ORIGINAL ARTICLE

Impact of forest disturbances on soil properties: a case study in Mon State, Myanmar

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ABSTRACT

Communities in Myanmar rely heavily on forests for various uses, but there have been few studies on disturbance to tropical evergreen forests in the country. There is a growing need to evaluate the responses after disturbances relating to soil condition to inform sustainable forest management practices to all regulating agencies. This study assessed the impact of forest disturbances on soil properties in a tropical evergreen forest ecosystem in Myanmar. Soil samples were collected from the sites with three different types of forest disturbance, namely 1) shifting cultivation (≥15 years post-abandonment), 2) landslide (20 years post-landslide), 3) selective logging (>30 years post-logging), and 4) old growth forest (no recorded history of disturbance over the last 80 years), to determine the effects of forest disturbances on soil carbon (C), nitrogen (N), available phosphorus (AP), pH, and bulk density (BD). Soil C, N, and AP concentrations were significantly higher in old growth forest soils than in the other disturbed forests, while BD was lowest in old growth forest soils. There were no significant differences in soil properties between soil depths, except in BD. Selective logging area soils had the lowest C, N, and pH values, and AP may be severely depleted in areas of shifting cultivation. Our results confirm that forest disturbances can alter soil properties and that the impacts differ among forest disturbance types. Forest areas were slashed and burned for cultivation, cleared by landslides, and selectively logged during harvesting time, and after abandonment, the soil conditions determined the recovery pattern of the forest. According to our results, a logging cycle of more than 30 years is essential to mitigate the influences of logging on soil nutrients.

Key words: Forest disturbance, Shifting cultivation, Selective logging, Landslide, Old growth forest

INTRODUCTION

Disturbance, which can be defined as a relatively discrete event that disrupts the structure of an ecosystem and changes resource availability or the physical environment, is an important process in many forest ecosystems (Powell, 2000). In recent decades, tropical forests have been degraded due to natural and anthropogenic disturbances, the main contributor to the decline in global biodiversity (Mishra et al. 2004). As a result of increasing demand for firewood, timber, pasture, shelter, and food crops, natural land cover (particularly tropical forests) is being degraded or converted to cropland at an alarming rate (Hall et al. 1993). Randrianarison et al. (2016) discussed how historical land use has had a lasting effect on vegetation and an even longer-term effect on soils; therefore, the land use history determines the soil and vegetation characteristics of secondary forest. In addition, the duration and type of disturbance, e.g., for woodlots, agriculture, and grazing, determine current soil properties (Yesilonis et al., 2016).

Criteria for judging the regeneration success of disturbed ecosystems have been based on the inspection of visual aboveground indicators (Mummey, Stahl, & Buyer, 2002), and soil components, in most cases, have received little attention. Therefore, it is crucial to understand how soils respond to natural and anthropogenic forest disturbances to inform sustainable forest management systems while conserving soil fertility in the long term. Forest disturbances and their associated impacts on soil conditions may determine forest capacity at both local and global scales.

In the early 1990s, Myanmar had a total forest cover of approximately 442,000 km² (Leimgruber et al. 2005). The annual deforestation rate between 1990 and 2015 was 4,071 km², representing 0.6% of the country’s total area (Republic of the Union of Myanmar, 2016). According to the Global Forest Resource Assessment conducted in 2015, 42.92% of Myanmar’s total area is still forested. The main causes of land degradation are demographic pressure, expansion of agricultural land, overgrazing, shifting
cultivation, illicit logging, excessive use of fuel wood, installation of industrial plants, and mining (MOF 2005). To date, very few investigations have examined the impacts of different forest disturbances in Myanmar on soils, particularly in tropical evergreen forest. Fukushima et al. (2007) reported adequate fallow vegetation recovery and no significant decrease in total carbon (TC) and total nitrogen (TN) in the surface soil to sustain continuous swidden land fallow for 12 years in deciduous forest in the Bago Yoma region in Myanmar. Thein et al. (2007) also discussed how, with targeted logging of deciduous (teak and commercial hardwood) species in deciduous forest in Myanmar, there were no significant impacts from selective logging on vegetation in terms of basal area, except in Dipterocarpus, where it also had a detrimental effect on soil condition. According to these two studies, the vegetation and soil were not severely affected after disturbances in deciduous forest; however, they were significantly impacted in tropical evergreen forest. Effective sustainable forest management practice requires qualitative data on the influence of disturbances. Therefore, in this study, we examined soil physiochemical properties after disturbances in tropical evergreen forest.

We predicted that old growth forest would display high soil nutrient values and that different forest disturbance types would have significant impacts on current soil quality. We examined both natural and anthropogenic forest disturbances. The objectives of this study were 1) to analyze the impacts of different forest disturbances on current soil physiochemical properties and 2) to compare soil quality among forest disturbance types.

**METHODOLOGY**

**Study site**

This study was conducted in the Kyaik Htee Yoo forest reserve (17° 25’ 38.20”N, 97° 4’ 39.47”E, Fig. 1), one of the major watersheds of the Sittaung River, Kyaik Hto Township, Mon State, Myanmar. The forest reserve covers a total land area of 156 km². Mon State has a tropical climate...
climatic climate. The monthly lowest temperature is 25.6°C in January, and the highest temperature is 29.4°C in April. Annual precipitation is 5,500 mm (MOI 2002); precipitation peaks in July and August. According to the first Schematic Soil Map of Myanmar, which is based on a soil classification system used by the International Society of Soil Science (FAO, 1974), the soil type at our study site is mainly granitic red brown. All forest stands share the same climate and parent material, and similar topography. Elevation ranges from 280 to 878 m. The entire forest reserve is covered by tropical evergreen forest (Stamp 1924, Davis 1960). Based on field observations, the most common dominant species in all disturbance types are Archidendron jiringa, Styrax serrulatum, Anisoptera scaphula, Abarema bigemina, Microcos paniculata, Heterophragma adenophylla, Ilex sulcata, Cedrela serrata, Glochidion glaucifolium, and Ficus glomerata. Data were collected during November and December 2015. Detailed site information for each disturbance type and old growth forest is given in Table 1.

Areas with four different types of forest disturbance were selected for this study: 1) shifting cultivation areas (≥15 years post-abandonment), 2) landslide-affected areas (20 years post-landslide), 3) selective logging (>30 years post-logging) and 4) old growth forest areas (no disturbance history over the last 80 years – used as a reference site). The old growth forest study areas were located at higher elevation ranges than the other forest disturbance types, which explains why the sites had remained undisturbed while forest areas at lower elevations had undergone disturbance by anthropogenic activities, including selective logging and shifting cultivation.

### Disturbance history

As early as 1970, the entire study area was covered with natural tropical evergreen forest that had been disturbed by both natural and anthropogenic factors. Since the 1970s, local communities in some areas of the natural forest have practiced significant shifting cultivation with a short cultivation period of 1 y. All sample plots were located in areas that were ≥15 years post-abandonment (i.e., the forest was no longer under a fallow cycle). In 1996, severe landslides caused by heavy rains occurred in some areas of the study site. We were unable to obtain more detailed scientific data concerning the landslides. The study plots were located in the depletion zone, where surface soil was lost during the landslides. The selective logging site was cut more than 30 years ago, with hardwood commercial species such as Dipterocarpus alatus and Anisoptera scaphula mostly targeted. All sample plots were laid out in areas of >30 years post-logging (single harvest only). The distribution of logged areas was related to the placement of crude roads and trails. All selective logging operations proceeded according to the Myanmar Selection System (MSS) and followed the National Code of Practice for Forest Harvesting (MOF 2000). MSS is a method of harvesting tree species with prescribed minimum girth limits within the boundary of the annual allowable cut. Under the MSS, the forests are organized into felling series, each of which is divided into 30 blocks of approximately equal yield capacity, and the entire felling series is worked in the course of a 30-year felling cycle. All types of forest disturbance had occurred once.

In 2001, the Myanmar Forest Department, Ministry of

### Table 1. Site details for each disturbance type and old growth forest

| Location       | Elevation | Top IVI species                      |
|----------------|-----------|--------------------------------------|
| Shifting Cultivation | 280 m–434 m | Microcos paniculata, Heterophragma adenophylla, Archidendron jiringa |
| Landslide      | 283 m–454 m | Microcos paniculata, Ficus glomerata, Abarema bigemina |
| Selective Logging | 339 m–473 m | Abarema bigemina, Cedrela serrata, Anisoptera scaphula |
| Old Growth Forest     | 413 m–878 m | Ilex sulcata, Styrax serrulatum, Glochidion glaucifolium |

IVI = Important Value Index
Environmental Conservation and Forestry, designated the study area as a forest reserve to protect the disturbed environment. All information concerning forest disturbances was obtained from two sources: official data from the township forest department and extensive interviews with locals.

Soil analysis

Land use changes such as deforestation, conversion of rangeland to cropland, and cultivation are known to cause changes in soil physiochemical and biological properties (Houghton et al. 1999). Among the physical indicators, soil texture, aggregation, moisture, porosity, and bulk density (BD) have been used in studies, and among the chemical indicators, TC and TN, mineral nutrients, organic matter, and cation exchange capacity, among others, are well established (Cardoso et al. 2013). The soil organic carbon affects important functional processes in soil, such as the storage of nutrients (mainly N), water holding capacity, and stability of aggregates (Gatto et al. 2009). It is also a key component of soil fertility, especially under tropical conditions, which must be considered in assessments of soil health (Cardoso et al. 2013). Nitrogen is one of the macronutrients that are needed in the greatest quantities by plants and is generally one of the most limiting to plant growth due to lack of environmental availability (Schoonover & Crim 2015). Phosphorus is second only to nitrogen in the amount needed for optimal plant growth and is one of the essential elements categorized as macronutrients (Schoonover & Crim, 2015). Soil pH is a key indicator because it is directly correlated with nutrient availability/solubility, and it also affects microbial activity (Cardoso et al. 2013). Therefore, pH can be used to predict the potential for nutrient availability in a given production system (Cardoso et al. 2013), and bulk density can better represent the effects of soil use and management (Beutler et al. 2002).

Başaran et al. (2008) showed that soil properties (C, BD, and pH) were affected by land use changes. Geostatistics reveal the dynamic relationships between soil properties and land use types. Previous studies reported that land use history affects soil properties and forest biodiversity (Dupouey et al. 2002) and that a decrease in soil nutrients can occur in forests after abandonment of cultivation (based on a long-term [>50 years] assessment; Compton & Boone 2000). In this study, to elucidate the main changes in soil characteristics after disturbances, we investigated the soil nutrients TC, TN, and AP, and soil physiochemical properties pH (H₂O, KCl) and BD.

Soil sampling

In November and December 2015, soil samples were collected from 50 sample plots. We established 50 plots of 30 × 30 m in each type of forest disturbance area: 15 plots in shifting cultivation areas, 15 plots in landslide-affected areas, 10 plots in selectively logged areas, and 10 plots in old growth forest areas. In each plot, triplicate soil samples were collected from two soil depths (0–10 cm and 10–20 cm) using a 100-mL soil core.

Laboratory analysis

We collected 300 soil samples and analyzed the soil properties of each sample. BD was determined using a core method. Field-moist soil samples were air-dried and gently sieved through 2-mm screens to remove stones, roots, and large organic residue prior to chemical analysis. Dry soils were milled, and TC and TN were analyzed using an NC analyzer (SUMIGRAPH NC-22 A; Sumika Chemical Analysis Service, Ltd.). Available phosphorus (AP) was determined using the Bray II method (Sparks et al. 1996). Soil pH (H₂O) and pH (KCl) were measured in mixtures of 1:2.5 (soil:water) and (soil:KCl), respectively, using a glass electrode pH meter (HM-30P, TOA-DKK, Ltd.).

Statistical analysis

One-way analysis of variance (ANOVA) was used to compare soil properties (TC, TN, AP, pH (H₂O) and pH (KCl), and BD between different forest disturbance types. P ≤0.05 was considered to indicate a significant difference. Significant differences between forest disturbances at two soil depths were tested using Fisher’s least significant difference (Turkey’s HSD) post hoc tests for each soil property. Relationships between soil property indices were determined by Pearson’s correlation matrix. For principle components analysis (PCA), the soil (0–20 cm) variables of TC, TN, AP, BD, and pH (H₂O) were standardized and normalized (\( \bar{X} = 0 \) and \( \sigma = 1 \)). All statistical analyses were performed with SPSS ver. 23.0.0 and PCORD ver. 5.

RESULTS

Soil chemical and physical properties

Several significant effects were found within the
different forest disturbances (Table 2). Soils under old growth forest presented the highest TC, TN, and AP values and there were significant differences between old growth forest and disturbed forests for these soil properties. TC and TN values were lowest in selective logging areas. The pH values in landslide and old growth forest soils were higher than those of all other disturbed forests. The pH values in landslide and old growth forest soils were higher than those of all other disturbed forests. The pH values in landslide and old growth forest soils were higher than those of all other disturbed forests.

The PCA revealed two main soil gradients with eigenvalues ≥1 in the study area (Table 3). The first two principal components in the PCA explained 72% of the total variance in the observations (Fig. 3, Table 3). The highest loadings for PC1 (51% of the total variance) included TC, TN, BD, and pH (H₂O). The only significant factor in PC2 (21% of the total variance) was AP.

Nutrient storage pools in different forest disturbance types

Old growth forest yielded the highest TC, TN, and AP storage values (Table 4). Under shifting cultivation, TC and TN values were higher than those under landslide and selective logging areas. Old growth forest TC and TN values were about two times higher than those from shifting cultivation and three times higher than those from landslide and selective logging. Under shifting cultivation, the AP value was three times lower than in old growth forest and two times lower than in landslide and selective logging areas.
Soils integrate long- and short-term history through their physical and chemical characteristics, biological activity, and spatial landscape arrangement (Fanning et al. 1989). PC1 best separated the soil properties from disturbed forests and old growth forest (Fig. 3), forming two main groups of disturbed and undisturbed forests. The PC1 indicators with the highest loading values are well known for their close correlation with soil nutrients. The PCA also revealed variations in the soil properties among the sites in the disturbed forests, and most of the disturbed forest sites possessed lower soil nutrient values. The old growth forest possessed the highest values of TC and TN, and the disturbed forests had lower values of soil nutrients and high BD values. The PCA also indicated that soil nutrient levels clearly reflected the history of forest disturbance. Compton et al. (2000) reported that important ecosystem processes, such as C storage and N retention, were influenced by soil properties and reflected historical land use types. The results of the PCA included several outliers in the landslide and old growth forests; however, ranges were similar for topography, soil type, and vegetation type among all sample plots. These results suggest that further studies are needed on the vegetation in the study area. In the present study, forest disturbance type has been shown to be a critical factor in determining current soil TC, TN, and AP conditions following conservation initiatives.

We expected to find a strong impact in the selective logging areas due to the removal of large amounts of biomass. There were also differences in the mean values of...
soil physiochemical properties according to forest disturbance type. TC, TN, and AP values were highest in old growth forest, in line with our hypothesis. Although there are limitations to the interpretation of our results because of the lack of baseline soil data in our study site before forest disturbances, our results indicate that most soil properties are strongly influenced by forest disturbance type.

Soil physiochemical properties

**Carbon and nitrogen**

We expected TC and TN to be correlated because they are both related to the amount of organic matter in the soil (Kahle et al. 2002, Takoutsing et al. 2014). The clear group separation pattern that can be seen in Fig. 2 also shows that forest disturbances were a critical factor in determining changes in soil TC and TN. According to Pal et al. (2013), higher organic C concentrations were found in soils under forest land than under equivalent cleared sites, and soil organic carbon was rapidly lost following the removal of trees in such environments. This is consistent with our finding (Fig. 2) that soils in old growth forest whose canopy cover had not been cleared for 80 years possessed the highest TC and TN values. Higher C and N concentrations in surface layers under forest land reflect the larger quantity of biomass input to the soil surface and hence organic matter accumulation (Wilson et al. 2008). Soil properties such as the organic TC and TN content had the lowest values in soil in selective logging areas compared with the soils under other disturbed forests (Table 2, Fig. 2). This suggests that selective logging causes the most severe damage in terms of TC and TN accumulation among the forest disturbance types examined in this study. The major impact of selective logging is not only the removal of tree biomass but also the removal of the topsoil as a result of log dumps, haulage roads, elephant skidding, and large skid trail construction, all of which result in the loss of soil nutrients.

**Available phosphorus**

The AP value could be divided into three groups: old
growth forest, disturbed forests except shifting cultivation, and shifting cultivation (Fig. 2). The soil under shifting cultivation was lower in AP than that under the disturbed and old growth forests. This may be because the AP requirement of cultivated crops was higher, and the absorbed AP was removed from the field in the cultivated soil. Another explanation is the occupation of fast-growing species, which uptake nutrients after shifting cultivation. This finding is in agreement with George & Buvaneswaran (2001), who postulated that rapid nutrient absorption by fast-growing species would lead to a decrease in soil nutrients. This suggests that longer periods of time are required for soils to recover soil P concentrations in the cultivated soil.

**pH and bulk density**

Soil acidity observed in the study area may be due in part to high annual precipitation. Precipitation has been shown to eliminate base cations from the surface horizon through leaching, thereby decreasing pH and increasing soil acidity. The pH (H₂O) values under shifting cultivation and selective logging were relatively low compared to those in other areas, and the differences between pH (H₂O) and pH (KCl) in those areas were also small. This suggests that practicing shifting cultivation and selective logging might reduce the concentrations of basic cations due to the uptake, leaching, and loss of soil organic matter through the removal of biomass. pH (H₂O) values of around 4.5 were observed after 20–30 years of abandonment in evergreen forest in Madagascar, and the pH value was not related to the age of abandonment (Randrianarison et al. 2016). In the present study, the differences between pH (H₂O) and pH (KCl) were large compared to the values reported by Randrianarison et al. (2016). This indicates that the soils in our study area contained high concentrations of exchangeable cations, and suggests the possibility that the soil could be acidic after absorption of the exchangeable cations by plants. Therefore, further studies are needed to investigate exchangeable cations in soils.

BD varied significantly not only depending on forest disturbance type but also between the topsoil and subsoil layers. Soil was the most compact, with the highest BD values, in selective logging areas. This is caused by elephant logging operations and the construction of skid trails. BD values were lowest in old growth forest, where the C concentration was highest (Table 2). Normally, BD values decrease where soil C is relatively high ( Başaran et al. 2008). The high BD associated with selective logging influences both the physical and chemical properties of soil.

**Ecological implications**

We have shown that forest disturbances influenced soil chemistry in our study site. The impacts of forest disturbance on soil chemistry reflect the characteristics of each forest disturbance type. Differences in soil properties may be the result of the complex interactions of forest disturbances. Forest areas were slashed and burned for cultivation, cleared by landslides, and selectively logged during harvesting time, and after abandonment, the soil conditions determined the recovery pattern of the forest.

There was a significant difference in TC and TN concentrations between old growth forest and all other forest disturbance types (Table 2). These differences may indicate that TC and TN contents require at least several decades to return to their original state before disturbance. This is consistent with the findings of Zarin et al. (1995) and Cheng et al. (2016). The lowest AP value, which occurred in soils under shifting cultivation, reflected AP removal by agricultural practices and uptake of more nutrients by fast-growing species. However, soil under shifting cultivation had not only the lowest AP value but also the second-lowest N concentration (Table 2).

The lowest TC and TN concentrations, found in selective logging areas, resulted from a combination of lower C inputs due to limited biomass C return on harvested land and greater C losses due to aggregate road construction and disruption by elephants during log milling (Fig. 3a). In comparison, low values of TC and TN in landslide areas demonstrate the changes in soil properties that typically follow landslides (Adams et al. 1987). The similar patterns of TC, TN, and AP in the landslide and selective logging areas indicated that the disturbance caused by selective logging on soil chemistry was as strong as those caused by the collapse of the surface soil with a landslide. Many studies (Brouwer et al. 1996, Hedin et al. 1995, Hughes et al. 2000, Keller et al. 2001) have suggested that a 30-year logging cycle in humid tropical forests may be too short for atmospheric nutrient deposition to restore all lost base cations, which could result in nutrient depletion to these forests over time (Zarin et al. 1995, Cheng et al. 2016). The MSS 30-year rotation harvesting practice is entirely based on the increment of stand growth without taking soil conditions into consideration. To date, research on the impacts of selective logging on soil nutrients in Myanmar has been very limited, and most of the studies focused on forest vegetation. According to our results, a logging cycle of more than 30 years is essential to mitigate the influences of logging on soil nutrients. Further study on nutrient budgets under selective logging is therefore needed.
This study has shown that different forest disturbance types influence soil chemistry in different ways. The results obtained from this study are the first to provide essential information required by regional and state government agencies to develop effective forest management and improve soil resources. We suggest further quantitative study of nutrient changes following forest disturbance to be consistent with sustainable forest use. In our study, we assumed that vegetation was similar among sites based on vegetation categories and field observations. However, further research on the vegetation in each site is also needed.

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### Appendix 1. Soil physico-chemical properties among all plots

| Plot No | C (gC/kg) 0-10 cm | N (gN/kg 0-10 cm) | AP (mgP/kg 0-10 cm) | pH (KCl 20 cm) | pH (H₂O 20 cm) | BD (g cm⁻² 10 cm) |
|---------|-------------------|-------------------|---------------------|----------------|----------------|------------------|
| Shift   | Cultivation       |                   |                     |                |                |                  |
| 1       | 6.08              | 7.34              | 0.48                | 0.53           | 12.00          | 10.22            |
| 2       | 7.98              | 7.77              | 0.58                | 0.53           | 15.82          | 12.97            |
| 3       | 3.06              | 9.38              | 0.26                | 0.88           | 9.15           | 6.02             |
| 4       | 10.37             | 5.70              | 0.68                | 0.36           | 12.37          | 9.17             |
| 5       | 14.78             | 12.19             | 0.96                | 0.72           | 32.08          | 30.82            |
| 6       | 11.12             | 12.35             | 0.77                | 1.06           | 10.85          | 10.49            |
| 7       | 7.15              | 14.41             | 0.62                | 1.41           | 14.28          | 8.94             |
| 8       | 4.96              | 11.34             | 0.22                | 1.28           | 16.98          | 16.14            |
| 9       | 9.26              | 12.08             | 0.35                | 1.24           | 15.50          | 15.72            |
| 10      | 6.42              | 15.16             | 0.32                | 1.59           | 11.17          | 12.88            |
| 11      | 28.15             | 14.73             | 1.79                | 1.45           | 36.62          | 37.58            |
| 12      | 18.42             | 15.47             | 0.82                | 1.55           | 45.29          | 53.87            |
| 13      | 25.48             | 19.57             | 2.04                | 1.57           | 25.23          | 25.26            |
| 14      | 23.16             | 19.06             | 1.90                | 1.57           | 29.63          | 23.19            |
| 15      | 21.46             | 14.91             | 1.81                | 1.34           | 21.63          | 14.52            |
| Landsl  | ide               |                   |                     |                |                |                  |
| 1       | 4.98              | 1.21              | 0.50                | 0.30           | 112.84         | 115.09           |
| 2       | 7.11              | 5.88              | 0.54                | 0.65           | 104.02         | 84.86            |
| 3       | 19.43             | 21.94             | 1.00                | 1.68           | 29.06          | 15.27            |
| 4       | 8.60              | 8.23              | 0.47                | 0.82           | 9.46           | 8.48             |
| 5       | 14.26             | 3.51              | 0.95                | 0.49           | 150.89         | 113.02           |
| 6       | 5.49              | 1.71              | 0.63                | 0.34           | 77.43          | 63.37            |
| 7       | 7.67              | 6.95              | 0.59                | 0.73           | 23.19          | 14.75            |
| 8       | 10.72             | 8.11              | 0.49                | 0.91           | 14.11          | 12.53            |
| 9       | 8.10              | 11.77             | 0.59                | 1.10           | 49.05          | 33.89            |
| 10      | 14.46             | 5.76              | 1.26                | 0.45           | 16.99          | 8.44             |
| 11      | 11.63             | 4.97              | 1.12                | 0.44           | 7.39           | 8.59             |
| 12      | 13.53             | 6.73              | 1.25                | 0.70           | 10.15          | 8.48             |
| 13      | 10.57             | 10.08             | 0.89                | 1.08           | 14.27          | 15.20            |
| 14      | 17.50             | 14.75             | 1.54                | 1.19           | 23.72          | 26.95            |
| 15      | 25.47             | 17.31             | 2.10                | 1.58           | 31.43          | 43.47            |
| Select  |ive Logging       |                   |                     |                |                |                  |
| 1       | 12.34             | 4.79              | 1.12                | 0.28           | 30.92          | 23.66            |
| 2       | 11.58             | 8.08              | 0.94                | 0.70           | 26.71          | 19.00            |
| 3       | 14.54             | 4.50              | 1.17                | 0.09           | 35.48          | 18.71            |
| 4       | 8.73              | 9.70              | 0.82                | 0.82           | 51.89          | 40.22            |
| 5       | 9.82              | 6.31              | 0.85                | 0.73           | 100.20         | 75.55            |
| 6       | 8.36              | 7.28              | 0.79                | 0.66           | 18.86          | 11.92            |
| 7       | 13.18             | 8.09              | 1.20                | 0.18           | 44.98          | 35.48            |
| 8       | 8.50              | 11.46             | 0.72                | 1.40           | 29.66          | 20.46            |
| 9       | 5.69              | 8.83              | 0.55                | 1.04           | 25.33          | 24.02            |
| 10      | 4.63              | 8.45              | 0.26                | 1.07           | 58.80          | 86.26            |
| Old     | Growth Forest     |                   |                     |                |                |                  |
| 1       | 14.01             | 10.01             | 1.25                | 1.01           | 33.34          | 23.98            |
| 2       | 16.92             | 13.92             | 1.58                | 1.38           | 161.02         | 217.65           |
| 3       | 14.48             | 10.88             | 1.44                | 1.12           | 192.39         | 221.02           |
| 4       | 53.79             | 39.18             | 3.45                | 2.66           | 56.88          | 43.05            |
| 5       | 46.22             | 31.45             | 2.86                | 1.96           | 54.88          | 40.96            |
| 6       | 32.73             | 33.66             | 2.24                | 2.34           | 32.56          | 28.02            |
| 7       | 21.63             | 29.32             | 1.64                | 2.17           | 20.32          | 31.99            |
| 8       | 30.91             | 32.60             | 2.27                | 2.41           | 17.46          | 24.55            |
| 9       | 40.42             | 27.00             | 2.65                | 2.06           | 31.02          | 22.32            |
| 10      | 17.42             | 19.24             | 1.42                | 1.46           | 32.29          | 20.32            |