MAGNITUDE OF NUTRIENT INFUXES FROM ATMOSPHERIC SOURCES TO A CENTRAL AMERICAN PINUS CARIBAEA WOODLAND

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SUMMARY

(1) The following influxes of macro-nutrients in bulk precipitation were measured during 1 year in the Mountain Pine Ridge savanna, Belize (kg ha⁻¹): Ca 1.96; Mg 0.28; K 3.40; Na 9.34; and P 0.12.

(2) The quantities of water-soluble nutrients in aerosols caught by an artificial filter over the same period were also measured, and these measurements converted to estimates of filtration by canopies of Pinus caribaea Morelet, var. hondurensis, after calibration of the filter catch on that by pine foliage. Annual canopy filtration by natural and thinned 30-year-old pine strands were found to comprise only 8.1-37.8% and 3.2-15.9% of bulk influx, respectively, with Ca and K showing little augmentation from this source and Mg the greatest relative to bulk influx.

(3) The influx of K from atmospheric sources is probably adequate to meet the requirement for this element by the first cycle of pine-stand development in this area, but the influx of other elements is insufficient and tree growth is presumably drawing upon soil reserves.

(4) However, conventional timber harvesting at the end of the first rotation will remove only a portion of accumulated nutrients and, provided that the remainder are not lost from the site, subsequent rotations can be sustained by the atmospheric accessions measured.

INTRODUCTION

The lowland pine savannas of Central America are the native habitat of Pinus caribaea Morelet, var. hondurensis, a softwood species of extreme importance in tropical forestry (Lamb 1973). The pine savannas characteristically occur upon soils of very low fertility that are derived from quartz-rich coastal alluvial deposits or deeply weathered granites (Parsons 1955; Romney 1959; Taylor 1962). Despite this low fertility, suppression of fires in these savannas for several decades has precipitated the development of a woodland of P. caribæa (Munro 1966; Kellman 1976), and atmospheric influxes have been identified as the most likely source of nutrients driving this woodland development (Kellman & Hudson 1982). However, there are as yet no estimates available of the magnitude of atmospheric influxes to these ecosystems, although scattered data exist for influxes elsewhere in the tropics (Kellman, Hudson & Sanmugadas 1982). Moreover, all estimates of atmospheric influx in the tropics have so far comprised only estimates of bulk precipitation (sensu Whitehead & Feth 1964) despite there being reason to suppose that filtration of aerosols by tree canopies may augment this considerably. Estimates of tree-canopy filtration in several other areas have suggested a significant augmentation from this source (White & Turner 1970; Art et al. 1974; Mayer & Ulrich 1974; Miller & Miller 1980; Lovett, Reiners & Olson 1982; Lovett & Lindberg 1984). Moreover, conifer foliage is, in theory, an efficient
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filter, and the open canopies of the Central American savanna woodlands, exposed to continuous onshore trade winds, may be expected to be especially effective in this role. Finally, high Na levels have been recorded in the soil solutions beneath *P. caribaea* stands in Belize, despite this element being highly mobile and almost absent from the exchange complex (Kellman & Sanmugadas 1985). This suggests that oceanically derived aerosols are being filtered by the pine canopies.

The object of this study was to estimate the total influx of plant macro-nutrients to a Central American pine woodland, including both bulk precipitation and canopy filtration components, and to compare the magnitude of these influxes with the quantities sequestered in pine stands and the quantities expected to be removed when these are harvested. A further objective was to explore the effects of pine canopy depth and density upon the quantities of materials filtered.

The study was carried out in the western part of the Mountain Pine Ridge savanna of Belize (17 °N, 89 °W). The area is a granite plateau of 500 m elevation and receives a mean annual rainfall of 1560 mm, with a pronounced dry season from February to April (Walker 1973). Soils consist of coarse sandy loam topsoil of varying depth, overlying a clay-rich subsurface horizon. Topsoils were acid (pH 4.7–5.0), of low cation exchange capacity (5–10 mEq per 100 g), of low base saturation (1–3%) and were low in available phosphorus (1 μg g⁻¹). Further details of the soils are provided by Kellman (1979) and Kellman & Sanmugadas (1985).

The area was last reported burned in the late 1940s (Johnson & Chaffey 1973), and the even-aged stands of *P. caribaea* that have developed since then have been managed for future timber production. In addition to fire protection, management has so far comprised thinning of pine to densities of approximately 500 stems ha⁻¹ at least once in each rotation of 50+ years, and clearing of any other trees and shrubs that are assumed to compete with pine. Recently, some limited use has been made of prescription burning to reduce fuel accumulation and fire hazard.

**METHODS**

*Bulk precipitation*

The input of water-soluble Ca, Mg, K, Na and P in bulk precipitation was measured at the settlement of Augustine from July 1982 to June 1983, using a collector mounted at tree-top level in a hillside clearing on the edge of the savanna. The collector consisted of a polyethylene funnel 176.7 cm² in area draining to a 10 l polyethylene collecting bottle enclosed in a box. To prevent entry of insects, the funnel throat was plugged with a wad of acid-washed fibreglass which was changed regularly. Water volumes were measured and samples taken for chemical analysis at weekly intervals whenever rainfall had occurred. As interest was focused upon plant-available nutrient influxes, no attempt was made to measure separately any dry fallout received during weeks without rain. For similar reasons, dry fallout accumulated on the funnel after earlier rainfall in any week was not flushed off before sampling for that week. On three occasions, when logistical difficulties prevented a weekly sample being taken, the influx over 2 adjacent weeks was averaged. Funnels, tubes and collecting bottles were changed twice during the year when discoloration of their surfaces suggested that some algal growth had occurred.

Forty ml samples of solution were placed in small polyethylene bottles and 0.5% chloroform was added as a preservative. Samples were stored in the dark at approximately 5 °C for up to a year until return to Canada for chemical analysis. Storage under similar
conditions, but at room temperature, has been shown to have no effect upon the concentration of these elements in solution over a 3-month period (Kellman, Hudson & Sanmugadas 1982).

**Foliage filtration**

Estimates of the quantity of nutrients filtered by plant canopies presents a particularly intractable experimental problem because of the difficulties of separating filtered materials from foliar leachates. Past attempts to estimate this component of atmospheric influx have involved simulated foliage filters (Schlesinger & Reiners 1974; deCatanzaro & Binkley 1981), elimination of foliar leaching with acrylic spray (Art et al., 1974), comparison of throughfall composition in different seasons (Mayer & Ulrich 1974), regression techniques (Miller, Cooper & Miller 1976; Lakhani & Miller 1980; Lovett & Lindberg 1984), measurement of foliage catch when exposed to known aerosol loads (White & Turner 1970; Wedding et al. 1975; Wiman 1981), simulation modelling (Lovett, Reiners & Olson 1982), and isotope ratios (Gosz, Brookins & Moore 1983). In this study, the architectural simplicity of the pine woodland canopy facilitated some aspects of filtration estimates, while the remoteness of the study area from technical support and laboratory facilities imposed other constraints. The approach adopted involved a combination of two techniques that have been used by others: artificial filters, and the washing of foliage before and after exposure to aerosol impaction.

The quantity of water-soluble nutrients caught by an artificial mesh filter exposed adjacent to the bulk precipitation collector was measured at weekly intervals throughout 1 year. Similar filters were placed for shorter periods of time within pine stands of differing density, and their catch compared with that by a filter exposed above the canopy, to estimate the reduction in filtration associated with different canopy densities and depths. Catches with the artificial filters were calibrated against those by pine foliage over short periods of time, expressing foliage catch per unit weight of foliage. Sodium was used as the tracer in this and all other filtration comparisons because of its abundance and hence ease of measurement. Its use assumes that the filtration of Na relative to other elements in any observation period did not differ between filter mesh and pine foliage.

A separate set of measurements was used to characterize pine-canopy morphology. The foliage comprising the canopies of *P. caribaea* consists of relatively discrete aggregations of needles, rarely extending more than 20 cm from twig apices, and normally comprised of needles produced in several recent growth flushes. Because the species exhibits multiple intra-annual growth flushes (Chudnoff & Geary 1973), it is not possible to specify the ages of the needles in these aggregations. They are hereafter referred to as ‘whorls’, a usage which is not intended to imply either needles arising from one node, or those of a specified age. Field sampling sought to characterize the weight, density and vertical distribution of these whorls in the stands studied.

The weekly catch of nutrients by the exposed filter throughout 1 year was reduced proportionately to the observed reduction in catch by within-canopy filters. The catch by an average whorl within stands was then estimated from the filter :whorl calibration, and this catch multiplied by the estimated whorl density at that level within each stand. Weekly catch estimates were summed over a year to arrive at an annual canopy catch for each layer, and these summed between layers to arrive at an annual catch by the entire stand canopy.
Artificial filters

The artificial filter comprised a circular tube of polypropylene mesh, 6·5 cm diameter and 25 cm tall, composed of 1 mm diameter filaments woven 2 mm apart. The mesh tube was mounted in a 15 cm diameter polyethylene funnel, identical to that used in sampling bulk precipitation, and stayed vertically by four nylon-fishing-line filaments attached to a heavy elastic band positioned below the funnel edge (Fig. 1a). The funnel throat was plugged with fibreglass and connected to a collecting bottle as in the bulk precipitation collector.

The volume of solution collected by the funnel with filter was measured and sampled for chemical analysis whenever bulk precipitation was measured, and samples were treated with chloroform and stored as described above. The weekly catch of water-soluble nutrients was measured as the difference between the quantities collected by the funnel and filter collector and the bulk precipitation funnel collector. When calibrating the filters on foliage, each filter was removed from its funnel and rinsed for 5 min in a polyethylene sack containing the collected rainfall (if any) which was then used to rinse the collecting funnel before being sampled for chemical analysis. When little or no rain had fallen in the observation period, filters and funnels were rinsed with 1 l of distilled water which was then sampled for chemical analysis. The distilled water used in this, and other, rinsing procedures was always sampled before use and any Na contamination detected used to correct measured Na concentrations after rinsing.

Sets of artificial filters were maintained for 1 month in adjacent unthinned and thinned stands of *P. caribaea* approximately 30 years old, located 4·5 km south of the settlement of Augustine. One stand had been thinned 1 year before sampling and contained 489 stems ha⁻¹. The unthinned stand comprised a small area (≥30 x 50 m) within the thinned stand and contained 2978 stems ha⁻¹ (≥2 cm dbh). In each, a pole was raised on which were mounted three artificial filters and funnels, connected by tubes to collecting bottles at its base. One filter was mounted at the top of each pole and two others at lower heights on brackets that placed them 50 cm from the pole on opposite sides. Each filter was located at the median height of whorls in three vertical canopy segments, each containing one third of the total estimated whorls in that stand (Fig. 4).

![Figure 1](image-url)
TABLE 1. Regression equations for Na catch by artificial filters within stands (x) upon Na catch by artificial filter above the canopy (y) for *Pinus caribaea* stands in Belize, Central America. Data in mg; n = 9

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Regression equation</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unthinned stand:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper filter</td>
<td>$x = 0.1381 \log_{10} y + 0.2034$</td>
<td>0.90</td>
</tr>
<tr>
<td>Middle filter</td>
<td>$x = 0.0891 \log_{10} y + 0.1333$</td>
<td>0.93</td>
</tr>
<tr>
<td>Lower filter</td>
<td>$\log_{10} x = 0.6753 \log_{10} y + 0.7883$</td>
<td>0.89</td>
</tr>
<tr>
<td>Thinned stand:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper filter</td>
<td>$x = 0.1354y + 0.0299$</td>
<td>0.98</td>
</tr>
<tr>
<td>Middle filter</td>
<td>$x = 0.0790y + 0.0343$</td>
<td>0.90</td>
</tr>
<tr>
<td>Lower filter</td>
<td>$x = 0.1021 \log_{10} y + 0.1423$</td>
<td>0.92</td>
</tr>
</tbody>
</table>

To sample exposed conditions, a third pole with a single filter at its top was raised on a ridge crest approximately 100 m away, with the filter located above the pine canopy.

Solutions caught by the funnels and filters were measured and sampled nine times during the 1-month exposure period, whenever measurable rainfall had occurred. The quantity of Na caught by each filter within a stand was regressed upon that caught during the same period by the exposed filter, using both transformed and log-transformed data. The regression equations providing the best estimates of the dependent variables (Table 1) were used to convert exposed filter catches made throughout the year of observations at Augustine to within-canopy filter catches in the two stands.

**Filter calibration**

The apical whorls of pine seedlings that had developed mature foliage were used in filter calibration because these possessed the straight stems that were necessary for experimental mounting. Whorl sets used in each calibration run (8–9 pairs per set) were arbitrarily selected to include a variety of foliage volumes, but to avoid those with excessively long needles or those which contained recently flushed foliage, which was found to wilt prematurely. The size frequency distribution of whorls used in calibration are shown in Fig. 3, together with the frequency distribution of a stand-wide sample of whorls (see below). Whorls were separated into pairs approximately equal in foliage volume and morphology, and one member of each pair was assigned to an exposed subset and the other to an unexposed subset. Both subsets were soaked and rinsed together for 30 min in tap water, then for a further 15 min in 1 l of distilled water. Whorls of the unexposed subset were then hung to dry overnight in an enclosed room, after which they were stored in a closet for the duration of the exposure period. The stem of each whorl in the exposed subset was enclosed in two sealed polyethylene sleeves, then stayed vertically with three nylon filaments in the centre of a 32 cm diameter bowl lined with a heavy polyethylene sack (Fig. 1b). Each whorl was then exposed to the ambient airstream adjacent to an artificial filter and bulk precipitation collector at the site of the annual collectors. Exposure lasted for 5–7 days, depending upon the rainfall quantity and state of the foliage.

At the close of each exposure period, exposed foliage whorls were soaked and rinsed for 30 min in the water collected in the polyethylene liner of the bowl beneath each whorl. The water volume was then measured and a sample taken for chemical analysis, after which liners were discarded and new ones used for the next exposure period. Each whorl of the unexposed subset was soaked and rinsed in 0.5–1 l of distilled water for 30 min after which this was sampled for chemical analysis. At the close of each exposure period, all whorls
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Fig. 2. Relation between Na catch by foliage whorls and by artificial filters. Regression line used as calibration also shown. \( r = 0.45 \) (\( P < 0.05 \)); \( y = 0.0549x + 0.0073 \).

used were oven dried at 65 °C after which the needles of each whorl were removed and weighed. The quantities of Na released in the second washing of the fifty unexposed foliage whorls used were consistently small relative to those released by exposed foliage (\( \bar{X} = 0.0028 \) mg (g of foliage)\(^{-1} \), range 0–0.0081; cf. Fig. 2). This suggests that the washing and rewashing procedure used was unlikely to have introduced large experimental errors into the results.

The total Na received in the form of bulk precipitation on a bowl 32 cm in diameter was estimated from the measured bulk receipt during the exposure period and deducted from the bowl + whorl Na yield to give a gross whorl yield. This was divided by the foliage dry weight to give a gross yield per g of exposed foliage. From this was deducted the mean Na yield per g of unexposed foliage for that calibration run. The resulting figure represented net Na catch per g of exposed foliage, and was used in conjunction with the Na catch by the artificial filter in developing a filter calibration. A total of eight calibration runs was performed during the 1983 and 1984 field seasons, the data from two of which were rejected because there was no measurable catch on the artificial filter.

Estimates of Na catch per g of exposed foliage showed a great deal of variability between whorls in each exposure period. The resulting correlation with catch by the artificial filter was weak but significant (\( r = 0.45, n = 50, P < 0.01 \)), and a linear regression of foliage catch upon filter catch was used as the calibration (Fig. 2).

Pine-foliage sampling

The weight of pine whorls, and their vertical distribution on trees, were sampled in an area adjacent to the stands studied immediately after the thinning of pine by a forestry work crew. The area was traversed in parallel lines, approximately 20 m apart, enumerating all felled pine trees that were not so deeply buried in slash as to be unidentifiable. The dbh at 1.4 m of each tree was measured, as was the height to each branch and the number of whorls supported by that branch. A total of fifty trees were sampled in this way. In a separate systematic sample in the same area, 183 whorls were collected by taking the closest whorl on a felled tree to points spaced 5 paces apart along parallel traverse lines. Whorls were oven-dried at 65 °C, after which foliage was removed and weighed.
Tropics tended of in collected and Pine the mean spectrophotometry analysis with data, spectrophotometry. Chemical Water bulk samples were analyzed by spectrophotometry using an autoanalyser.

RESULTS

The total annual influx of macro-nutrients in bulk precipitation measured in the Mountain Pine Ridge savanna is given in Table 3 and the seasonal pattern of weekly inputs is shown in Fig. 5. Annual totals fall within the lower range of those recorded elsewhere in the tropics (Kellman, Hudson & Sanmugadas 1982). Sodium was the dominant element collected with progressively lesser quantities of K, Ca, Mg and P being recorded. The input of Mg was especially low relative to that recorded in other tropical areas. Inputs of Ca, Mg and P showed no distinct seasonal pattern, while those of K, and to a lesser degree Na, tended to be concentrated in the wet season.
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**Fig. 3.** Foliage dry-weight frequency distributions of *Pinus caribaea* whorls used in (a) filter calibration and \((n = 50; \bar{x} = 19.1; \text{median} = 17.6)\) (b) a standwide systematic sample \((n = 183; \bar{x} = 14.1; \text{median} = 20.3)\).

**Fig. 4.** Vertical frequency distribution of foliage whorls in (a) unthinned and (b) thinned stands of *Pinus caribaea*. (-- --), boundary of the three layers of equal whorl abundance. *, Height of artificial filters within each layer.
TABLE 3. Total annual influx in bulk precipitation and in aerosol filtration by canopies in unthinned and thinned stands of *Pinus caribaea* in Belize, Central America. Data in kg ha\(^{-1}\) year\(^{-1}\). Total influx as a % of bulk influx also shown

<table>
<thead>
<tr>
<th>Element</th>
<th>Source</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>Na</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulk precipitation</td>
<td>1.96</td>
<td>0.28</td>
<td>3.40</td>
<td>9.34</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>Canopy filtration:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unthinned stand</td>
<td>0.19</td>
<td>0.11</td>
<td>0.28</td>
<td>1.62</td>
<td>0.029</td>
<td></td>
</tr>
<tr>
<td>Thinned stand</td>
<td>0.07</td>
<td>0.04</td>
<td>0.11</td>
<td>0.67</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td>Total influx:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unthinned stand</td>
<td>2.15</td>
<td>0.39</td>
<td>3.68</td>
<td>10.96</td>
<td>0.149</td>
<td></td>
</tr>
<tr>
<td>% of bulk influx</td>
<td>109.6</td>
<td>137.9</td>
<td>108.1</td>
<td>117.4</td>
<td>124.0</td>
<td></td>
</tr>
<tr>
<td>Thinned stand</td>
<td>2.03</td>
<td>0.32</td>
<td>3.51</td>
<td>10.01</td>
<td>0.132</td>
<td></td>
</tr>
<tr>
<td>% of bulk influx</td>
<td>103.7</td>
<td>115.9</td>
<td>103.2</td>
<td>107.1</td>
<td>110.4</td>
<td></td>
</tr>
</tbody>
</table>

The estimated annual catch of Na by filters located within unthinned and thinned pine stands, expressed as a percentage of that caught externally, is given in Table 4. The catches in both stands lie within the 17–28% range and show no consistent difference between stands or canopy depths.

The estimated annual catch of elements by canopy filtration in the two pine stands is given in Table 3. The augmentation of bulk influx by canopy filtration varies from 8.1 to 37.9% in the unthinned stand and from 3.2 to 15.9% in the thinned stand. Seasonal variation in estimated weekly canopy catch by the unthinned stand is shown in Fig. 6.
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Table 4. Estimated annual catch of Na ions by filters located within stands of *Pinus caribaea* in Belize, Central America. Data expressed as % of catch by a filter located above the canopy.

<table>
<thead>
<tr>
<th></th>
<th>Unthinned stand</th>
<th>Thinned stand</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper filter</td>
<td>28.0</td>
<td>21.8</td>
</tr>
<tr>
<td>Middle filter</td>
<td>18.6</td>
<td>17.3</td>
</tr>
<tr>
<td>Lower filter</td>
<td>19.3</td>
<td>18.9</td>
</tr>
</tbody>
</table>

![Graphs](a) (b) (c) (d) (e)

Fig. 6. Estimated weekly catch in aerosols of (a) Ca, (b) Mg, (c) K, (d) Na, and (e) P by the canopy of an unthinned 30-year-old stand of *Pinus caribaea* in Belize, Central America.

Canopy filtration of Ca and Mg tended to be somewhat larger in the dry than in the wet season, while that of K and Na showed no distinct seasonal pattern. Estimated filtration of P was highly irregular and variation probably reflects primarily the large experimental errors that are associated with the persistently low concentrations of this element in solutions.
The influx of nutrients from atmospheric sources is subject to some year-to-year variability, making any estimate based only on a single year's observations prone to unknown errors. The magnitude of this variability is poorly documented in tropical areas, but the absence of strong seasonal patterns and irregular large influxes during the year of observations in the Mountain Pine Ridge suggests that a relatively equable influx regime prevails and that this single year's observations may provide a reasonable estimate of longer-term conditions. A single large influx of K and P in bulk precipitation was recorded in July 1981 (Fig. 5) and is suggestive of contamination, possibly from bird droppings. However, ignoring the data for this week would not radically alter the overall conclusions of this study.

The low input of nutrients in bulk precipitation, relative to that recorded in most other tropical areas, probably reflects the remoteness of the sampling site from the ocean. Most other tropical sampling stations have been in closer proximity to the ocean, which provides a major source of aerosols for atmospheric deposition in humid climates (Junge & Werby 1958; Wilson 1959; Thornton 1965; Hingston & Gaalitis 1976; Miller 1979). The Mountain Pine Ridge savanna lies approximately 50 km from the ocean in the rain shadow of the Maya Mountains. Areas on the east flanks of these mountains, that receive heavy orographic rainfall, may be the sites of greatest influx of oceanically derived aerosols, leaving areas in the lee of the mountains subject to air masses that are depleted both of moisture and nutrients. The extensive areas of coastal pine savanna that exist in Belize and Nicaragua probably receive a significantly larger influx of nutrients than that measured in the Mountain Pine Ridge.

The elemental composition of both bulk precipitation and filtered materials in the Mountain Pine Ridge differs from that of seawater in possessing larger proportions of Ca, K and P relative to Na (Table 5). Such differences are characteristic of most data sets on atmospheric influxes, other than those derived at sites extremely close to the ocean (e.g. White & Turner 1970; Westman 1978), and indicate enrichment of these elements from non-marine sources. Crozat (1979) has reported appreciable K-enrichment of filtered aerosols in West Africa and suggested that guttation of K-rich water by tropical forest trees is the most likely source. In that area, K enrichment was most pronounced during the wet season, a phenomenon also observed in this study (Fig. 5), and it is possible that the extensive areas of tropical forest that surround the Mountain Pine Ridge savanna were contributing to the input of this element. The extensive areas of limestone terrain that occur to the west and north of the study area may be a source of augmented Ca input in dust, especially in the dry season (cf. Fig. 6). However, in Central America, a more likely source

**Table 5. Quotients of the concentration of individual elements to concentration of Na in seawater and in bulk precipitation and canopy-filtered aerosols in Belize, Central America**

<table>
<thead>
<tr>
<th>Element</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>Na</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seawater</td>
<td>0.039</td>
<td>0.120</td>
<td>0.036</td>
<td>1</td>
<td>0.000005</td>
</tr>
<tr>
<td>Bulk precipitation</td>
<td>0.210</td>
<td>0.030</td>
<td>0.364</td>
<td>1</td>
<td>0.013</td>
</tr>
<tr>
<td>Filtered aerosols:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unthinned stand</td>
<td>0.117</td>
<td>0.068</td>
<td>0.173</td>
<td>1</td>
<td>0.018</td>
</tr>
<tr>
<td>Thinned stand</td>
<td>0.104</td>
<td>0.060</td>
<td>0.164</td>
<td>1</td>
<td>0.018</td>
</tr>
</tbody>
</table>
of non-marine elements is volcanic activity. In Honduras, a brief period of very large Ca and Mg inputs was attributed to nearby volcanic activity by Kellman, Hudson & Sanmugadas (1982). While such large influxes probably represent exceptional events, it is possible that the extensive vulcanism in the region is also responsible for smaller, but more persistent, enrichment of the atmosphere by aerosols containing these, and other, elements.

The filtration of nutrients by the *P. caribaea* canopies that has been estimated in this study is low relative to estimates made for other forest canopies (White & Turner 1970; Art *et al.* 1974; Mayer & Ulrich 1974; Miller & Miller 1980; Lovett, Reiners & Olson 1982; Lovett & Lindberg 1984). A crude verification of the magnitude of these estimated catches can be provided by a comparison of the influx of elements in throughfall beneath pine canopies in the area with those in bulk precipitation. As throughfall deposition includes both products of foliar leaching and filtration, it should normally exceed independent estimates of filtration if significant foliar absorption of elements is not occurring. In Table 6 data are provided on the enrichment of four cations in throughfall beneath a pine stand in the Mountain Pine Ridge. Data were taken from Kellman & Sanmugadas (1985) and Kellman, Miyanishi & Hiebert (1985) and cover 10 weeks of sampling in 1981 and 1982, including both wet- and dry-season conditions. The pine stand from which the data come was of similar age to the two stands used in this study and possessed 1570 stems ha⁻¹, making it of intermediate stem density relative to these stands. The data do not include a stemflow component, but this is probably small due to the near-horizontal branching pattern and the very rough bark of the pines.

The data show that Ca influx beneath the canopy was virtually identical to that in adjacent open area, while the influx of K was slightly less than in the open, suggestive of foliar uptake of this element. While these results are surprising, especially for K which is usually characterized as a highly leachable element (Tukey 1970; Parker 1983), they do conform to the very low pine-canopy filtration contribution estimated for these two elements in this study (Table 3). In contrast, both Na and Mg showed enrichment in throughfall, but to a degree larger than the filtration contribution independently estimated for these two elements (Table 3). However, throughfall enrichment of these two elements was well below the worldwide enrichment averages for these two elements reported by Parker (1983). These data thus suggest that the filtration estimates made for Na and Mg may be underestimates, unless leaching of these two elements from pine foliage comprised 65–70% of the throughfall enrichment. This foliar leaching proportion lies within the extreme upper range of those suggested probable by Parker (1983), implying that any errors in this study are likely to have involved underestimates of canopy filtration. As Na was the tracer element used in filter calibration, its measurement should have been subject to fewer experimental errors than those for other elements. On this basis we conclude that the pine-canopy filtration estimates made are of the correct order of magnitude, but may

<table>
<thead>
<tr>
<th>Element</th>
<th>Throughfall influx (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca</td>
<td>98.6</td>
</tr>
<tr>
<td>Mg</td>
<td>205.0</td>
</tr>
<tr>
<td>K</td>
<td>92.8</td>
</tr>
<tr>
<td>Na</td>
<td>156.1</td>
</tr>
</tbody>
</table>
underestimate true values somewhat. The most likely source of such underestimation is the loss of some filtered materials from foliage whorls during calibration exposure, as a result of blow-off, rain-splash or water-drip from very long needles. Belot & Gauthier (1975) have observed that aerosols caught by foliage in a wind-tunnel experiment tend to form aggregates that are easily dislodged. These losses are also likely to be the major source of experimental error contributing to the weak correlation between foliage and filter catches (Fig. 2).

The relatively high concentration of Na ions in soil solution beneath pine stands (Kellman & Sanmugadas 1985) remains enigmatic if filtration of this element by pine canopies is as low as estimated in this study. We believe that the most plausible explanation for this phenomenon is that relatively large quantities of Na are being retained, accumulated, and recycled by this species. Chemical analysis of the foliage of *P. caribaea* has shown it to have Na concentrations that are almost 10 times those of other common trees and shrubs in the savanna (Kellman 1976), and burning of fuels beneath a pine stand was estimated to mineralize over 4 times the quantity of Na that was released when adjacent open savanna was burned (Kellman, Miyanishi & Hiebert 1985). Both phenomena imply preferential accumulation and cycling of Na by *P. caribaea*, and we suggest that the high concentrations of this element in soil solutions beneath pine are the result of continuous mineralization of Na-rich pine litter.

The total nutrient accessions from atmospheric sources did not show strong seasonality comparable to that found in Venezuela by Lewis (1981) and in Honduras by Kellman, Hudson & Sanmugadas (1982). In these two areas, both experiencing less rainfall and a more pronounced dry season than the Belize study site, a major influx of nutrients in bulk precipitation coincided with early wet-season rains. Such a lack of seasonality probably facilitates effective nutrient capture by the plants of the savanna ecosystem. Plants of infertile environments are characteristically obligate slow growers (Chapin 1980) and may be incapable of rapidly absorbing large nutrient flushes. However, soils in the savanna have been shown to be capable of rapidly immobilizing nutrient accessions which are thereafter presumably available for more gradual plant uptake (Kellman 1985; Kellman, Miyanishi & Hiebert 1985; Kellman & Sanmugadas 1985).

The catch of materials by artificial filters within pine-stand canopies (Table 4) showed a substantial reduction in filtration within canopies, but no clear changes in filtration effectiveness with either canopy depth or density, and the difference in annual catch by the two canopies corresponds approximately to their differences in foliage density (1:2.33). Presumably, a pronounced gradient in foliar filtration exists across the upper canopy boundary in both stands and the catch by the uppermost whorls of the tallest trees may have been underestimated substantially in this study. However, as these comprise only a small proportion of total canopy whorls in each stand (Fig. 4), this is unlikely to have introduced large errors into the estimates of total canopy catch. The absence of a canopy density effect indicates that any increased airflow resulting from canopy thinning does not result in a compensatory increase in filtration by the remaining foliage. While the effect of thinning upon atmospheric accessions of Ca and K will be negligible, thinning will have a slight negative impact upon long-term rates of Mg and P accumulation in this ecosystem. Stands of pine older than 30–35 years are rare in the savanna, making it impossible to specify how stand foliage density and filtration capacity would change over the second half of a 60-year rotation. However, it seems unlikely that stem densities higher than those measured in the unthinned stand would develop, and thinning operations would normally keep foliage density below those levels throughout the latter half of the rotation.
Atmospheric nutrient influxes

Table 7. Estimated quantities of four nutrients sequestered in aboveground tissues of unthinned and thinned stands of Pinus caribaea in Belize, Central America, compared to quantities of nutrients received over the 30-year growth period under different assumptions of canopy filtration. All data in kg ha⁻¹.

<table>
<thead>
<tr>
<th></th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unthinned stand</td>
<td>102.6</td>
<td>32.3</td>
<td>94.6</td>
<td>12.1</td>
</tr>
<tr>
<td>Thinned stand</td>
<td>62.6</td>
<td>19.5</td>
<td>53.5</td>
<td>7.0</td>
</tr>
<tr>
<td>30-year atmospheric influx:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bulk precipitation</td>
<td>58.8</td>
<td>8.4</td>
<td>102.0</td>
<td>3.6</td>
</tr>
<tr>
<td>Bulk precip. + thinned stand canopy filtration</td>
<td>60.9</td>
<td>9.6</td>
<td>105.3</td>
<td>4.0</td>
</tr>
<tr>
<td>Bulk precip. + unthinned stand canopy filtration</td>
<td>64.5</td>
<td>11.7</td>
<td>110.4</td>
<td>4.5</td>
</tr>
</tbody>
</table>

The magnitude of atmospheric influxes in this study may be compared to the quantities of nutrients immobilized in developing P. caribaea stands in the area using allometric regressions developed by Stewart & Kellman (1982). These regressions provide estimates for aboveground tissues only, and so are minimal estimates. However, they permit an assessment of whether atmospheric influxes of nutrients over the 30-year growth period have been sufficient to fuel the present pine-stand development. The quantities of nutrients sequestered in aboveground tissues in the two stands studied are provided in Table 7, together with the estimated influxes of nutrients from atmospheric sources over the 30-year growth period. Influxes of K have probably been sufficient to compensate for growth demands by pine, but those of the other three elements fall well short of demands. During the first cycle of woodland development on the savanna soils, the difference is presumably being met from soil reserves, and Kellman & Hudson (1982) have reported deficits in levels of exchangeable Ca and Mg in the soil beneath a 24-year-old pine.

The savanna’s soil reserves, while limited, are apparently sufficient, in combination with atmospheric influxes, to sustain this initial growth cycle, and subsequent logging by conventional extraction methods (bole and bark only) will remove only a portion of those nutrients sequestered in aboveground tissues. Stewart & Kellman (1982) estimate that the following proportion of nutrients sequestered in aboveground biomass are left on site after this form of timber extraction: Ca 49%; Mg 59%; K 63%, P 69%. It is unlikely that these accumulations of elements will become immobilized in organic material in a tropical environment where decomposition rates are high and accumulations of dead organic material are small. A potentially more serious growth-limiting process in future rotations is the immobilization of accumulated P in Fe and Al compounds in the sesquioxide-rich savanna soils. However, despite rapid disappearance of P from soil solutions (Kellman & Sanmugadas 1985), pine stands have accumulated quantities of P in their tissues far in excess of those detected in the soil by Truog extraction (Stewart & Kellman 1982). This suggests that soil-immobilized P is available for pine growth, perhaps through mycorrhizal activity. Consequently, provided that accumulated reserves of nutrients left in logging residues are not dissipated by leaching or runoff, before the establishment of the next timber rotation, they, in combination with atmospheric influxes, would be adequate to meet the nutrient demands of the next rotation of pine. Indeed, provided that whole-tree harvesting, or other nutritionally costly forms of management, are not employed, a modest increase in soil fertility and tree growth rates may be expected on these infertile savanna soils after multiple rotations of P. caribaea.
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REFERENCES

Atmospheric nutrient influxes


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