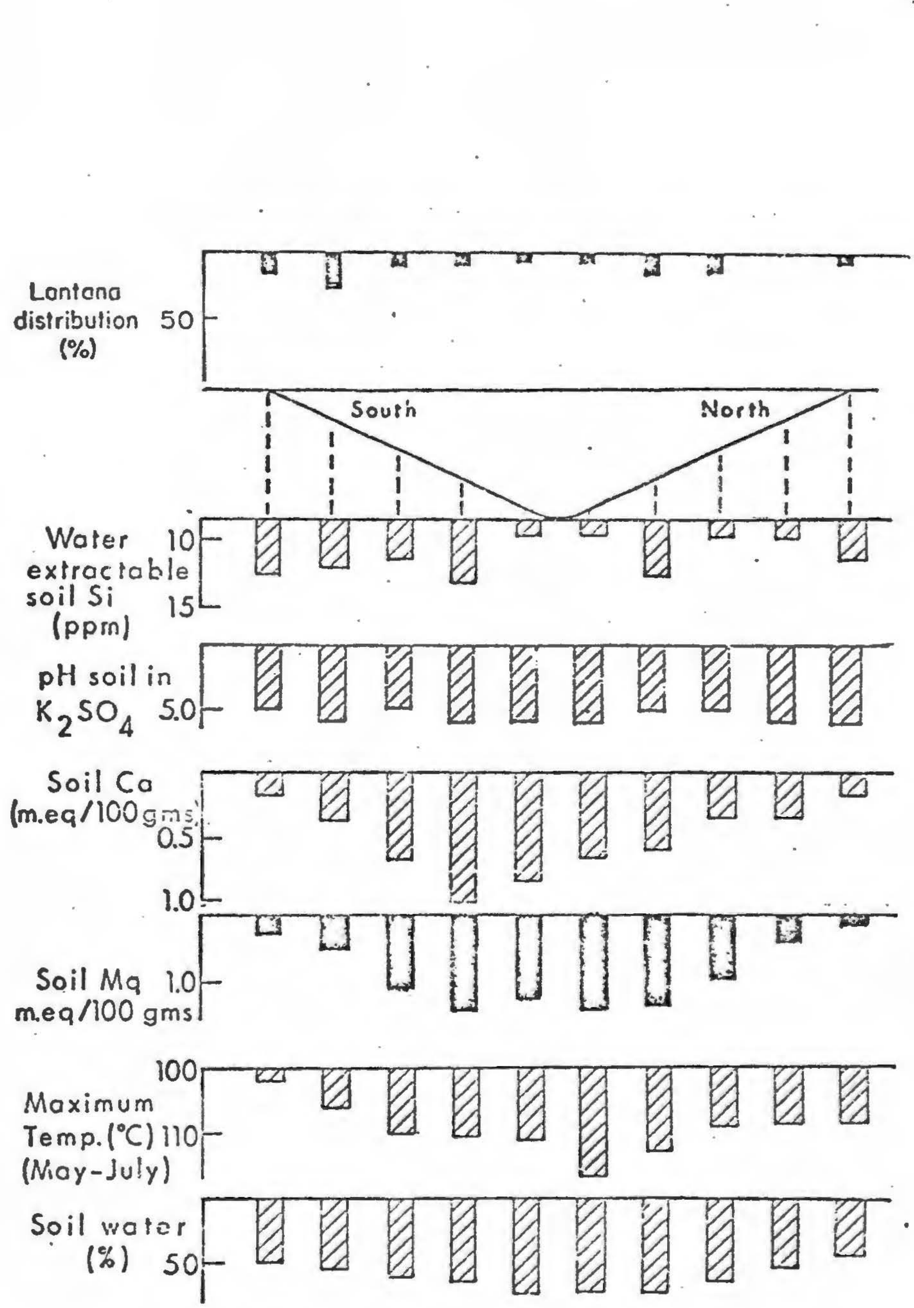
Erechtites hieracefolia (L.) Raf. ex DC. American burnweed is a member of the Senecia tribe of the Asteraceae (formerly Compositae). It is an erect winter annual 0.5 - 2 m high found in waste lands especially after clearing and burning, hence its name 'fireweed' or 'burnweed'. Stems and branches are marked with many, small longitudinal ridges. Leaves are thin, lanceolate or ovate-lanceolate, toothed and often deeply notched 2 - 18 cm long. Flower heads are greenish-white, arranged at the ends of stems and branches.

Elephantopus mollis (H.B.K.). Hawaiian elephants foot is a member of the Vernonia tribe of the Asteraceae (formerly Compositae) and is an erect, perennial herb, 0.3 - 1.3 m high, somewhat woody. Stems are green, covered with white, fine to coarse hair. Leaves are firm, dull green, thinly hairy to rough above, soft-haired and resinous, especially on veins on lower surface. Oblong leaves have serrated edges and are sharply pointed at the tip. Flowers are white and are formed in clusters.

Nephrolepis exultata (L.) Schott (Sword fern). This species of the sword fern group, Davaliaceae, is one of five known in Hawaii. This group of ferns is common in forests, growing in tufts. The long, narrow, arching fronds are cut into many narrow segments along each side of an axis, the tip of which continues to unroll and produce pinnae. These pinnae are jointed to the axis. Beneath the stiff frond near the edge of the pinnae are numerous sori which have a circular or kidney-shaped covering (Neal, 1948).

APPENDIX III

REGRESSION RELATIONSHIPS BETWEEN WEED SPECIES DISTRIBUTION PATTERNS AND ENVIRONMENTAL FACTORS



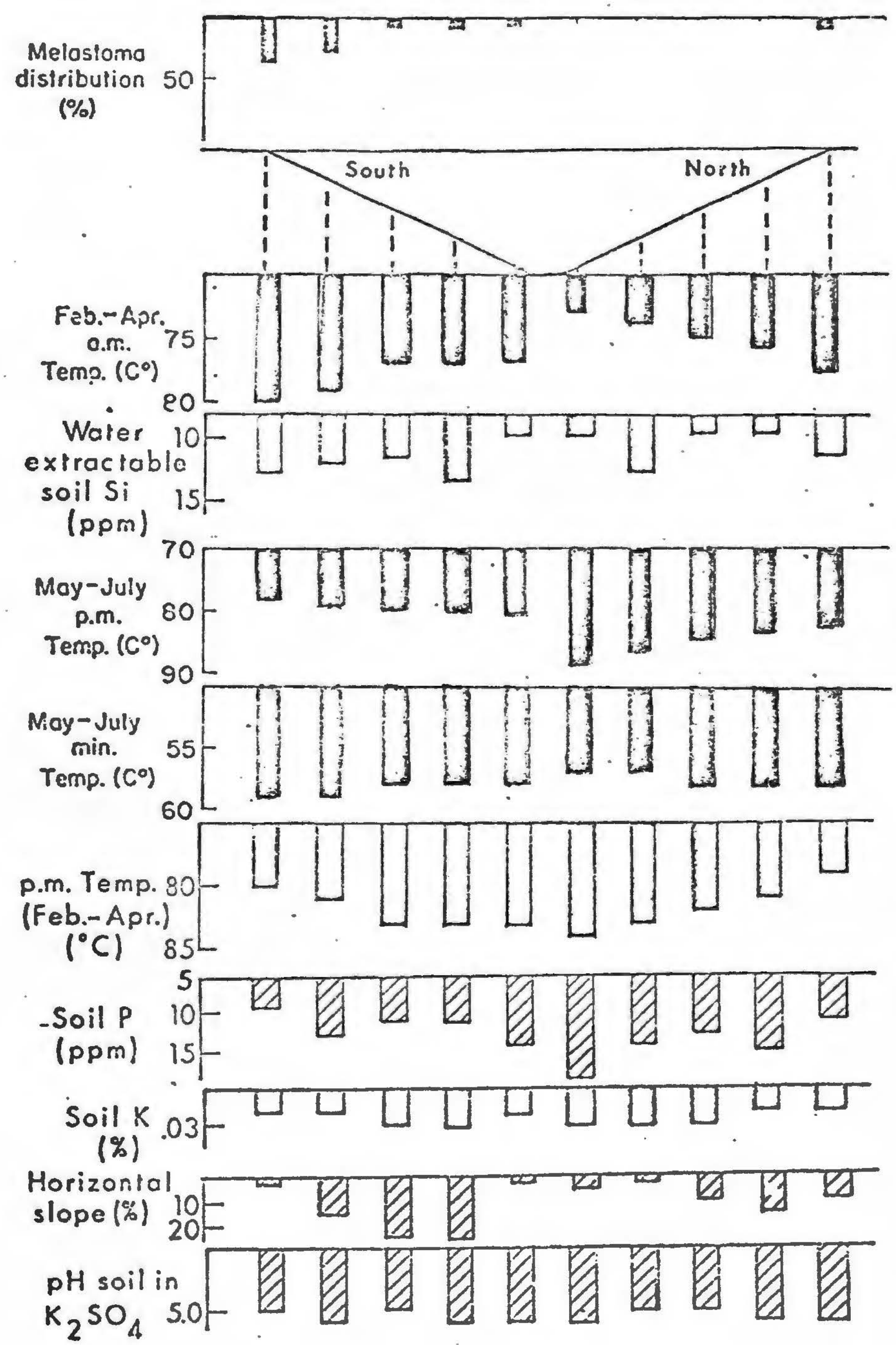
APPENDIX FIGURE 1. DISTRIBUTION OF *Lantana camara*, AS INFLUENCED BY ENVIRONMENTAL FACTORS.

APPENDIX TABLE 1. STEP-WISE BUILD UP ON MULTIPLE REGRESSION EQUATION FOR *Lantana camara*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Lantana camara*	R	Inc. in R^2
Soil Silicon (x_1)	$Y=-15.4+2.2x_1$	0.361**	0.130
Soil pH in K_2SO_4 (x_2)	$Y=-186.6+2.2x_1+34.0x_2$	0.487**	0.107
Soil Calcium (x_3)	$Y=-222.8+2.5x_1+41.6x_2-10.2x_3$	0.571**	0.089
Soil Magnesium (x_4)	$Y=-182.0+2.8x_1+31.4x_2-14.9x_3+9.9x_4$	0.670**	0.123
May-July Max. Temp. (x_5)	$Y=12.7+2.5x_1+25.1x_2-12.5x_3+14.1x_4-1.5x_5$	0.723**	0.074
Soil Water (x_6)	$Y=-46.3+2.6x_1+30.9x_2-13.2x_3+15.7x_4-1.1x_5-0.2x_6$	0.734**	0.016

R = Regression coefficient

** = Significance at the 1% level



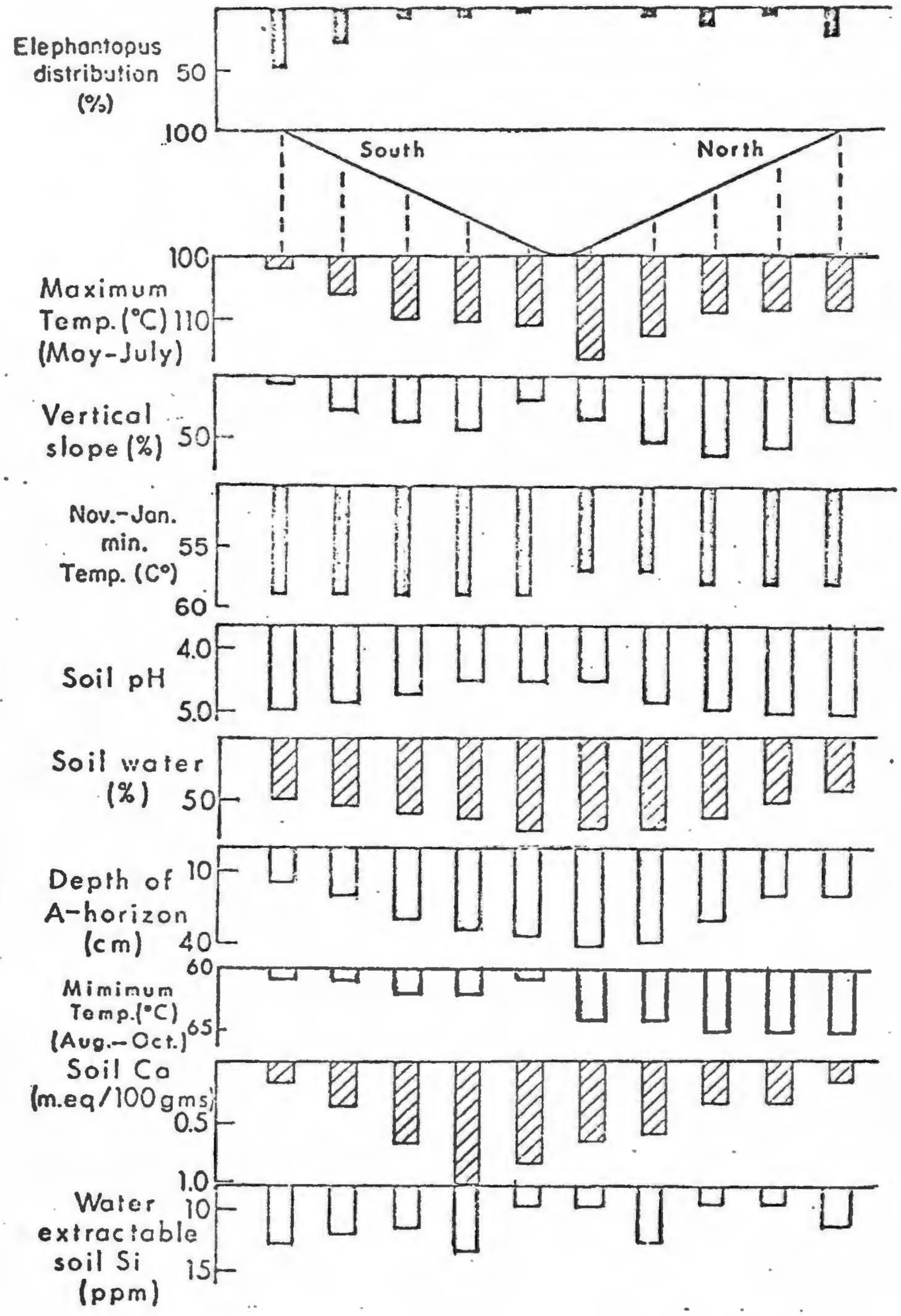
APPENDIX FIGURE 2. DISTRIBUTION OF Melastoma malabathricum, AS INFLUENCED BY ENVIRONMENTAL FACTORS.

APPENDIX TABLE 2. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Melastoma malabathricum*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Melastoma malabathricum*	R	Inc. in R^2
Feb.-Apr. a.m. Temp. (x_1)	$Y=-347.6+4.6x_1$	0.649**	0.422
Soil Silicon (x_2)	$Y=-329.8+4.1x_1+1.7x_2$	0.714**	0.088
May-July p.m. Temp. (x_3)	$Y=-771.4+7.4x_1+1.9x_2+2.3x_3$	0.743**	0.042
May-July min. Temp. (x_4)	$Y=-1489.3+15.5x_1+2.2x_2+3.0x_3+15.5x_4$	0.778**	0.053
Feb.-Apr. p.m. Temp. (x_5)	$Y=-3158.5+11.7x_1+2.1x_2+6.9x_3+19.8x_4+6.4x_5$	0.823**	0.072
Soil Phosphorus (x_6)	$Y=-3305.1+11.4x_1+2.3x_2+7.3x_3+21.7x_4+6.7x_5-0.7x_6$	0.838**	0.026
Soil Potassium (x_7)	$Y=-3263.1+11.2x_1+2.3x_2+7.4x_3+21.3x_4+6.8x_5-0.8x_6-224.6x_7$	0.853**	0.025
Hor. Slope (x_8)	$Y=-3697.4+13.9x_1+2.4x_2+9.0x_3+21.0x_4+8.1x_5-0.9x_6-335.1x_7+0.22x_8$	0.875**	0.039
pH in K_2SO_4 (x_9)	$Y=-3730.0+14.1x_1+2.4x_2+8.9x_3+20.0x_4+8.1x_5-0.9x_6-361.6x_7+0.2x_8+12.9x_9$	0.884**	0.016
Soil Water (x_{10})	$Y=-3922.5+14.4x_1+2.4x_2+9.1x_3+19.3x_4+10.1x_5-0.9x_6-432.2x_7+0.2x_8+26.5x_9-0.3x_{10}$	0.902**	0.031

R = Regression coefficient

** = Significance at the 1% level



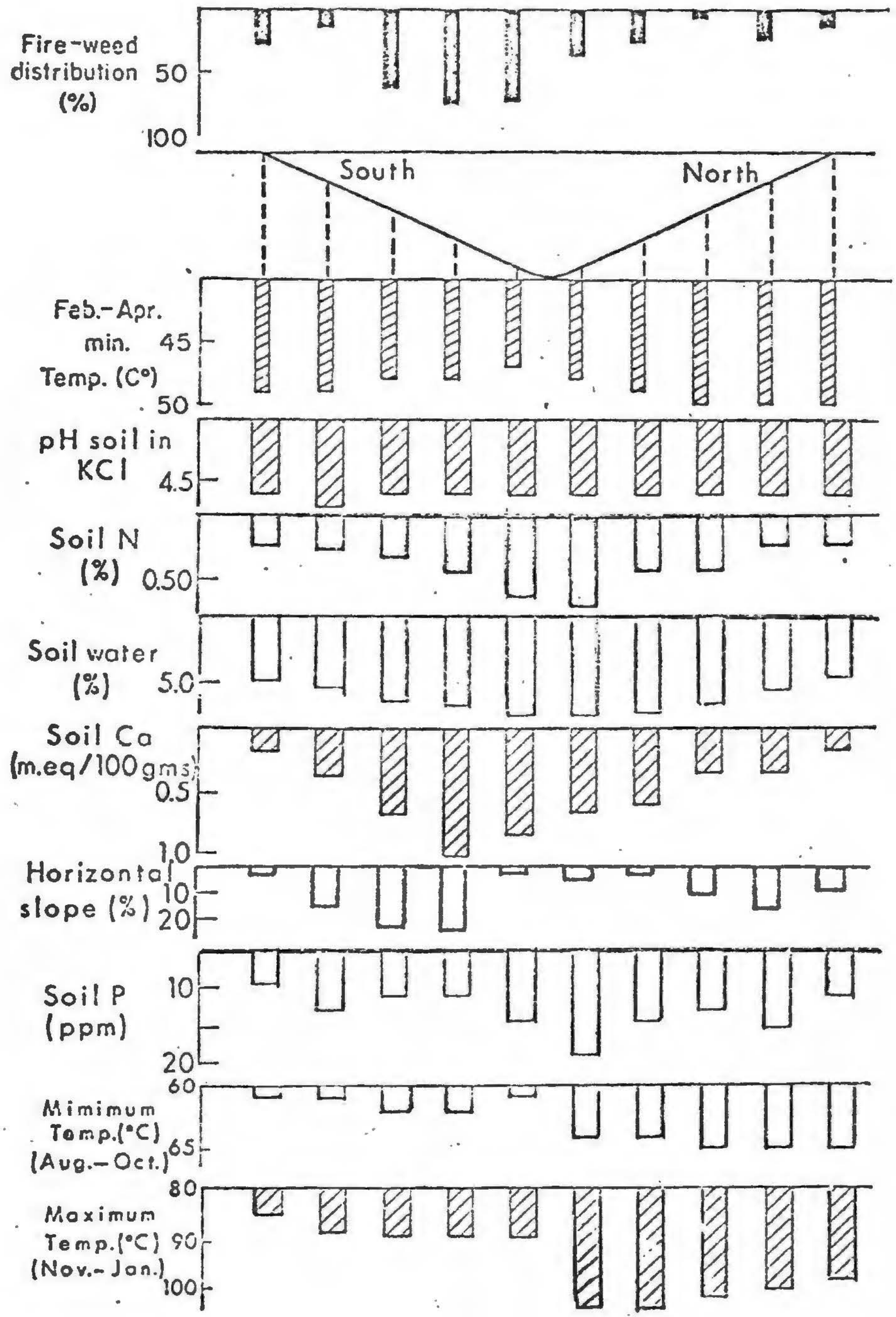
APPENDIX FIGURE 3. DISTRIBUTION OF <u>Elephantopus</u> <u>mollis</u>, AS INFLUENCED BY ENVIRONMENTAL FACTORS.

APPENDIX TABLE 3. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR <u>Elephantopus mollis</u>

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Elephantopus mollis*	R	Inc. in R^2
May-July Max.Temp.(x_1)	$Y=380.7-3.3x_1$	0.661**	0.437
Vert. Slope (x_2)	$Y=336.2-2.8x_1-0.3x_2$	0.733**	0.100
Nov.-Jan.Min.Temp.(x_3)	$Y=887.4-3.6x_1-0.4x_2-7.9x_3$	0.773**	0.061
Soil pH in water(x_4)	$Y=716.8-2.8x_1-0.4x_2-9.3x_3+31.9x_4$	0.805**	0.050
Soil water (x_5)	$Y=708.8-3.3x_1-0.3x_2-11.2x_3+49.1x_4+0.4x_5$	0.829**	0.040
Soil depth (x_6)	$Y=886.6-3.9x_1-0.4x_2-12.2x_3+51.9x_4+0.5x_5+0.8x_6$	0.841**	0.019
Aug.-Oct.Min.Temp.(x_7	$Y=1250.6-4.1x_1-0.3x_2-16.0x_3+54.5x_4+0.4x_5+0.7x_6-2.3x_7$	0.847**	0.009
Soil calcium (x_8)	$Y=1176.7-3.8x_1-0.3x_2-15.3x_3+57.6x_4+0.5x_5+0.8x_6-2.6x_7-4.4x_8$	0.853**	0.009
Soil silicon (x_9)	$Y=1046.8-3.6x_1-0.3x_2-14.4x_3+59.4x_4+0.8x_5+0.9x_6-1.9x_7-5.5x_8+0.8x_9$	0.859**	0.009

R = Regression coefficient

** = Significance at the 1% level



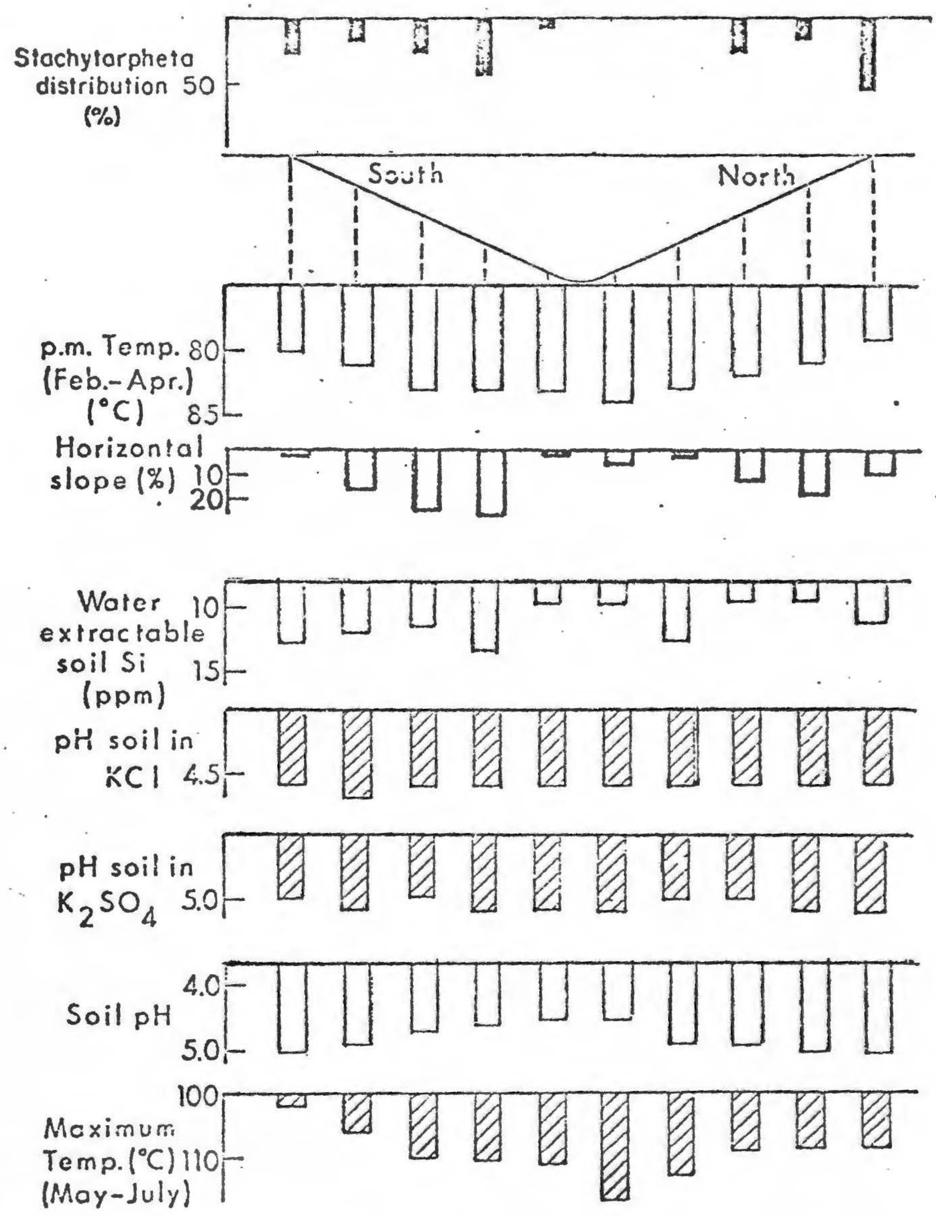
APPENDIX FIGURE 4. DISTRIBUTION OF Erechtites hieracifolia, AS INFLUENCED BY ENVIRONMENTAL FACTORS.

APPENDIX TABLE 4. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Erechtites hieracifolia*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Erechtites hieracifolia*	R	Inc. in R^2
Feb.-Apr. Min. Temp. (x_1)	$Y=1084.8-21.5x_1$	0.648**	0.419
Soil pH in KCl (x_2)	$Y=1099.9-21.5x_1-4.6x_2$	0.674**	0.035
Soil Nitrogen (x_3)	$Y=1343.6-25.7x_1-8.9x_2-44.3x_3$	0.711**	0.051
Soil Water (x_4)	$Y=1193.4-22.9x_1-14.9x_2-65.1x_3+0.7x_4$	0.736**	0.037
Soil Calcium (x_5)	$Y=1035.5-19.8x_1-15.4x_2-62.8x_3+0.7x_4+12.2x_5$	0.757**	0.030
Hor. Slope (x_6)	$Y=1047.2-19.9x_1-14.8x_2-63.4x_3+0.6x_4+14.8x_5-0.3x_6$	0.776**	0.029
Soil Phosphorus (x_7)	$Y=962.1-18.0x_1-14.0x_2-47.9x_3+0.6x_4+17.1x_5-0.3x_6-1.4x_7$	0.791**	0.023
Aug.-Oct. Min. Temp. (x_8)	$Y=1082.1-25.7x_1-14.5x_2-61.3x_3+0.5x_4+15.3x5-0.3x_6-1.5x_7+4.4x_8$	0.802**	0.017
Nov.-Jan. Max. Temp. (x_9)	$Y=508.5-26.1x_1-14.3x_2-36.9x_3+0.9x_4+16.2x_5-0.5x_6-1.4x_7+18.8x_8-3.7x_9$	0.839**	0.063

R = Regression coefficient

** = Significance at the 1% level



APPENDIX FIGURE 5. DISTRIBUTION OF Stachytarpheta urticaefolia, AS INFLUENCED BY ENVIRONMENTAL FACTORS.

APPENDIX TABLE 5. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stachytarpheta urticaefolia*

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Stachytarpheta urticaefolia*	R	Inc. in R^2
Feb.-Apr. p.m. Temp. (x_1)	$Y=662.1-7.8x_1$	0.488**	0.238
Hor. Slope (x_2)	$Y=685.5-8.2x_1+0.7x_2$	0.671**	0.213
Soil Silicon (x_3)	$Y=645.9-8.0x_1+0.7x_2+2.3x_3$	0.721**	0.069
Soil pH in KCl (x_4)	$Y=638.8-8.1x_1+0.7x_2+2.1x_3+2.6x_4$	0.734**	0.019
Soil pH in K_2SO_4 (x_5)	$Y=878.4-8.1x_1+0.7x_2+1.8x_3+8.1x_4-50.9x_5$	0.755**	0.031
Soil pH in H_2O (x_6)	$Y=641.8-5.9x_1+0.7x_2+1.6x_3+11.0x_4-69.8x_5+29.5x_6$	0.768**	0.021
May-July max. Temp. (x_7)	$Y=775.2-9.6x_1+0.7x_2+1.9x_3+12.9x_4-84.3x_5+49.6x_6+0.01x_7$	0.796**	0.044

R = Regression coefficient

** = Significance at the 1% level

APPENDIX TABLE 6. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR <u>Pteridium aquilinum</u>

ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Pteridium aquilinum*	R	Inc. in R^2
Soil pH in water (x_1)	$Y=-102.8+22.5x_1$	0.349**	0.122
Aug.-Oct.Min.Temp.(x_2)	$Y=-301.7+27.4x_1+2.8x_2$	0.514**	0.142
Soil depth (x_3)	$Y=-283.4+22.2x_1+3.0x_2-0.6x_3$	0.559**	0.049
Feb.Apr.Min.Temp.(x_4)	$Y=-194.9+36.2x_1+6.6x_2-1.1x_3-7.8x_4$	0.651**	0.110
Nov.Jan.Min.Temp.(x_5)	$Y=-672.7+27.9x_1+9.2x_2-1.1x_3-8.5x_4+6.8x_5$	0.691**	0.055
Soil Manganese (x_6)	$Y=-810.2+29.9x_1+8.9x_2-1.2x_3-6.9x_4+7.8x_5+2.1x_6$	0.729**	0.033
Vert. Slope (x_7)	$Y=-936.1+27.0x_1+9.7x_2-1.0x_3-6.3x_4+8.8x_5+2.2x_6-0.1x_7$	0.745**	0.021
Soil Nitrogen (x_8)	$Y=-1041+27.9x_1+9.8x_2-1.2x_3-5.4x_4+9.7x_5+2.1x_6-0.1x_7+10.4x_8$	0.769**	0.022
Soil pH in KCl (x_9)	$Y=-1149+36.6x_1+9.4x_2-1.1x_3-3.4x_4+9.8x_5+2.0x_6-0.1x_7+24.6x_8+2.8x_9$	0.785**	0.038
May-July Min.Temp. (x_{10})	$Y=-836.9+36.2x_1+5.6x_2-0.9x_3+4.5x_4+16.9x_5+1.4x_6-0.2x_7+30.0x_8+3.4x_9-15.5x_{10}$	0.791**	0.024

R = Regression coefficient

** = Significance at the 1% level

APPENDIX TABLE 7. STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Nephrolepis exultata*

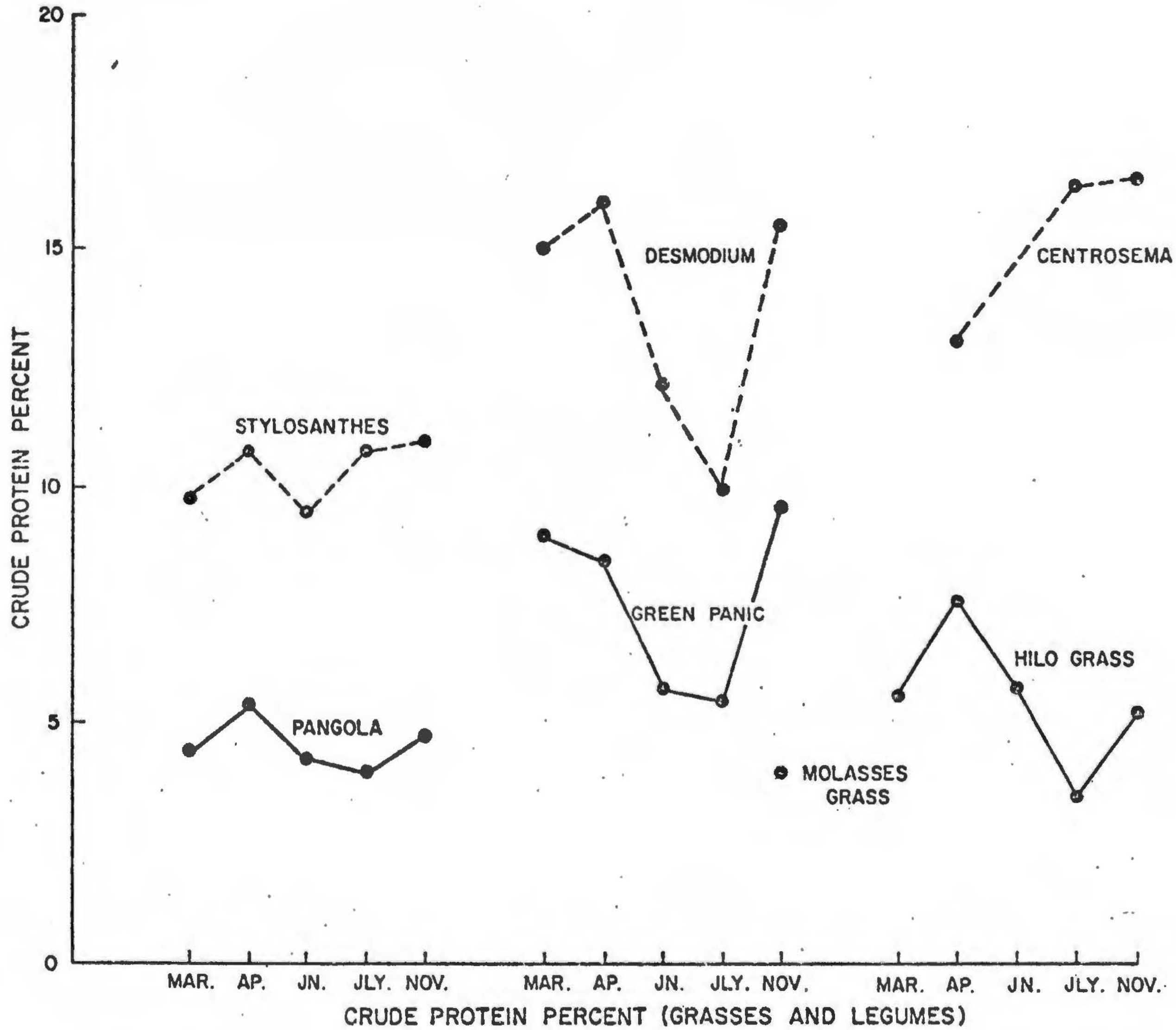
ENVIRONMENTAL FACTORS ENTERED	STEP-WISE BUILD UP OF MULTIPLE REGRESSION EQUATION FOR *Nephrolepis exultata*	R	Inc. in R^2
Feb.-Apr. Min.Temp. (x_1)	$Y=-502.7+10.6x_1$	0.361**	0.130
Soil Magnesium (x_2)	$Y=-721.8+14.8x_1+13.4x_2$	0.462**	0.084
Hor. Slope (x_3)	$Y=-702.0+14.5x_1+12.3x_2-0.4x_3$	0.509**	0.045
Soil Phosphorus (x_4)	$Y=-662.2+14.1x_1+12.4x_2-0.4x_3-1.5x_4$	0.551**	0.045
Soil Potassium (x_5)	$Y=-661.6+13.9x_1+11.5x_2-0.5x_3-1.3x_4+443.3x_5$	0.574**	0.027

R = Regression coefficient

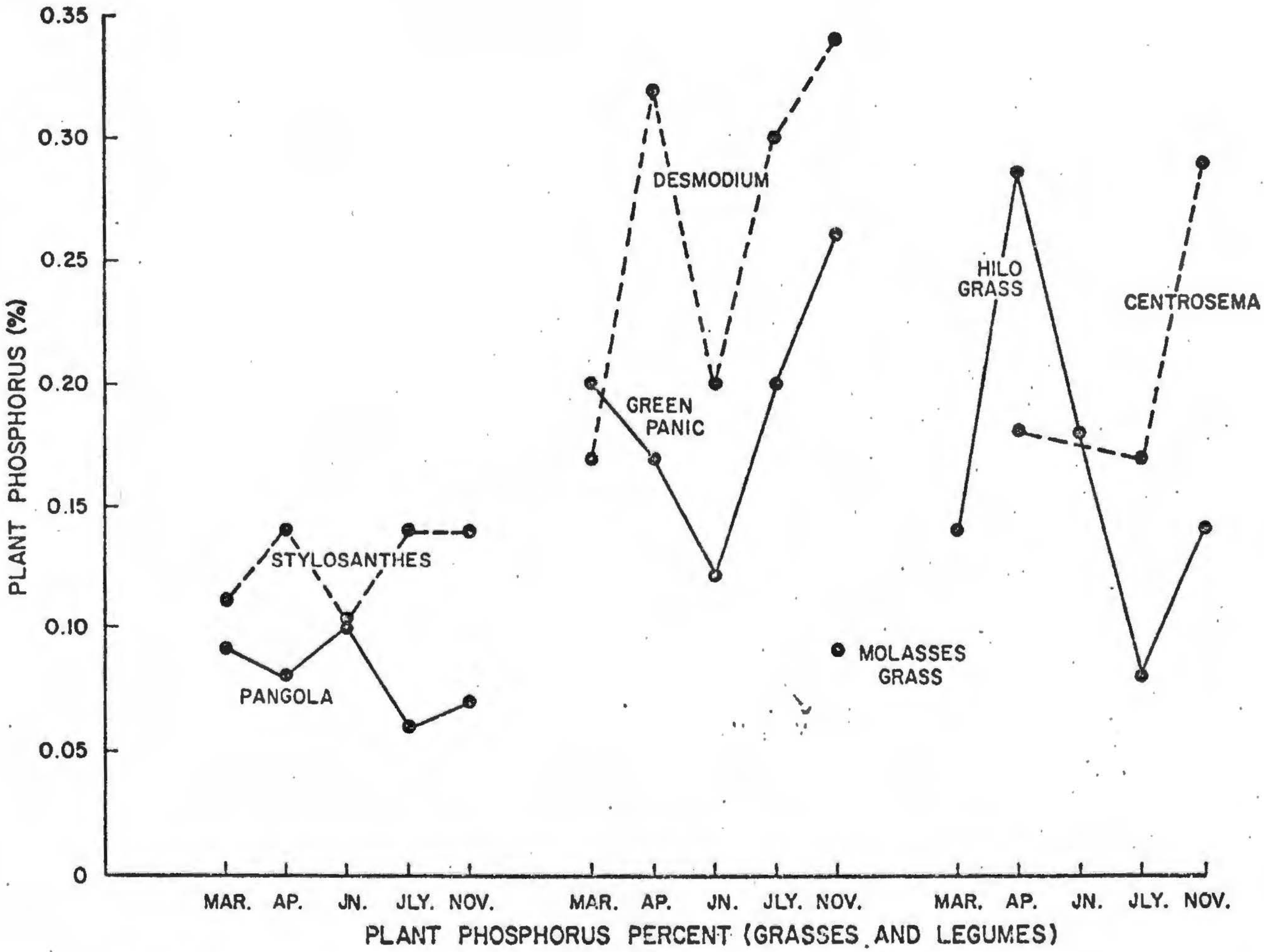
** = Significance at the 1% level

APPENDIX IV

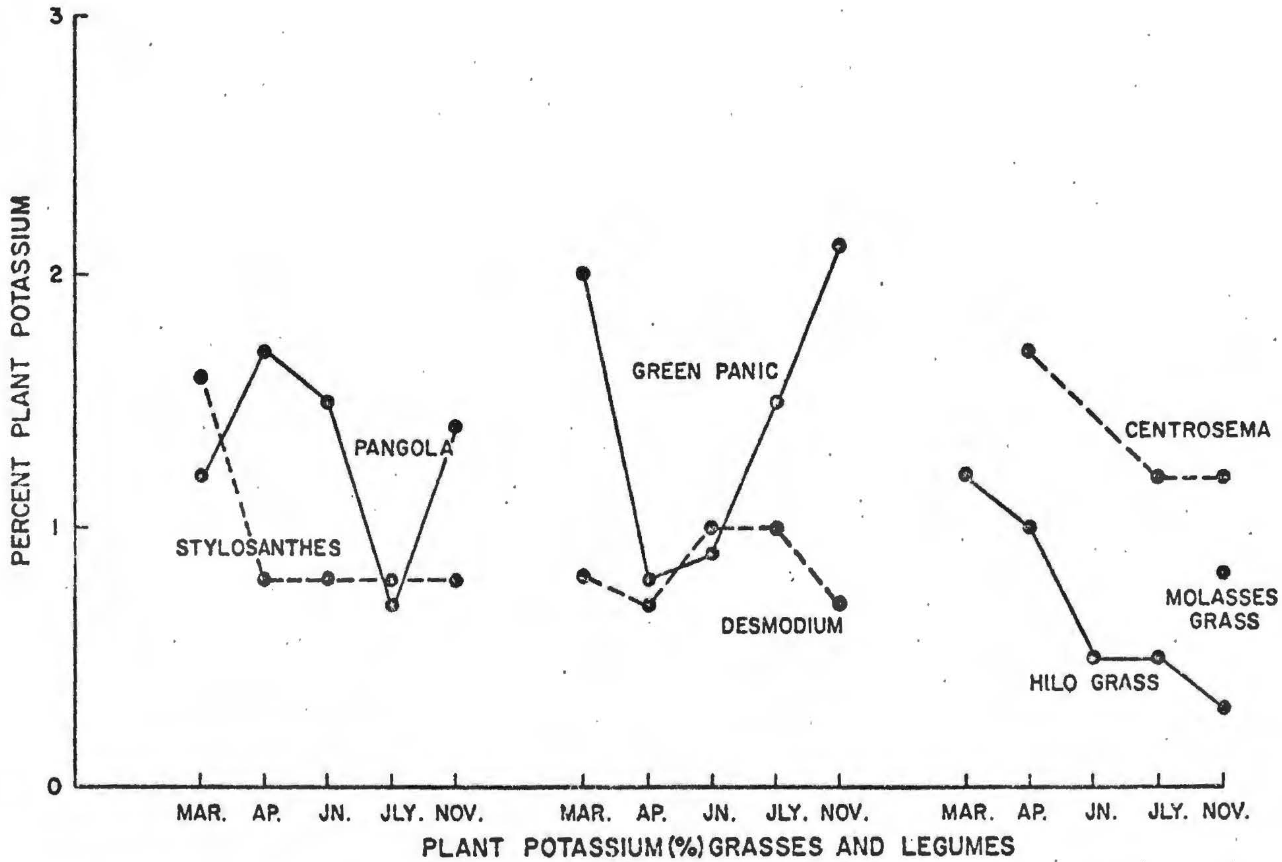
SEASONAL VARIATION IN CRUDE PROTEIN AND MINERAL CONTENT OF FORAGE SPECIES



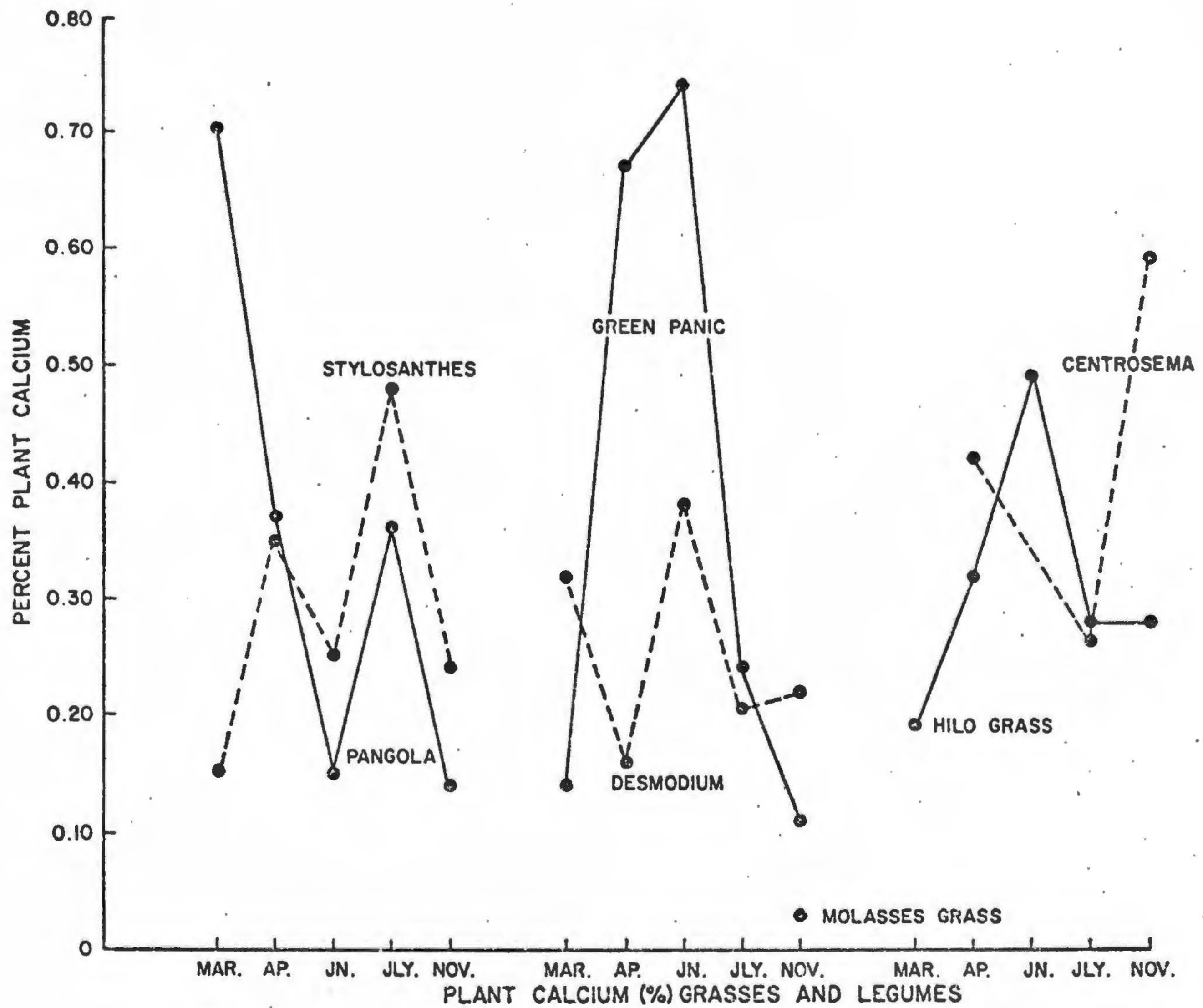
APPENDIX FIGURE 6. VARIATION IN THE CRUDE PROTEIN PERCENT OF FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



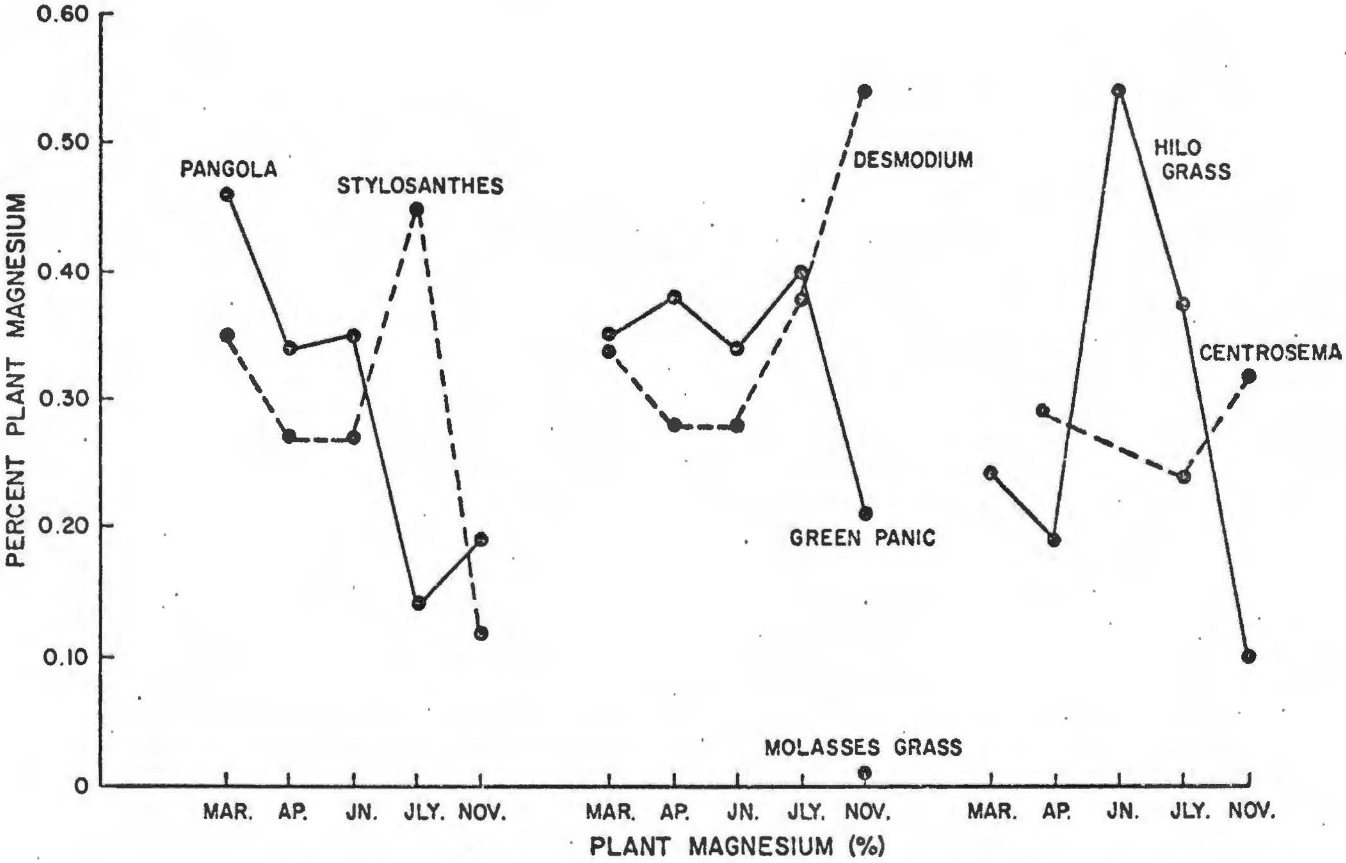
APPENDIX FIGURE 7. VARIATION IN PLANT PHOSPHORUS IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



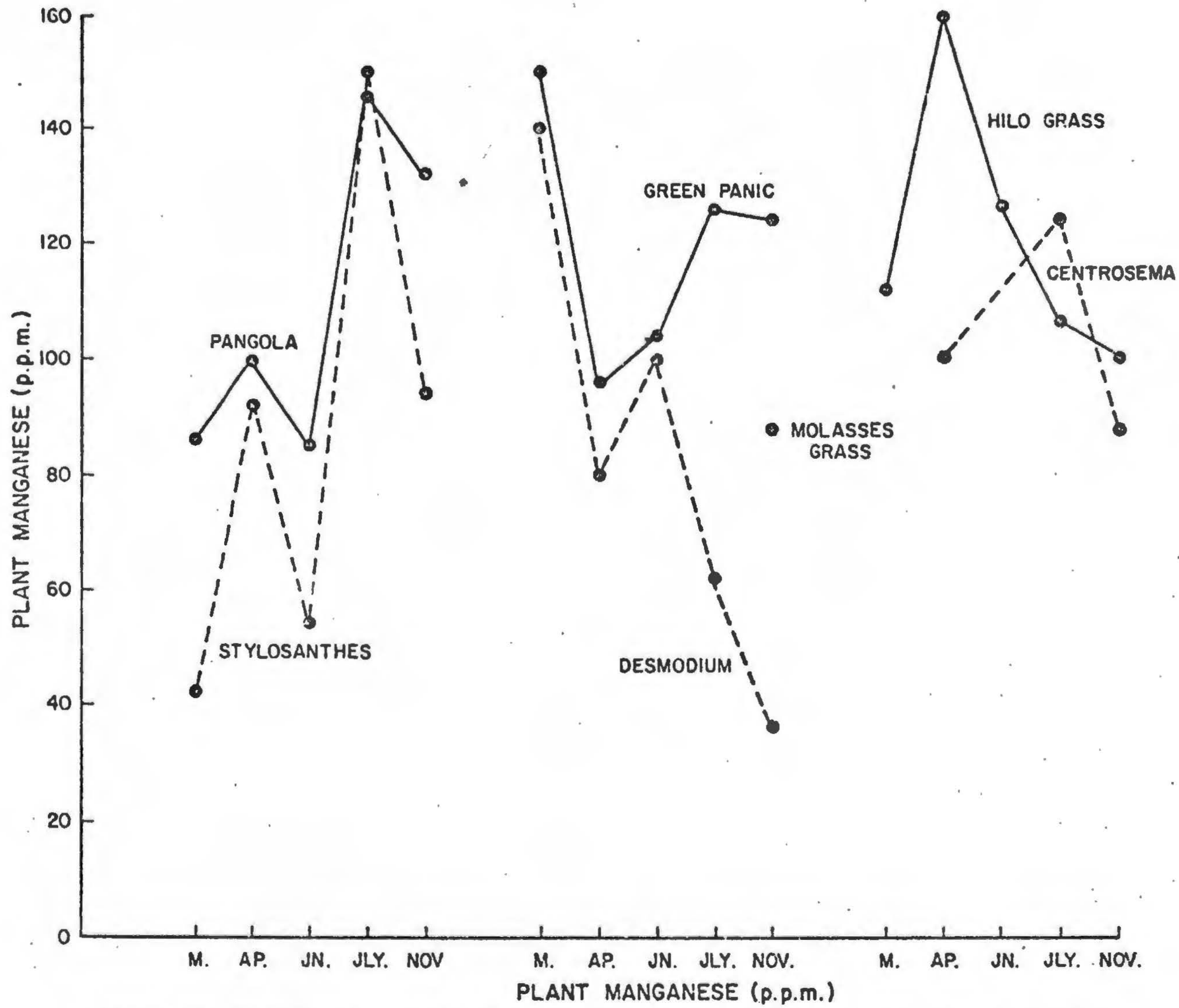
APPENDIX FIGURE 8. VARIATION IN PLANT POTASSIUM IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



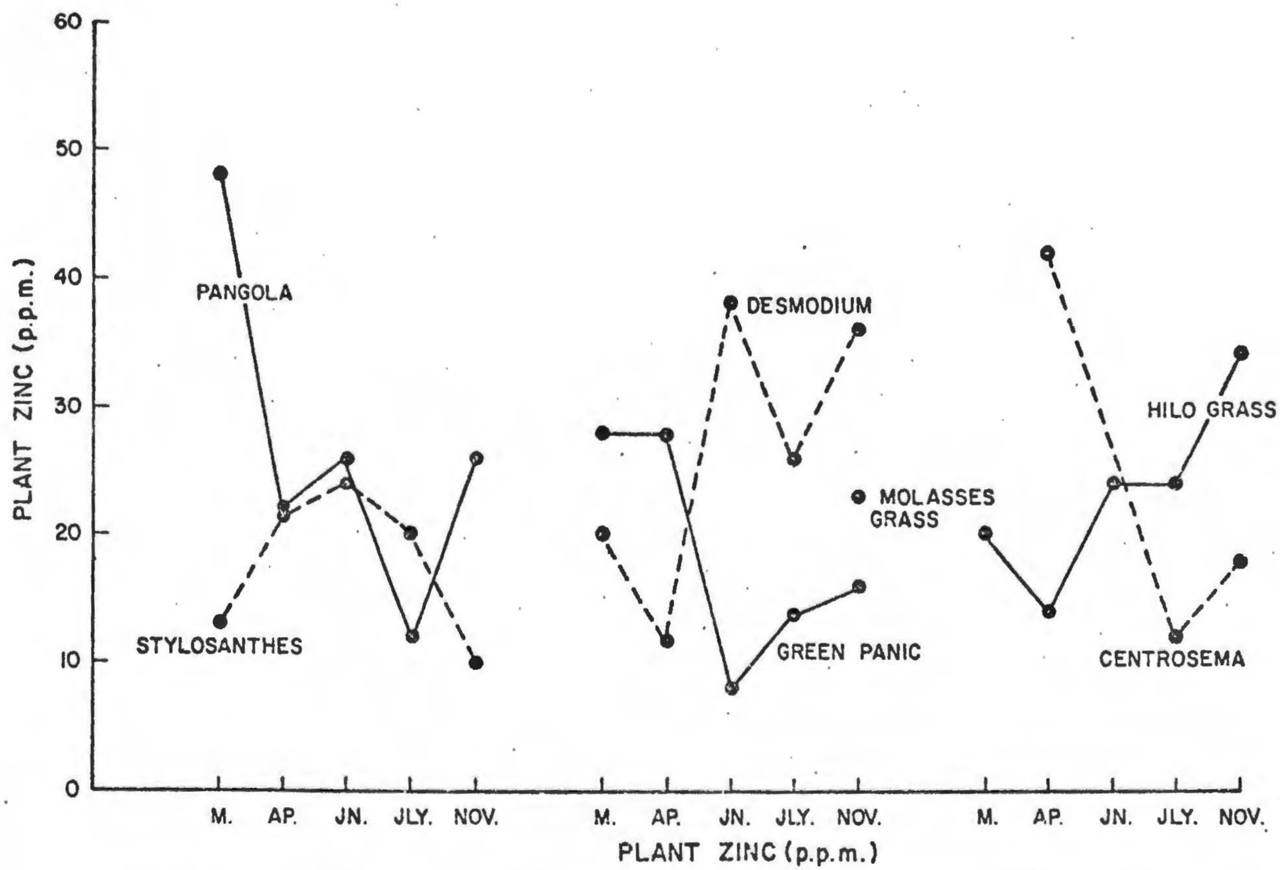
APPENDIX FIGURE 9. VARIATION IN PLANT CALCIUM IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



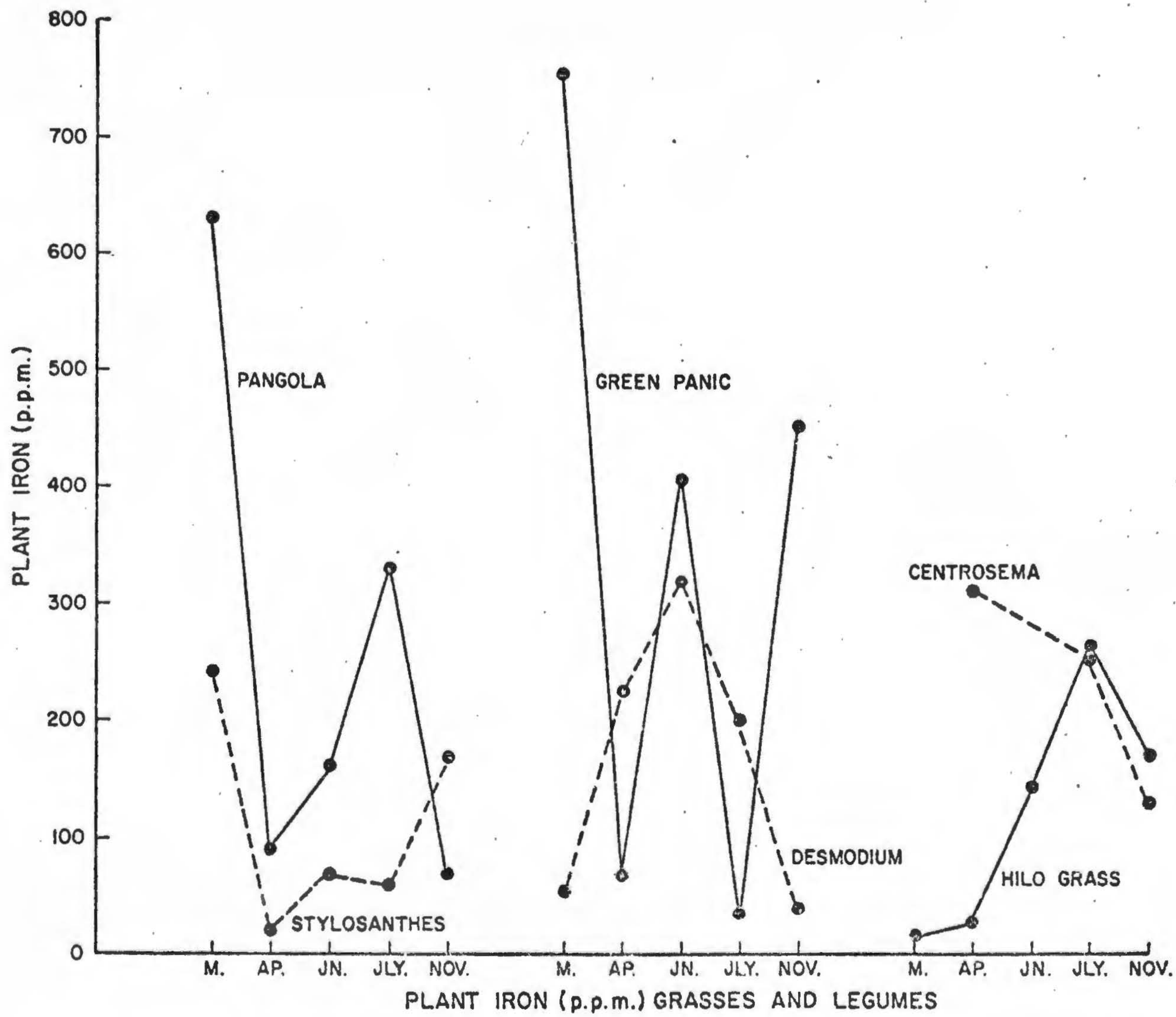
APPENDIX FIGURE 10. VARIATION IN PLANT MAGNESIUM IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



APPENDIX FIGURE 11. VARIATION IN PLANT MANGANESE IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



APPENDIX FIGURE 12. VARIATION IN PLANT ZINC IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.



APPENDIX FIGURE 13. VARIATION IN PLANT IRON IN FORAGE GRASSES AND LEGUMES AT DIFFERENT SAMPLING DATES.

APPENDIX V

CORRELATION MATRIX FOR ENVIRONMENTAL FACTORS

APPENDIX TABLE 8. CORRELATION COEFFICIENTS (r) OF ENVIRONMENTAL FACTORS df = 38, 4 = 0.310 (5%), r - 0.405 (1%)

		Soil H2O	pH H2O	pH KCl	pH K2SO4	Soil N	Soil P	Soil K	Soil Ca	Soil Mg	Soil Mn	Soil SiO_2	Vert. slope	Hor. slope	Soil depth
	Soil H2O														
	pH H2O	.662													
	pH KCl	.515	.193												
	pH K2SO4	.359	.040	.832											
	Soil N	.159	.443	.553	.571										
	Soil P	.165	.269	.087	.073	.403									
	Soil K	.049	.215	.113	.204	.191	.147								
	Soil Ca	.264	.034	.135	.235	.070	.175	.195							
	Soil Mg	.617	.313	.257	.326	.129	.035	.053	.398						
	Soil Mn	.434	.506	.032	.045	.461	.339	.134	.659	.598					
	Soil SiO_2	.014	.025	.156	.029	.099	.064	.032	.166	.069	.082				
	Vert. slope	.027	.246	.057	.088	.144	.249	.097	.028	.006	.135	.078			
	Hor. slope	.111	.331	.039	.223	.102	.011	.328	.176	.101	.114	.033	.062		
	Soil depth	.174	.252	.249	.033	.531	.264	.103	.207	.137	.129	.163	.279	.097	
Feb. - April	am Temp.	.479	.652	.073	.020	.468	.393	.033	.173	.449	.574	.225	.543	.031	.504
Feb. - April	pm Temp.	.646	.528	.001	.010	.547	.253	.103	.447	.653	.655	.040	.202	.050	.459
Feb. - April	max. Temp.	.544	.673	.015	.015	.499	.335	.061	.212	.473	.607	.252	.530	.061	.495
Feb. - April	min. Temp.	.459	.298	.009	.046	.419	.003	.030	.446	.447	.423	.075	.339	.036	.273
May - July	am Temp.	.503	.654	.012	.007	.516	.413	.096	.221	.454	.603	.209	.461	.023	.543
May - July	pm Temp.	.316	.593	.015	.053	.387	.395	.057	.029	.252	.426	.251	.458	.163	.411
May - July	max. Temp.	.572	.657	.012	.027	.575	.397	.061	.339	.531	.654	.175	.301	.030	.579
May - July	min. Temp.	.459	.629	.012	.048	.453	.338	.104	.199	.435	.591	.126	.405	.089	.497
Aug. - Oct.	am Temp.	.476	.569	.037	.033	.420	.353	.137	.250	.513	.562	.126	.504	.093	.485
Aug. - Oct.	pm Temp.	.405	.604	.012	.067	.368	.309	.097	.037	.361	.481	.207	.572	.097	.359
Aug. - Oct.	max. Temp.	.383	.619	.017	.048	.427	.359	.059	.029	.303	.492	.260	.489	.169	.437
Aug. - Oct.	min. Temp.	.059	.193	.017	.045	.012	.215	.039	.207	.073	.056	.254	.592	.018	.197
Nov. - Jan.	am Temp.	.660	.663	.009	.032	.602	.323	.047	.337	.595	.683	.194	.298	.022	.523
Nov. - Jan.	pm Temp.	.121	.424	.017	.056	.205	.321	.029	.163	.059	.229	.283	.534	.136	.291
Nov. - Jan.	max. Temp.	.222	.506	.017	.059	.272	.339	.052	.099	.163	.330	.257	.558	.132	.340
Nov. - Jan.	min. Temp.	.202	.493	.014	.077	.274	.336	.059	.113	.153	.329	.161	.398	.203	.295

		Feb. - April				May - July				Aug. - Oct.				Nov. - Jan.		
		am Temp.	pm Temp.	max. Temp.	min. Temp.	am Temp.	pm Temp.	max. Temp.	min. Temp.	am Temp.	pm Temp.	max. Temp.	min. Temp.	am Temp.	pm Temp.	max. Temp.
Feb. - April	am Temp.															
Feb. - April	pm Temp.	.603														
Feb. - April	max. Temp.	.924	.700													
Feb. - April	min. Temp.	.064	.608	.114												
May - July	am Temp.	.931	.742	.878	.199											
May - July	pm Temp.	.912	.396	.789	.184	.879										
May - July	max. Temp.	.873	.806	.799	.479	.934	.721									
May - July	min. Temp.	.918	.627	.802	.161	.926	.873	.883								
Aug. - Oct.	am Temp.	.929	.762	.796	.210	.949	.753	.866	.859							
Aug. - Oct.	pm Temp.	.907	.539	.903	.181	.826	.876	.621	.765	.774						
Aug. - Oct.	max. Temp.	.920	.447	.884	.147	.372	.971	.728	.865	.725	.917					
Aug. - Oct.	min. Temp.	.614	.119	.515	.671	.525	.764	.289	.567	.444	.653	.740				
Nov. - Jan.	am Temp.	.779	.906	.876	.554	.802	.536	.864	.678	.739	.653	.638	.835			
Nov. - Jan.	pm Temp.	.781	.039	.684	.495	.704	.934	.483	.722	.576	.817	.911	.930	.306		
Nov. - Jan.	max. Temp.	.862	.247	.779	.392	.783	.964	.581	.733	.676	.994	.955	.882	.432	.900	
Nov. - Jan.	min. Temp.	.795	.229	.629	.314	.749	.960	.565	.809	.529	.805	.904	.765	.323	.923	.934