SEASONAL CAMBIAL ACTIVITY, LITTERFALL, AND FOLIAGE DECOMPOSITION RATES FOR *Pinus oocarpa* IN HONDURAS

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RESUMEN

Un rodal de *P. oocarpa* cerca de Siguatepeque, Honduras, fue estudiado con el propósito de determinar la estacionalidad del crecimiento y estimar las tazas de caída y de descomposición del follaje. Se midió la estacionalidad del crecimiento del cambium por medio de bandas dendrométricas. Más del 80 por ciento del crecimiento anual ocurrió durante los meses más lluviosos (julio a octubre). El cambium no creció e incluso tuvo contracciones durante marzo y abril que corresponden a los meses más secos.

El promedio del incremento diametral para 21 árboles en un sitio de baja calidad fue 0.51 - 0.57 cm/año (medido por dos años) y 0.87 cm/año en el mejor sitio (medido por un año). Durante la estación seca (marzo a mayo) cayó más de 50 por ciento de la hojarasca anual (1.7 toneladas/ha/año). Después de 3, 11 y 29 meses, la descomposición del follaje de *Byrsonima crassifolia* fue por lo menos dos veces más rápida que la de *P. oocarpa,* pero en ningún caso se había perdido más del 50 por ciento del peso original después de 11 meses de descomposición. En análisis químico del follaje de diferentes edades, de la hojarasca recién caída y de la hojarasca en varias etapas de descomposición indicó que los árboles de *P. oocarpa* en este sitio pudieron ser deficientes en P y N. Adaptaciones autoecológicas e interacciones entre crecimiento y descomposición son

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discutidas y presentadas como consideraciones en la selección de *P. oocarpa* para plantaciones.

INTRODUCTION

Pinus oocarpa Schiede is one of seven species in the closed-cone pine group, subsection Oocarpae (2). Three of these seven species: 1) *P. radiata* D. Don., 2) *P. attenuata* Lemm. and 3) *P. muricata* D. Don. are native to California. The remaining four species: 1) *P. patula* Schiede and Deppe, 2) *P. oocarpa* Schiede, 3) *P. greggii* Engelm. and 4) *P. pringlei* Shew. are native to Central America and Mexico. The most successful exotic pine plantations include *Pinus radiata* in winter-rainfall climates, *Pinus patula* in afforestation efforts in summer-rainfall areas of subtropical highlands, and *Pinus caribaea* Morelet in afforestation of tropical lowland and of some mid-elevational sites. These successful plantings have, until recently, overshadowed the potential of *P. oocarpa.*

Recently, the Commonwealth Forestry Institute provenance studies (5) have recommended *P. oocarpa* as an alternative tropical plantation species for mid-elevation sites, especially on degraded or naturally infertile soils. The greater demand for plantations on degraded sites has contributed to an estimated *P. oocarpa* planting rate in 1983 of 20,000 ha per year (17). This significant increase compares to a worldwide *P. oocarpa* plantation area of 23,000 ha in 1977 and 93,000 ha in 1982.

The general altitudinal range for *P. oocarpa* is between 600 and 2400 meters. Its latitudinal range is from 12°45'N in Nicaragua to 27°00'N in Mexico. In Honduras this pine occurs most often between 600 to 1700 m (14) and hybridizes at lower elevations of this range with *P. caribaea* (19). In the Honduran interior *P. oocarpa* stands are poorly stocked, but natural regeneration can occur despite continual exposure to grazing, fire and erosion. In central Honduras logging has removed most of the better formed trees, leaving poorly formed trees as the seed source for naturally regenerated stands. Efforts to offset this dysgenic exploitation include the designation of seed stands (8) and the distribution of quality seed from the seed bank of the Honduran Forestry School.

Although *P. oocarpa* is the most widely distributed of the Mexican and Central American pines (1) and has an increasing importance as a plantation species, no growth or nutrient cycling information is available from naturally occurring stands. For example, in a recent *P. oocarpa* review article (6) and annotated bibliography (7) most of the reported growth information was from exotic plantations.

The survival and growth of *P. oocarpa* trees on severely degraded soils may reflect efficient nutrient utilization or uptake processes. For example, nutrient uptake mechanisms such as internal translocation from senescing needles or from litterfall decomposition could be especially important. This study was undertaken to: 1) secure seasonal growth information from native *P. oocarpa* stands and 2) to compare seasonal growth patterns with foliage nutrient concentrations and decomposition processes.

SITE DESCRIPTION

The study area was located in the *P. oocarpa* experimental forest of the Honduran National Forestry School (Escuela Nacional de Ciencias Forestales or ESNACIFOR) at 14^{o}32'N latitude and 87^{o}50'W longitude at 1100 m. Average monthly rainfall and temperature data (Table 1) and rainfall and temperature data during the study period (Figure 1) were summarized from data taken at the forestry school meterological station, located approximately 6 km from the study areas.

Table 1. Mean monthly rainfall and mean daily temperature maxima and minima from Siguatepeque, Honduras. Number of years of observation are 8 for rainfall and 3 for temperature data (after Robbins, 1983).

	J	F	M	A	M	J	J	A	S	O	N	D	Mean Annual Values
Rainfall (mm)	21	13	6	18	161	188	182	142	205	208	59	44	1247
Maximum temperature (°C)	24.9	25.5	29.1	30.6	29.8	28.0	28.1	27.6	28.1	27.6	26.7	25.1	27.6
Minimum temperature (°C)	11.0	10.9	11.5	12.2	13.1	14.5	13.4	13.3	12.5	13.3	11.3	10.4	12.3

The study areas were two naturally regenerated *P. oocarpa* stands, one on a relatively good site and one on a relatively poor site. The lesser quality site was designated as plot 1 (Figure 2). Plot 1 was a stand of low stem density on soil less than 30 cm deep, was near the top of a 15-20 degree slope, and was representative of much of the pine forest area in the school forest.

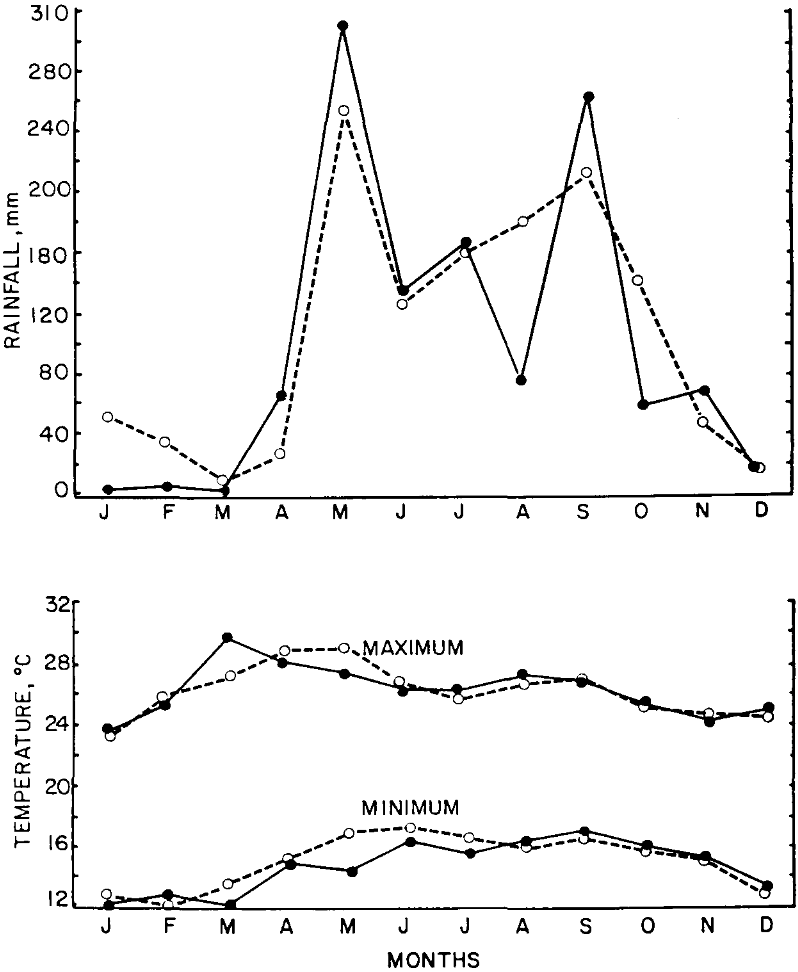

Figure 1. Monthly average rainfal and temperature maximum and minimum values from Siguatepeque, Honduras. Broken lines are 1977 and solid lines are 1978.

The better quality site, plot 2, was also of low stem density, but was on deeper soil (over 80 cm), was along the lower portion of a 15-20 degree slope, and was representative of better site conditions of the school forest. The deeper soil in plot 2 was due in part to downhill movement of soil. The age of these pine stands, estimated by ring counts of two large and

Figure 2. *Pinus oocarpa* study plot 1, near Siguatepeque, Honduras.

two small individuals from each stand was 25-40 years. Both stands were on silica-rich, ignimbrite parent material of volcanic origin, material that is extensive in this area and that can limit root growth by a hardpan. Simmons (18) classified the soils in the Siguatepeque area as Lithic Ustorthents (Ojojona soil series). He described these soils as:

"Surface soils, about 10 cm deep, are dark grayish brown, friable, very fine sandy loam to silt loam with a pH of about 6.3. The subsoil reaching to a depth of 20-30 cm is yellowish brown friable silt loam to clay loam with pH of about 5.5. This horizon rests on partially weathered solid rock. Soil depth varies with rock outcrops common but there are inclusions of areas with soils as deep as a meter. Soil profiles are commonly stony from surface to bedrock. Fertility is said to be moderate. ."

MATERIALS AND METHODS

CAMBIAL ACTIVITY

Twenty-one trees in plot 1 and seven trees in plot 2 were randomly selected for study. None of the study trees had a crown that was severely crowded or topped by other trees. Tree size ranged from 10-33 cm d.b.h. and from 15-35 cm d.b.h. on plots 1 and 2, respectively. At 1.3 m height on each bole of the 28 trees the loose bark was scraped away with a machete and dendrometer bands were installed (22). Initial band readings were taken on September 20, 1976. For logistical reasons and to compensate for variable tensions of initial band placement, the first three months of data were not analyzed. The seven bands in plot 2 were read monthly for one year from January, 1977 to January, 1978. The 21 bands in plot 1 were read monthly for two years, from January, 1977 to January, 1979.

LITTERFALL

To estimate litterfall amount and seasonality ten litterfall traps were placed in plot 1 on September 20, 1976. These square traps, 0.5 x 0.5 m, had nylon screen bottoms suspended 20 cm above the forest floor. Traps were placed 5 m apart in two rows of five. The first trap position was selected at random. During two years all litter in these was collected monthly (September, 1976 to September, 1978), oven dried at 70°C for 72 hours and weighed.

FOLIAGE DECOMPOSITION RATES

The decomposition rate of *P. oocarpa* needles was compared with the decomposition rate of *Byrsonima crassifolia* (L.) HBK leaves. *Byrsonima crassifolia* was selected as a broadleaf comparison species because it was a frequent savanna species throughout the study area. In September, 1976 eighteen 35-45 g subsamples of *P. oocarpa* needles and eighteen 15-25 g subsamples of *B. crassifolia* leaves were collected from the lower branches of ten trees per species. To approximate decomposition of cast foliage, only needles or leaves that appeared to be near senescense were collected. Twelve of these subsamples (six per species) were weighed fresh, oven dried at 70°C for 72 hours, and reweighed to estimate the initial dry weight of each subsample. The fresh foliage subsamples (12 per species) were each placed into 20 x 30 cm nylon decomposition bags (1 mm mesh). Bags were stapled at 3 cm intervals around the edges to allow entry spaces for arthropods. These bags were divided into 12 pairs (one *P. oocarpa* and one *B. crassifolia* bag per pair) and on September 21, 1976 were placed on mineral soil in plot 1. The first pair was randomly placed in the plot. Based on this spot as a corner, the remaining eleven pairs were placed in two rows, each row with six pairs and with 5 m between pairs. Four sample pairs were randomly assigned for collection after 3, 12, and 24 months of decomposition. For logistical reasons, however, actual collections were made after 3, 11, and 29 months. Also, fewer than the programmed number of bags were collected after 3 and 11 months and only one undamaged subsample per species was available after 29 months. Collected foliage was oven dried for 72 hours at 70°C and weighed.

ANALYSES OF FOLIAR SAMPLES

Pinus oocarpa needles and *B. crassifolia* leaves from decomposition bags were chemically analyzed initially and after 3, 11, and 29 months of decomposition. For five months collections from all ten traps were combined in a single monthly sample for chemical analyses (Sept. 1976 to March 1977). On September 20, 1976 three subsamples of current year foliage from lower branches were collected from one 30-40 year-old pine in plot 1 and from two young (4 years old) pines in a nearby plantation. One plantation tree had yellow and the second had dark-green foliage. Three subsamples from each tree were combined and one composite sample per tree was analyzed for total N, P, K, Ca, Mg, and Mn (15).

To determine N levels in foliage from different branch positions, twelve additional needle samples were collected on November 9, 1977. Subsamples from similar positions on 3 separate branches were combined in a single sample for chemical analyses (15). The four branch positions were: 1) the proximal or yellow, clinging and nearly senescent needles; 2) needles one-third the distance from the branch base to the branch apex; 3) needles two-thirds the distance from the branch base to the branch apex and 4) the most apical, newest and assumably the current-year needles.

RESULTS AND DISCUSSION

CAMBIAL ACTIVITY

Trees on the better site (plot 2) grew faster than those on the poorer site (Figure 3, Table 2), and larger trees grew more

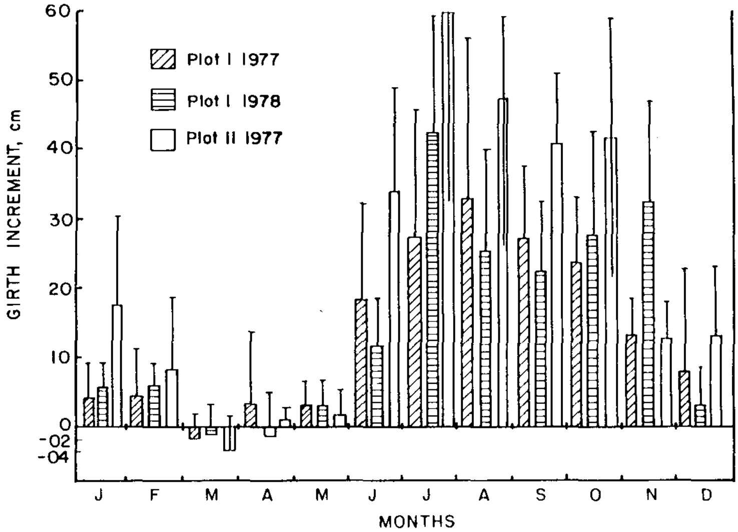

Figure 3. Mean monthly girth increments for 21 *P. oocarpa* trees in plot 1 and for 7 trees in plot 2. Notice stem skrinkage during March and April. Vertical bars are one standard deviation from the mean.

Table 2. Mean annual diameter increment (MAI) of *Pinus oocarpa* trees in two plots near Siguatepeque, Honduras. Plot 2 is the better quality site.

d.b.h. size class (cm)	Plot 1 No. of trees	Plot 1 1977 (cm/yr)	Plot 1 1978 (cm/yr)	Plot 2 No. of trees	Plot 2 1977 (cm/yr)
10 - 14	6	.33	.49	0	—
15 - 24	9	.48	.59	4	.84
25 - 29	4	.64	.59	0	—
30 - 34	2	.84	.65	3	.90
MAI	21	.51	.57	7	.87

than smaller trees (Figure 4, Table 2). In 1977 the mean annual diameter increment was 37 percent greater on plot 2 than on plot 1. This difference was apparently related to greater water and/or nutrient availability in plot 2, the plot with deeper soil. The greater girth increment of large diameter trees (Table 2) may reflect a greater photosynthetic area and/or more extensive root systems for larger trees.

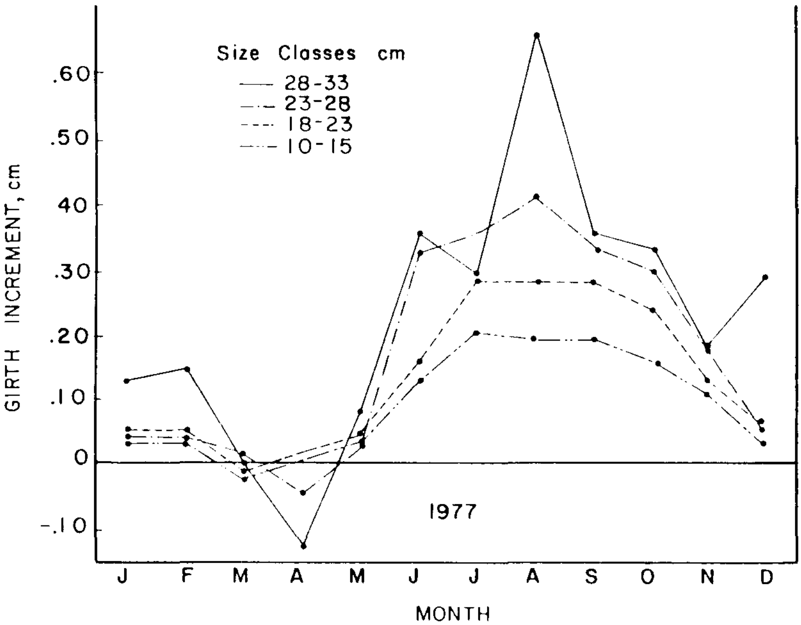

Figure 4. Mean monthly girth increments of 21 *Pinus oocarpa* trees in Plot 1, Siguatepeque, Honduras.

Monthly cambial activity and rainfall patterns for *P. oocarpa* were greater from June to November and less from December to May (Figures 1 & 3). On both plots and for both study years less than 20 percent of total annual rainfall and less than 20 percent of total annual cambial activity occurred during the 6 driest months (Nov. - Apr.). During both study years there was no measurable cambial activity and sometimes negative girth increments (stem and/or bark shrinkage) during the driest months of March and April (Figure 3). This cambial inactivity and the consistency of an annual dry season in central Honduras suggested that for this area the clearly identifiable rings in *P. oocarpa* wood were produced annually.

The onset of the rainy season in May was followed by an increase in cambial activity with maximum monthly girth increments from July to October (Figure 3). During 1978 the rainy season had an intermittent dry period during August ("canicula"). Also during this month, and to a lesser extent during August, 1977 when a "canicula" was less apparent (Figure 2), a decrease in cambial activity also occurred. Another indication that cambial activity was related to rainfall was a comparison of total monthly increments during November of 1977 and 1978 (Figure 3). For November there was greater cambial activity during 1978, the year with greater rainfall. A bimodal peak in cambium activity was reported for *Pinus elliottii* in Florida (11). Peak cambial activity for *P. elliottii* occurred during March and September but did not appear to be correlated with times of greater rainfall as was the case with *P. oocarpa.* Cambial activity of *P. elliottii* in Florida, however, may be more influenced by environmental stimuli other than rainfall, since photoperiod fluctuations and temperature extremes can be greater there than in Honduras.

A pattern similarity between seasonal cambial activity and seasonal rainfall does not suggest that continuous water availability would result in continuous cambial activity. For example, the limited success of *P. oocarpa* plantations in areas with uniformly distributed rainfall (4) and the tendency for this pine to foxtail on certain lowland sites (9) suggest a physiological importance of a dry season dormancy. Active growth during the rainy season may temporarily exhaust some factors essential for growth or accumulate substances that inhibit growth (10). Until the effects of uniform rainfall on the growth and development of *P. oocarpa* are more clearly understood, plantations of this pine will probably be more successful in tropical and subtropical climates with marked dry seasons.

LITTERFALL

Over 50 percent of a total annual litterfall of approximately 1.7 t/ha/a occurred during March, April, and May (Figure 5). It may be that stress during the driest months (March and April) contributed to increased needle fall. During May the casting of senescent but clinging needles by wind and/or rain probably

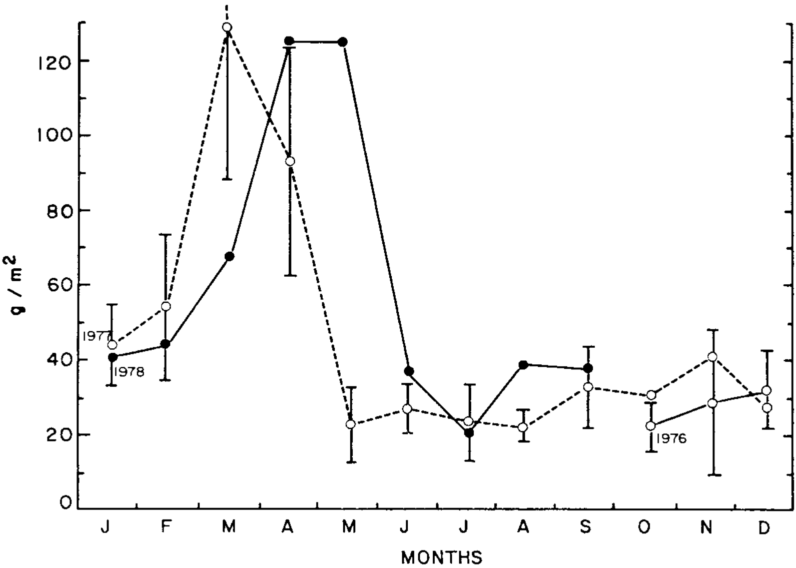

Figure 5. Mean monthly litterfall mass during 24 months in *P. oocarpa* plot 1, near Siguatepeque, Honduras. Vertical bars are one standard deviation from the mean.

contributed to peak needle fall during this first month of the rainy season. The 3 months of greatest litterfall (March to May) were also the months of least cambial activity (Figures 3 and 5).

DECOMPOSITION RATES

After 11 months of decomposition *B. crassifolia* leaves were decomposing nearly twice as fast as *P. oocarpa* needles (Table 3). At this point *B. crassifolia* leaves had lost 40 - 44 percent and *P. oocarpa* had lost 21 - 26 percent of their original dry weight. For both species the time required for 50 percent of the original foliage to mineralize had not been attained after 11 months. This is a slow decomposition rate for tropical conditions. A UNESCO review (20) reported a 2.5 to 19 month range (6 mo mean) for complete decomposition of non-coniferous foliage in tropical and subtropical climates.

If the 43 percent dry weight loss after 29 months for *P. oocarpa* needle decomposition is representative, then this pine foliage decomposes at a rate similar to coniferous foliage in temperate forests. For example, after two years of decomposition *Pseudotsuga menziesii* litter in Washington had lost up to 50 percent of original dry weight (3), *Pinus radiata* foliage in New Zealand had lost 50.6 percent (21), and several conifers in Finland had lost between 41.3 and 52 percent (13). It may be that the extended dry season in the subtropical *P. oocarpa* forest is as effective in reducing the activity of decomposer organisms as is the cold weather season in temperate coniferous forests. Decomposer activity in the *P. oocarpa* forest may have been further reduced because of nutrient deficiencies (especially N and P) and acid soils.

After 3, 11, and 29 months, the amounts of N in decomposing *P. oocarpa* foliage was essentially unchanged, while N amounts in *B. crassifolia* foliage rapidly decreased and sustained a level of approximately 50 percent less than the initial amount (Table 3). This suggested an initially low N concentration in pine needles or perhaps N inaccessability to microorganisms. Other decomposition studies in conifers (3 and 21) have shown a rapid reduction in foliar P concentrations during the first three months of decomposition, especially when P is not limiting. *P. oocarpa* needles were low in P initially, suggesting a possible deficiency, and remained low after up to 29 months of decomposition (Table 3). The mineralization of N, P, K and Mg during decomposition was more rapid for *B. crassifolia* foliage than for *P. oocarpa* needles. A reason for this could be the presence of more decay resistant structural and chemical components in *P. oocarpa* needles.

For both species, the concentrations and absolute amounts of Ca in foliage remained the same or increased during decomposition (Table 3). This increase reflected the immobile nature of this element as well as the structural durability of the species used for this study. The variable concentrations of Mn in the foliage of both species (Table 3) was probably the result of Mn accumulation during needle and foliage aging, since old foliage was initially placed in decomposition bags. The high Mn concentrations, however, suggested a possible Mn toxicity in foliage or soils, a possibility not directly examined by this study.

FOLIAR NUTRIENT CONCENTRATIONS

With the exception of N, the levels of foliar P, K, Ca, Mg, and Mn in *P. oocarpa* foliage (Table 4) were within the ranges

Table 3. Foliar nutrient concentrations and absolute percents of initial amounts (in parentheses) of *Pinus oocarpa* needles and *Byrsonima crassifolia* leaves at different stages of decomposition.

Species	Decomposition period (Months)	Number of subsamples	Dry mass loss (percent)	Percent N	P	K	Ca	Mg	Mn
Pinus oocarpa	0	3	0	.72	.06	.53	.12	.11	.02
				(100)	(100)	(100)	(100)	(100)	(100)
	3	2	15 - 19	.87	.05	.28	.20	.08	.02
				(98–103)	(71)	(43–45)	(135–142)	(59–62)	(81–85)
	11	3	21 - 26	.90	.05	.08	.33	.06	.02
				(95–99)	(62–66)	(11–12)	(204–219)	(40–43)	(74–79)
	29	1	43	1.20	.07	.05	.25	.05	.01
				(95)	(66)	(5)	(117)	(25)	(28)
Byrsonima crassifolia	0	3	0	1.50	.07	.96	.84	.22	.01
				(100)	(100)	(100)	(100)	(100)	(100)
	3	2	27 - 60	1.58	.07	.26	1.61	.21	.01
				(42–47)	(40–73)	(11–20)	(77–140)	(38–70)	(40–73)
	11	3	40 - 44	1.82	.06	.07	1.88	.22	.02
				(68–73)	(48–51)	(4)	(125–134)	(56–57)	(112–120)
	29	1	64	2.03	.08	.07	1.64	.12	.04
				(49)	(41)	(3)	(70)	(20)	(144)

Table 4. Chemical analyses of *Pinus oocarpa* foliage collected from trees near Siguatepeque, Honduras.

Date	Tree age (yrs)	Needle color	Needle age (yrs)	Number of subsamples per analysis	Percent N	P	K	Ca	Mg	Mn (ppm)
Sept. 1976	30 – 40	green	current	3	.99	.075	.73	.14	.06	484
Sept. 1976	30 – 40	green	current	3	1.03	.076	1.01	.10	.10	180
Sept. 1976	4	green	current	3	.94	.068	.77	.09	.13	248
Sept. 1976	4	yellow	current	3	.76	.071	.76	.14	.06	426
Oct.–Feb. 1976	–	brown	litterfall	10	.33 to .38	.01 to .08*	1.11 to 1.80*	1.36 to 1.66*	.06 to .08	167 to 217*
Nov. 1977	30 – 40	green	current	1	.81 – 1.01**					
Nov. 1977	30 – 40	green	1 – 3	1	.71 – 1.07**					
Nov. 1977	30 – 40	green	3 – 5	1	.63 – .69**					
Nov. 1977	30 – 40	green/ yellow	5 – 8	1	.18 – .64**					

* Range of five values, one composite analysis per month.
** Range of three values, each value is a 3 tree composite sample.

reported from foliar analyses in many other pines (12). Liegel's dissertation (12) contains a summary of foliage element concentrations for many pine species. The range of nitrogen concentrations in current year *P. oocarpa* foliage was 0.81 to 1.03 percent, levels similar to the 0.84 to 1.04 percent range reported for *P. caribaea* (12) and the 0.80 to 1.00 percent range reported for *P. elliottii* (16), but less than the nitrogen values from most other pines. For example, nitrogen deficiency levels for *P. radiata* were designated at less than 1.60 percent, since chlorosis was sometimes visible at lower concentrations (21). It may be, however, that *P. radiata* is more nutrient demanding than other pine species, since in addition to relatively high requirements for nitrogen it also has a high P requirement. *P. oocarpa,* on the other hand, may be one of the least nutrient demanding pines, a quality that could continually increase its importance as plantations are more widely considered for degraded tropical sites. Phosphorus levels below 0.10 percent were considered as critical for *P. radiata* (21). Phosphorus levels reported here for *P. oocarpa* and values reported for *P. elliottii* and *P. caribaea* (12) range between 0.05 and 0.10 percent, with a 0.075 to 0.080 range as a possible critical level. By these criteria *P. oocarpa* trees in this study would be considered as borderline deficient in phosphorus (Table 4). Alternately, the P requeriment for *P. oocarpa* may be minimal.

An important consideration when comparing foliage element concentrations is sampling methodology. For *P. caribaea,* Liegel (12) sampled the second and third needle flush inward in the top one-third of the tree. *P. oocarpa* samples were current needles from lower branches. Despite different sample positions foliage from these two pines had similar nitrogen concentrations (Table 4). When foliage from more comparable positions on *P. oocarpa* trees were analyzed, the N concentrations were 0.71 percent and 1.07 percent. This was less than the 0.84 to 1.04 percent N concentration range reported for *P. radiata.* The oldest *P. oocarpa* needles had less than 0.64 percent N. Nitrogen could have been leached by rain from these oldest *P. oocarpa* needles or redistributed from the older to younger, more actively growing, tissues.

SUMMARY

A *P. oocarpa* stand in central Honduras was studied to determine seasonal diameter growth patterns and to estimate litterfall and foliage decomposition rates. Mean annual diameter increment was 0.87 cm/a on a high quality and 0.51-0.57 cm/a on a low quality site. Over 80 percent of annual diameter increment occurred during the six months with greatest rainfall (June to November). More than 50 percent of the total annual litterfall was cast during the three driest months (March to May), the months just prior to the onset of greatest cambial activity. Neither *P. oocarpa* nor *B. crassifolia* foliage had lost 50 percent of the original dry mass after 11 months, a rate slower than most other tropical studies. *Pinus oocarpa* needles decomposed twice as slowly as *B. crassifolia* foliage.

Efficient nutrient use on degraded sites could involve the redistribution of mobile elements (especially N) from senescent foliage to more actively growing plant parts. Also, slow decomposition rates of *P. oocarpa* needles could release nutrients into the soil at a pace that facilitates continual nutrient uptake with minimal nutrient loss from leaching. The efficiency of such nutrient recycling mechanisms could be of fundamental importance in explaining the survival and eventually managing this pine for increased growth rates on nutrient poor sites.

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MEMORIA DEL SEMINARIO REGIONAL DE FITOPROTECCION

Keith L. Andrews, Héctor Barletta
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La publicación registra 29 trabajos científicos desarrollados por destacados especialistas en fitoprotección de Centroamérica, México, Estados Unidos y Sudamérica sobre diferentes tópicos presentados en un Seminario Regional sobre Fitoprotección que se celebró en la Escuela Agrícola Panamericana, El Zamorano, en abril de 1984.

La obra publicada en la revista científica CEIBA de la EAP, aborda un capítulo relacionado con la enseñanza de la fitoprotección en Centroamérica a nivel de Agrónomo, Ingeniero Agrónomo y Post-grado la cual es de interés especial para fitopatólogos, entomólogos, malezólogos y especialistas en manejo integrado de plagas.

Asimismo, registra en tres capítulos los avances en las investigaciones en los campos entomológicos y malacológicos, haciendo énfasis en babosas y plagas de frijol y maíz.