

Lianas and Environmental Factors in the Mo Singto Biodiversity Research Plot, Khao Yai National Park, Thailand

KANOK LERTPANICH ^{1*} AND WARREN Y. BROCKELMAN ^{1,2}

¹ *Department of Biology, Faculty of Science, Mahidol University, Rajdhevee, Bangkok 10400, THAILAND*

² *Center for Conservation Biology, Institute of Science and Technology for Research and Development, Mahidol University, Salaya, Nakhon Pathom 73170, THAILAND*

ABSTRACT.—This study investigated the abundance and species diversity of lianas (woody climbing plants) on the Mo Singto Long Term Biodiversity Research plot, Khao Yai National Park, in relation to environmental factors. A stratified sample of 40 20×20-m quadrats on the 30-ha plot was taken in 4 kinds of habitats: hilltop, slope, valley, and secondary forest. There were no significant differences in either abundance or species diversity among habitat types, in spite of some significant differences in soil texture and available cations between secondary and primary forest sites. Multiple regressions of abundance and species richness on a variety of topographic and vegetation measures and soil variables failed to find any significant effects on the lianas. While individual species of lianas may be limited by physical factors and tree distribution, the community as a whole is robust to such variation.

KEY WORDS: lianas; diversity; density; environmental factors

INTRODUCTION

Climbing plants may be classified into 4 fundamental climbing strategies (Gentry, 1985): lianas, which are woody, relatively thick-stemmed climbers; vines, which are thin-stemmed succulent or sub-woody climbers usually referred to as herbaceous vines; hemi-epiphytes or stranglers, which begin life as epiphytic seedlings with roots later reaching the ground; and also woody hemi-epiphytes which begin their life as terrestrial climbers and later send out adventitious root systems possibly losing contact with the ground. The last group

contains herbaceous species that climb appressed to tree trunks and limbs, usually via adventitious roots. Most species included in this study are lianas; herbaceous species, monocotyledonous rattans, and stranglers are excluded from the analysis.

In both Old and New World tropical forests, lianas contribute a substantial portion of the stems and the leaf biomass, and usually close to half of trees have lianas in their crowns (Putz, 1984a; Gentry, 1991). Lianas make up about 1/3 of the canopy foliage in Thai forests, as estimated from the percentage of leaf litter contributed by lianas (Ogawa et al., 1965). Lianas are therefore important in terms of both forest structure and productivity, and yet relatively little research has so far been devoted to their distribution and ecology. This study evaluates for the first time the ecological

* Corresponding author.

Tel: (662) 4391035

Fax: (662) 4391035

E-mail: lertpanich@yahoo.com

distribution of liana species in a Thai forest, located in the Mo Singto long-term biodiversity research plot, Khao Yai National Park, central Thailand. The study is preliminary and will be expanded when the full database of tree and liana stems is available for the Mo Singto plot. First, some growth and reproductive characteristics of lianas will be briefly described.

Lianas can reproduce by either seeds or by the vegetative growth of stems or shoots (Penalosa, 1984, Caballé, 1994). Successful climbing shoots may lean on the ground and produce an additional adventitious root system, ramify, and finally branch out and become new individuals or ramets. Longitudinal growth of the stem occurs after fissuring in many liana species (Caballé, 1994), in which the plant has a cleavage in the shoot structure. Other methods of vegetative reproduction also occur, such as production of stolons, flagella, basal shoot sprouts, and lignotuber formation (Prósperi et al., 2001). Expansion in secondary areas or gaps tends to be by vegetative propagation rather than by seed systems (Penalosa, 1984; Putz, 1984a). Seed reproduction occurs mainly during the dry season (Putz and Windsor, 1987). As in the case of trees, seeds are dispersed either by wind or by animals. Gentry (1982, 1983) states that wind dispersal tends to occur more in the dry forest than in wet forests. In wet forests seed dispersal occurs mostly by mammals and birds. After seed germination, the young liana requires high atmospheric humidity (Jacob, 1976).

Some studies have reported correlations between liana abundance and both physical and biological limiting factors. Limiting factors may affect liana abundance in various ways. Gentry (1991) reported that in the Neotropics, liana abundance increases with seasonality of rainfall, although it is not clear what the proximate effects are. The liana growth form demands high light intensity (Putz, 1984a); hence disturbed forests seem to provide more favorable conditions for lianas than undisturbed forests (Richards, 1996; Gerwing and Farias, 2000; Laurence et al., 2001). Tree-fall gaps

and forest margins also have high liana abundance and light intensity (Fox, 1968; Williams-Linerra, 1990). There are also altitudinal gradients in liana abundance. Putz and Chai (1987) reported that lianas in Lambir National Park, Sarawak, Malaysia, were twice as abundant in the valleys as on hilltops. The same result has been reported in a South African forest (Balfour and Bond, 1993). The altitudinal gradient was closely associated with the level of base nutrients in the soil except for nitrogen concentration (Balfour and Bond, 1993). However, altitude is confounded with a variety of physical factors. Soil nutrients per se are probably less important in limiting liana abundance than biotic factors such as the availability of climbing supports (Balfour and Bond, 1993). Proctor et al. (1983) found that lianas in Gunung National Park, Sarawak, more frequently occur in alluvial forests, where nutrients come with the floods, than in higher altitude forest, but soil fertility was not positively correlated with liana abundance. Gentry (1991) found that liana density in 32 neotropical forests varied with soil fertility; a similar result has been found in Mexican forest (Ibarra-Manriquez and Matinez-Ramos, 2002).

An important requirement for liana maturity is mechanical support; hence host plants are also a limiting factor. Lianas are not randomly distributed on their potential host trees (Hergaty, 1991). Trees with long branch-free boles and deep-crowns are not suitable for lianas to reach the canopy (Putz, 1984b). Lianas on Barro Colorado Island, Panama, more frequently climb rough-barked trees compared with smooth-barked trees (Putz, 1982). Regarding host diameter, lianas are more abundant on trees less than 70 cm dbh; trees larger than that are usually without lianas (Clark and Clark, 1990). The host tree preferences of lianas on the Mo Singto plot will be analyzed in a future paper.

In this paper we attempt to test whether liana diversity (species richness) and density in a subsample of quadrats in the Mo Singto plot are correlated with a variety of physical and biological variables.

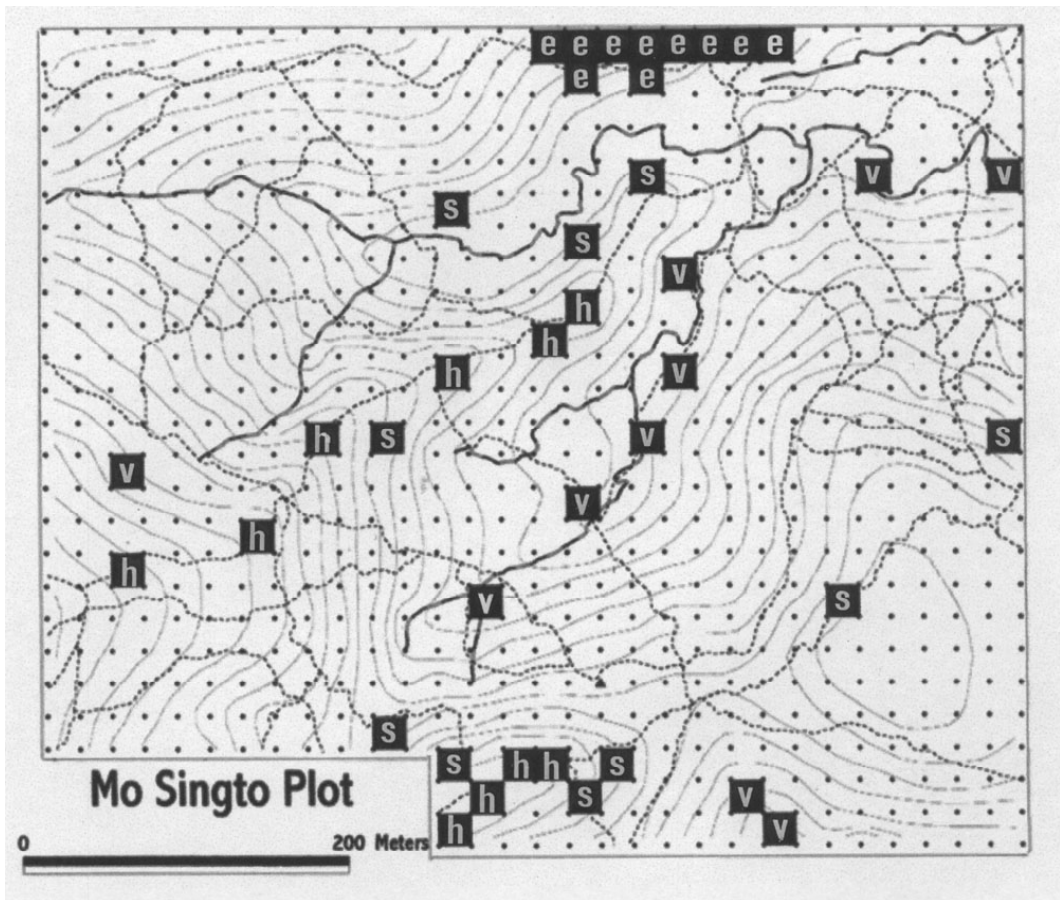


Figure 1. The Mo Singto Biodiversity Research Plot showing the sample quadrats (h = Hilltop, s = Slope, v = Valley and e = Secondary forest habitat)

MATERIALS AND METHODS

Study site

The 30-ha Mo Singto permanent biodiversity research plot lies in Khao Yai National Park which covers 2172 km² at 14° 10–35′ N and 101° 05–50′ E. The main mountain plateau is 600–1000 m and its top covers 834 km². The research plot lies 0.5–1.0 km west of park headquarters and lies at 825–890 m altitude. The southwest monsoon from the Indian Ocean influences the annual precipitation of 2000–3000 mm, which falls mostly during May to October. The dry season begins in November and ends in April. Average annual temperature is 23°C (range 5°C – 30°C)

and average humidity is 86% (Royal Forest Department data). The park provides habitat for 25 large mammal species, at least 40 small mammal species, and 318 species of birds (Graham, 1991; Srikosamatara and Hensel, 1996). The vegetation on the plateau above about 500 m altitude, and on the study site, is seasonal evergreen or semi-evergreen, with a canopy mostly 20–30 m tall with emergent trees reaching 40–55 m (Brockelman, 1998).

The Mo Singto plot is 500 × 600 m in size and has been surveyed into 20 × 20 m quadrats with a theodolite, each corner marked with an 180 plastic stake. The plot contains several hills, ridges and valleys and spans about 90 m in elevation (Fig. 1).

Liana data collection

The analysis was confined to 40 quadrats selected from 4 different "habitat" types. The plot was divided into hilltop, slope, and valley habitats and 10 quadrats were randomly selected from each type. In addition, 10 quadrats were placed in a strip of secondary forest at the north edge of the plot. This forest, now about 20 years old, is regenerating from former grassland resulting from old agricultural areas created more than 40 years ago before the park was gazetted.

All lianas ≥ 1 cm in diameter 1.3 m above the ground that were rooted in the ground and climbing host trees were censused in the study. Those with multiple branches (ramets) below 1.3 m in height were noted down as single individuals, or genets. They were included within a quadrat if the main host tree and rooted main stem were within the quadrat boundary. The specimens were compared with the reference collection at the Center for Conservation Biology, ISTRD (now located in the National Center for Genetic Engineering and Biotechnology (BIOTEC), Science Park, Pathum Thani). Voucher specimens of nearly all lianas on the Mo Singto plot have been deposited in the Royal Forest Department (BKF), Chiang Mai University Biology Herbarium (CMU), the Arnold Arboretum, Harvard University (A), and the National Herbarium of the Netherlands in Leiden (L). A total of about 120 species of lianas have been found on the Mo Singto Plot, of which 92 occurred in the 40 quadrats included here.

Soil sampling

Six soil cores 0–20 cm deep were taken in each of the 40 sample quadrats and pooled. The samples were oven-dried and analyzed for texture (percentage of sand, silt and clay), pH, organic matter, phosphorus, potassium, and cation exchange capacity. Soil analysis was based on Soil Survey Staff Methods (1975), and was done at the soil science laboratory, Department of Agricultural Technology, King Mongkut Institute of Technology Ladkrabang, Bangkok.

Trees and canopy

The number of trees per quadrat < 70 cm and the number ≥ 70 cm in diameter at breast height (dbh) were used as independent variables, as well as canopy height and "distinctiveness." Canopy height is the mean of 9 measures of the highest canopy parts, over the 9 points in or on the quadrat boundary spaced 10 m apart. These were measured with an optical rangefinder (Ranging Rangefinder, Forestry Suppliers, Jackson, MS, USA) (Brockelman, 1998). "Distinctiveness" was taken as the coefficient of variation (SD/mean) of these 9 measures, and was a measure of canopy unevenness or roughness. Both measures should have some relation with light penetration into the understory of the forest and therefore potentially affect liana growth.

Data analysis

The total number of rooted stems (genets) and the number of species per sample quadrat were used as dependent variables for two types of analysis. First, ANOVA was used to test for differences in abundance and diversity among the 4 habitat types. Second, multiple regression was used to describe the relation between liana density and diversity in all 40 samples and the environmental factors. The environmental factors included as independent variables were altitude above sea level, terrain slope, canopy height, canopy unevenness or distinctiveness, number of trees < 70 cm in diameter at breast height (dbh), number of trees ≥ 70 cm in dbh, and the following soil characters: pH, percentages of sand, loam and clay, percentage organic matter, and concentrations of phosphorus, potassium. The multiple regression analysis yielded r^2 (coefficient of determination), r (total correlation with independent variables), standard error of the estimate, and the Durbin-Watson value. The Durbin-Watson value indicates independence of the standard error. The regression tests the relation between the dependent variable and the independent variables one by one, and discards them if no significant relation is found. The analysis also provides beta (standardized coefficient) values,

in which a higher value indicates that an independent variable is more related with dependent variables than others.

RESULTS

Habitat differences

The ANOVA analysis revealed no significant differences in either liana abundance or diversity among the 4 types of habitats (abundance: $F = 0.78$, $P > 0.10$; diversity: $F = 1.64$; $P > 0.10$). Table 1 lists the liana abundance, diversity, and other variables for the 40 sample quadrats. Density was highest in the hilltop habitat at 17.1 stems on average, and lowest in the slope habitat with 13.2 stems. Species richness averaged highest in the hilltop habitat (31.1 species) and lowest in the slope habitat (23.3 species). Abundance and species richness were correlated and in the same rank order among habitats (Table 1), so it appears that species richness increases with sample size and is not independently affected by environmental variables in the plot.

There are significant differences in some soil variables between habitats. Table 2 shows selected variables that varied significantly

among habitats; phosphorus, potassium and organic matter did not vary significantly and are not shown. The secondary forest had the most distinct soil type, with the highest values for clay fraction, pH, and cation exchange capacity. In spite of this, the density and diversity of lianas had intermediate values in this habitat.

Liana density and environmental factors

The regression of liana density on the environmental factors had a coefficient of determination (r^2) of 0.31, meaning that environmental factors explained only 31% of the variation in liana density. The stepwise tests for each variable also found no significant relation between density and any of the variables (Table 3). The highest coefficient was for number of trees < 70 cm dbh. The value for the number of host trees < 70 cm dbh had the strongest positive relation with liana density but this relation was not strong or significant.

Liana diversity and environmental factors

The regression between liana diversity and environmental factors gave results similar to those with liana density (Table 4). The environmental factors explained only 29% of

Table 1. Mean abundance, diversity, and values for some soil variables for the four "habitats", with significance levels for differences among groups (ANOVA).

| | Area | | | | p-level |
|---|----------------|---------------|-----------------|-------------------|---------|
| | Valley habitat | Slope habitat | Hilltop habitat | 2° Forest habitat | |
| Density (per 20x20 m ²) | 26.3 | 23.3 | 31.1 | 28.6 | 0.51 |
| No. species (per 20x20 m ²) | 14.5 | 13.2 | 17.1 | 16.7 | 0.20 |
| Sand, % | 33.0 | 25.7 | 25.6 | 22.5 | 0.07 |
| Silt, % | 42.5 | 45.6 | 46.7 | 41.8 | 0.42 |
| Clay, % | 24.2 | 28.7 | 27.2 | 35.7 | 0.005 |
| PH | 5.1 | 4.5 | 4.4 | 5.2 | <0.001 |
| C.E.C. (cmol kg ⁻¹) | 13.0 | 14.6 | 14.9 | 17.1 | 0.007 |
| Total number of species | 61 | 57 | 61 | 67 | |

Table 2. The density and diversity of ≥ 1 cm dbh liana per sampling plots and their environmental factors data

| Plot name | Liana density | Liana diversity | Forest height (m) | Canopy distinctiveness | Sand fraction (%) | Silt fraction (%) | Clay fraction (%) | pH | Organic matter (g kg ⁻¹) | C.E.C. (cmol kg ⁻¹) | Trees < 70 cm dbh (stems) |
|-----------|---------------|-----------------|-------------------|------------------------|-------------------|-------------------|-------------------|------|--------------------------------------|---------------------------------|---------------------------|
| 3801v | 29 | 12 | 21.5 | 1.11 | 30.54 | 47.5 | 21.96 | 5.63 | 6.8 | 12.36 | 17 |
| 3702v | 6 | 5 | 29 | 1.16 | 28.69 | 46.14 | 25.17 | 5.42 | 5.72 | 13.54 | 8 |
| 2908v | 14 | 11 | 19.5 | 2.34 | 21.77 | 45.19 | 33.04 | 5.93 | 5.32 | 16.72 | 10 |
| 3211v | 21 | 14 | 29.4 | 1.8 | 42.5 | 35 | 22.5 | 4.9 | 3.41 | 11.51 | 18 |
| 3413v | 30 | 17 | 33.4 | 1.39 | 32.5 | 47.5 | 20 | 5.38 | 8.15 | 10.45 | 18 |
| 1812v | 35 | 19 | 22.3 | 1.59 | 23.64 | 48.68 | 24.89 | 4.69 | 5.75 | 14.48 | 21 |
| 3515v | 29 | 13 | 23.8 | 1.8 | 26.43 | 48.68 | 24.89 | 4.74 | 8.4 | 13.17 | 14 |
| 3518v | 22 | 16 | 22.5 | 1.27 | 47.31 | 33.98 | 18.71 | 5 | 7.3 | 11.15 | 21 |
| 4121v | 21 | 16 | 27.6 | 1.02 | 32.3 | 41.91 | 25.79 | 4.74 | 4.35 | 13.43 | 20 |
| 4521v | 56 | 22 | 15.7 | 2.41 | 44.1 | 30.5 | 25.4 | 5.02 | 5.9 | 13.64 | 14 |
| 2613s | 27 | 16 | 15.3 | 2.51 | 27.7 | 43.9 | 28.4 | 4.73 | 6.69 | 15.12 | 22 |
| 4008s | 28 | 15 | 21.6 | 2.01 | 23.64 | 50.36 | 26 | 4.6 | 5.13 | 14.46 | 21 |
| 3421s | 11 | 9 | 22.3 | 1.07 | 42.5 | 35 | 22.5 | 4.1 | 9.49 | 11.59 | 37 |
| 4513s | 17 | 12 | 12.9 | 2.31 | 25.56 | 58.21 | 16.23 | 4.54 | 5.95 | 10.37 | 19 |
| 2820s | 45 | 19 | 13.6 | 1.98 | 22.5 | 45 | 32.5 | 5.23 | 6.29 | 16.38 | 21 |
| 2604s | 10 | 8 | 19.2 | 1.85 | 42.5 | 40 | 17.5 | 4.5 | 6.46 | 10.76 | 12 |
| 3303s | 16 | 11 | 9.2 | 1.89 | 25 | 36.5 | 38.5 | 4.79 | 5.41 | 17.54 | 14 |
| 2803s | 11 | 8 | 15 | 1.77 | 22.66 | 43.83 | 33.51 | 4.28 | 9.66 | 16.29 | 18 |
| 3219s | 37 | 15 | 9.2 | 1.35 | 13.2 | 54.07 | 32.73 | 4.04 | 11.05 | 15.87 | 38 |
| 3202s | 31 | 19 | 14 | 2.29 | 12.21 | 49.06 | 38.73 | 4.56 | 6.17 | 17.32 | 21 |
| 3116h | 62 | 29 | 13.6 | 1.77 | 28.1 | 43 | 28.9 | 4.48 | 6.93 | 15.46 | 26 |
| 3217h | 20 | 13 | 13.9 | 0.5 | 29.32 | 38.5 | 32.18 | 4.17 | 10.39 | 17.14 | 40 |
| 2801h | 23 | 10 | 16.9 | 2.25 | 31.02 | 55.28 | 13.7 | 4.34 | 9.25 | 9.84 | 32 |
| 2413h | 32 | 19 | 19.2 | 1.98 | 20.64 | 48 | 31.36 | 4.52 | 7.31 | 16.97 | 25 |
| 3003h | 19 | 15 | 9.2 | 2.25 | 13.15 | 44.4 | 42.45 | 4.25 | 11.12 | 18.47 | 15 |
| 3103h | 30 | 18 | 12 | 2.37 | 20.3 | 44.2 | 35.5 | 4.5 | 7.01 | 17.65 | 27 |
| 2815h | 41 | 20 | 8.9 | 2.46 | 29.36 | 54.15 | 16.49 | 4.34 | 11.36 | 10.41 | 33 |
| 1809h | 22 | 14 | 23.1 | 1.56 | 42 | 31.15 | 26.85 | 4.66 | 5.97 | 14.35 | 24 |
| 2210h | 28 | 15 | 10.6 | 1.11 | 14.33 | 51.04 | 34.63 | 4.31 | 8.09 | 18.14 | 27 |
| 2902h | 34 | 18 | 11.7 | 1.92 | 27.89 | 56.96 | 15.15 | 4.45 | 6.68 | 10.35 | 27 |
| 3825e | 38 | 22 | 12.5 | 1.32 | 10.74 | 55.16 | 34.1 | 5.36 | 7.84 | 16.38 | 52 |
| 3725e | 27 | 12 | 8.5 | 2.46 | 17.5 | 52.5 | 30 | 5.25 | 6.93 | 15.43 | 24 |
| 3625e | 31 | 17 | 13.8 | 1.44 | 33.02 | 30.92 | 36.06 | 5.22 | 6.97 | 17.15 | 28 |
| 3525e | 16 | 12 | 8.6 | 0.99 | 30.47 | 33.42 | 36.11 | 5.08 | 6.61 | 17.91 | 31 |
| 3425e | 35 | 18 | 9.3 | 1.16 | 25.58 | 37.77 | 36.65 | 5.05 | 5.98 | 17.49 | 38 |
| 3325e | 20 | 12 | 8.8 | 1.51 | 15.23 | 44.87 | 39.9 | 5.2 | 5.87 | 18.52 | 27 |
| 3225e | 28 | 16 | 10.9 | 1.06 | 27.67 | 40.69 | 31.64 | 5.11 | 8.49 | 15.48 | 25 |
| 3125e | 18 | 15 | 15.5 | 1.23 | 25.32 | 39.15 | 35.53 | 5.12 | 7.17 | 16.74 | 32 |
| 3224e | 36 | 22 | 9.4 | 1.39 | 23.5 | 39 | 37.5 | 4.88 | 8.75 | 17.13 | 27 |
| 3424e | 37 | 21 | 10.8 | 1.77 | 15.64 | 44.99 | 39.37 | 5.25 | 6.79 | 18.68 | 22 |

h = Hilltop, s = Slope, v = Valley and e = Secondary forest habitat

Table 3. Coefficients table of regression between density and environmental factors

| | Unstandardized Coefficients | | Standardized Coefficients | t | Sig. |
|------------------------|-----------------------------|------------|---------------------------|--------|------|
| | B | Std. Error | Beta | | |
| (Constant) | 227.809 | 203.275 | | 1.121 | .273 |
| forest height | -.074 | .196 | -.105 | -.375 | .710 |
| elevation | -.019 | .038 | -.114 | -.495 | .625 |
| slope | -.061 | .157 | -.081 | -.387 | .702 |
| sand | -2.026 | 2.008 | -4.047 | -1.009 | .323 |
| silt | -2.114 | 2.017 | -3.410 | -1.048 | .305 |
| clay | -2.062 | 1.927 | -3.425 | -1.070 | .295 |
| pH | -.692 | 3.006 | -.066 | -.230 | .820 |
| organic | -.367 | .727 | -.144 | -.505 | .618 |
| phosphorus | .499 | .705 | .180 | .707 | .486 |
| potassium | .012 | .027 | .108 | .428 | .673 |
| cec | .283 | 1.580 | .168 | .179 | .859 |
| canopy distinctiveness | 2.360 | 2.345 | .261 | 1.006 | .324 |
| trees < 70 cmdbh | .226 | .134 | .436 | 1.686 | .104 |
| trees > 70 cmdbh | -1.085 | 1.813 | -.166 | -.598 | .555 |

Table 4. Coefficients table of regression between diversity and environmental factors

| | Unstandardized Coefficients | | Standardized Coefficients | t | Sig. |
|------------------------|-----------------------------|------------|---------------------------|--------|------|
| | B | Std. Error | Beta | | |
| (Constant) | 506.706 | 517.602 | | .979 | .337 |
| forest height | -.328 | .498 | -.185 | -.657 | .517 |
| elevation | -.060 | .096 | -.145 | -.628 | .536 |
| slope | .169 | .399 | .089 | .423 | .676 |
| sand | -4.662 | 5.113 | -3.695 | -.912 | .371 |
| silt | -4.799 | 5.135 | -3.072 | -.935 | .359 |
| clay | -5.800 | 4.908 | -3.822 | -1.182 | .248 |
| pH | .223 | 7.655 | .008 | .029 | .977 |
| organic | -.170 | 1.851 | -.026 | -.092 | .928 |
| phosphorus | 1.270 | 1.796 | .181 | .707 | .486 |
| potassium | .029 | .069 | .107 | .418 | .679 |
| cec | 3.117 | 4.024 | .732 | .775 | .446 |
| canopy distinctiveness | 5.377 | 5.971 | .236 | .901 | .376 |
| trees < 70 cmdbh | .396 | .341 | .303 | 1.160 | .257 |
| trees > 70 cmdbh | -1.875 | 4.616 | -.114 | -.406 | .688 |

the variation in liana diversity. The standard error was highly independent, and the Durbin-Watson value was 2.1. The overall relation between liana diversity and environmental factors was non-significant ($P = 0.71$), and no individual factors showed any significant coefficient. Cation exchange capacity showed the strongest relation with liana diversity (beta coefficient = 0.73), but it was not significant.

DISCUSSION

This preliminary analysis has revealed no significant differences in the overall abundance and diversity of lianas with respect to the habitat variation within the Mo Singto plot. More surprisingly, there was no gross difference in abundance or diversity between mature and secondary forest areas. Since lianas are pioneer colonizing species, we should expect them to be common in regenerating forest as well as in gaps in mature forest (Dewalt et al., 2000). The same species that occur in mature forest were found in the secondary forest, though not in the same relative abundance, so the secondary forest in a sense is not a separate community. Moreover, many of the potentially important animal dispersers (gibbons, pig-tailed monkeys, frugivorous birds) use both types of forest in the plot. The soil shows some differences between primary and secondary forest, such as more clay and exchangeable cations in the latter, but it all comes from the same parent material and has similar chemical characteristics. Gentry (1991) has concluded that liana diversity and abundance do not vary greatly between forest sites within the same continents, so we should not expect much variation between nearby sites within the same climate type.

The multiple regressions between liana diversity and density and a variety of environmental factors including topography, soil texture and nutrients and some gross vegetation characters did not reveal any significant effect by even a single

environmental factor. Many of the liana niches are possibly wider than the differences in environmental factors among sites on the plot. On the other hand, it is possible that the species in different sites replace one another in a manner so as to maintain the same overall abundance and diversity over the plot.

The number of trees < 70 cm dbh had highest effect on density and the second highest on diversity. This result suggests that the number of potential host trees is an important factor limiting liana density, or that younger regenerating forest (which has more stems < 70 cm in dbh) within the forest has the highest abundance of lianas. Diversity of lianas was most strongly affected by exchangeable cation concentration, which is an indication of overall soil fertility. No particular nutrient tested showed any greater effect on diversity.

Altitudinal variation on the plot is not sufficient to have any effect on liana abundance or diversity. Altitude does, however, affect the abundance of certain trees on the site (unpublished observations), and there are measurable differences in the height and canopy structure of the forest overall between hilltop and valley sites (Brockelman, 1998), with more protected valley and hill slope sites having higher and more complete canopy than hilltop areas. We have also noted (unpublished) that particular species of lianas are more abundant in some parts of the plot than others, and that some colonize new tree-fall gaps more aggressively than others.

In summary, we conclude that the overall density and diversity of lianas on the Mo Singto plot are not determined or affected much by environmental factors, although individual species might be. The analysis needs to be repeated with the entire liana database for the plot to detect more subtle effects, and it needs to be carried out for all individual species. The wide dispersion of most species apparently overwhelms such effects. If the physical environment does not determine species distributions directly, it is still possible that host tree preferences have limiting effects at the species or community level. Alternatively, the

species may not be partitioning the community according to physical gradients; the distributions of the species may be the result of chance, and may resemble a “lottery” which determines (or fails to determine) the composition of the community (Chesson and Warner, 1981; Hubbell, 2001; Hubbell and Foster, 1986). Much more analysis and long term observations on dispersal, recruitment, and species composition will be required to distinguish these alternatives.

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APPENDIX

Species list of ≥ 1 cm dbh lianas (genets) in survey of 40 sampling plots.

Acacia megaladena Desv., *Aganosma cymosa* (Roxb.) G. Don, *Aganosma schlechteriana* H. Lev., *Ampelopsis cantoniensis* Pl., *Anodendron affine* (Hook. & Arn.) Druce, *Anodendron paniculatum* A. DC., *Argyrea obtecta* (Choisy) Cl., *Argyria* sp., *Berchemia floribunda* Wall. ex Brongn., *Caelospermum truncatum* (Wall.) Baill. ex K., *Caesalpinia crista* L., *Callerya cinerea* (Bth.) Schot, *Celastrus approximata* Craib, *Celastrus monospermus* Roxb., *Combretum punctatum* Bl., *Combretum* sp., *Coptoselta flavescens* Korth., *Cosmostigma racemosa* (Roxb.) Wight, *Cyathostemma micranthum* (A. DC.) Sincl., *Dalbergia foliacea* Wall., *Dalbergia horrida* (Denn.) Mebb., *Desmos dumosus* (Roxb.) Saff. Var. glabrior, *Diplectria barbata* (Bl.) Franken & Roos, *Diploclisia glaucescens* (Bl.) Diels, *Elaeagnus conferta* Roxb., *Embelia sessiliflora* Kruz., *Epigynum griffithianum* Wight, *Erycibe elliptilimba* Merr. & Chun, *Erycibe subspicata* Wall ex G. Don, *Fagraea ceilanica* Thunb., *Ficus punctata* Thunb., *Ficus sagittata* Vahl., *Ficus villosa* Bl., *Ficus* sp., *Fissistigma parviflorum* (Scheff.) Merr., *Gnetum macrostachyum* Hk. f., *Gnetum montanum* Markgraf, *Gouania leptostachya* DC., *Grewia laevigata* Vahl, *Grewia* sp., *Gymnema inodorum* (Lour.) Decne., *Gymnema* sp., *Gymnema thorelii* Cost., *Hypserpa nitida* Miers, *Illigera pierrii* Gagnep., *Jasminum lanceolaria* Roxb., *Linostoma pauciflorum* Bl., *Melodinus cambodiensis* Pierre ex Spire, *Morinda cochinchinensis* DC., *Morinda umbellata* L., *Morinda villosa* Hk. f., *Mucuna macrocarpa* Wall., *Neuropeltis racemosa* Wall., *Oxyceros longiflora* (Lmk.) Yama., *Parameria laevigata* (Juss.) Mold., *Paramignya scandens* (Griff.) Craib., *Phyllanthus reticulatus* Poir., *Piper retrofractum* Vahl, *Piper ribesoides* Wall., *Poikilospermum suaveolens* (Lour.) Merr., *Pottsia laxiflora* (Bl.) O. K., *Premna flavescens* Ham. ex Cl., *Pterolobium microphyllum* Miq., *Reissantia indica* (Willd.) Halle, *Rhamnus nipalensis* (Wall.) Laws., *Rourea minor* (Gaertn.) Leenh., *Roureopsis stenopetala* (Griff.) Schell., *Sabia limoniacea* Wall. ex Hk. f. & Th., *Salacia chinensis* L., *Schefflera elliptica* (Bl.) Harms, *Spatholobus harmandii* Gagnep., *Sphenodesme pentandra* Jack, *Strophanthus caudatus* (L.) Kurz, *Tetracera indica* (Houtt. ex Christm. & Panz.) Merr., *Tetrastigma harmandii*

Pl., *Tetrastigma laoticum* Gagnep., *Toddalia asiatica* (L.) Lmk., *Trachelospermum asiaticum* (Sieb. & Zucc.) Nakai, *Uncaria laevigata* Wall. ex G. Don, *Uncaria laevigata* Wall. ex G. Don, *Uncaria macrophylla* Wall., *Uncaria scandens* (Sm.) Hutch., *Urceola micrantha* (Wall. ex G. Don)

Midd., *Uvaria cordata* (Dun.) Alst., *Uvaria dac* Pierre ex Fin. & Gagnep., *Uvaria fauveliana* (Pierre ex Fin. & Gagnep.) Ast., *Uvaria hirsuta* Jack, *Ventilago denticulata* Willd., *Vernonia elaeagnifolia* DC., *Vernonia solanifolia* Bth.

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