Part III

Nutrient Dynamics

Chapter 10

Grassland Biomass and Nutrient Content

10.1 Introduction

In the following sections a description of the above-ground biomass of the Nabou grassland site and its associated nutrient content will be given to illustrate the grassland, *i.e.* the pre-planting, situation. In subsequent chapters forest biomass and nutrient content, as well as rates of nutrients inputs, intra-system cycling, and outputs will be discussed.

10.2 Field and Laboratory Procedures

Estimates of the dead and live standing crop at the Nabou grassland site were made at the end of February (growing season) by clearing an area of $2{*}1$ m^2, and in May 1991 (start of the dry season) by clearing another $3{*}1$ m^2. All vegetation was cut at ground level after which litter layer and green plants (including any dead material still attached to the plants) were separated and put in pre-weighed plastic bags for transport. No attempt was made to sample the below ground-biomass. Field weights were recorded within a few hours after sampling with a Sartorius electronic weighing scales capable of weighing 6100 g with an accuracy of 0.1 g. All dry weights referred to in this chapter were obtained after drying of the samples in an oven, made available by TROPIK Wood Industries Ltd. at 70°C for at least 3 days.

The specific leaf area (SLA) of *Pennisetum polystachyon* grass was determined by measuring the surface area of 50 randomly picked, fresh leaves and recording their total dry weight. The surface area was determined shortly after sampling by carefully drawing the contours of each leaf on paper and measuring the total area by planimeter.

To determine the biomass of dead and green leaves, seed plumes and stems, 50 plants were randomly selected and cut at ground level in May 1991. Amounts of each component were bulked for 10 plants, placed in pre-weighed plastic bags, dried and weighed. In this way five replicas were obtained for each plant component described before.

Another 66 plants were sampled in a similar way between July 23 and August 10. To obtain additional information on biomass distribution with height of the plant, the length of each plant was measured, after which it was cut into three sections (0–0.7 m, 0.7–1.4 m and 1.4 m–top). The weights of dead leaves, fresh leaves and stems in each section were recorded. Seed plumes were not present as the flowering period had finished two months earlier.

A sunfleck ceptometer (Decagon Devices Inc., model SF-80) was used to determine canopy gap fraction and the absorbance of photosynthetic active radiation (PAR) at three levels within the vegetation during two days with clear-sky conditions. The canopy gap fraction was measured as the fraction of the light sensors receiving radiation above a certain treshold value, which represented the PAR value measured in the shadow of grass. After some experimenting the treshold value was set at 250 μmol m^{-2} s^{-1} (about 25% of incoming PAR). Measurements were made by inserting the probe horizontally above the litter layer (0.15–0.3 m) and at 1.0 m and 1.4 m within the vegetation (maximum height ±1.8 m). Incoming PAR was measured every few minutes in an adjacent area with low vegetation. A total of 217 measurements were made just above the litter layer on July 9 between 9:27 and 10:13 h with the sun angle increasing from 33° to 40°. Measurements at higher levels in the canopy were postponed to the next day to avoid effects of variations in sun angle on PAR and canopy gap fraction measurements. One hundred and ten measurements were made at the 1 m level on July 10, between 9:15 and 9:51 h, and another 106 measurements at 1.4 m between 9:51 and 10:09 h.

Two subsamples were taken from bulk samples of grass litter and fresh grass collected in February for analyses of macronutrients (N, P, K, Ca, Mg) and micronutrients (B, Mn, Zn). The oven-dry subsamples were sent to the Forest Research Institute, Rotorua, New Zealand, packed in paper enveloppes for analysis.

Macronutrients were digested with an H_2SO_4/H_2SO_4 solution on a digestion block (Parkinson and Allen, 1975). Nitrogen and P were simultaneously determined by automated colorimetric methods (indophenol blue method and vanadomolybdophosphoric yellow method respectively) whereas K, Ca and Mg were determined by atomic absorption. Manganese and Zn concentrations were established by atomic absorption after the material was ashed for four hours in a muffle furnace at 500 °C and the ash dissolved in hydrochloric acid. Boron was determined on the same digest using a curcumin colorimetric method. A more detailed description of the methods used by FRI is given in Nicholson (1984).

10.3 Grassland Biomass and Structure

Pennisetum polystachyon grass accounted for 92 and 93% of the total grassland biomass in February and May, 1991, respectively. The above-ground living biomass of *Pennisetum polystachyon* grass was 6486(±1747) kg ha^{-1} at the end of February and increased to 8239(±1427) kg ha^{-1} in May, which may be close to the maximum attained value as the vegetation started to die off soon after. The remainder was made up by ferns (*Dicranopteris linearis*), sensitivity grass (*Mimosa pudica*) and blue rats tail (latin name unknown) with a combined average biomass of 553(±689) kg ha^{-1} in February and 609(±190) kg ha^{-1} kg ha^{-1} in May, 1991. The productivity of Nabou grassland was 1809 kg ha^{-1} during the 76-day period. Production rates of mission grass and Nadi blue grass (which appeared recently in the grasslands near Nadi but has not yet spread to the Nabou area) are given in Table 10.1. These production rates were measured on

Table 10.1: *Production rates (dry weights in kg ha^{-1}) of mission grass (Pennisetum polystachyon) and Nadi blue grass (Dichanthium caricosum) as measured at Nacocolevu Research Station near Sigatoka by the Pastures Research Unit from the Ministry of Primary Industries of Fiji. (Mr. S. Chand, pers. comm.).*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mission grass	523	850	1100	1085	1090	220	190	190	198	225	500	475	6646
Nadi blue grass	475	775	1000	840	600	200	175	176	180	200	450	425	5496

trial plots (9 m^2) each at the nearby Sigatoka Research Center at Nacocolevu. The productivity was highest during the wet season (December–May) with a yield of 5123 kg ha^{-1} as compared to 1523 kg ha^{-1} during the dry season. The productivity of the Nabou grassland in March and April 1991 (1750 kg ha^{-1}) was somewhat lower than the corresponding value (2180 kg ha^{-1}) given in Table 10.1. The productivity of the grass vegetation was highly variable anyway in SW Viti Levu, depending on the site quality, and the figures presented here for Nabou grassland may be assumed representative (Mr. T.T. Rawaqa, pers. comm.).

The average gravimetric moisture content of the grass at the Nabou site decreased from 251% of dry weight in February to 158% in May, possibly reflecting increased moisture stress (*cf.* Section 5.3). The decrease in moisture content was less pronounced for the other species (159% *viz.* 133%).

The mass of litter standing crop was 10581(±146) kg ha^{-1} in February and had decreased to 6869(±1035) kg ha^{-1} in May 1991. Most of the grass died between May and July and the May estimate of litter mass may therefore be considered to be close to the annual minimum. A maximum litter mass of about 15000 kg ha^{-1} can be expected at the end of the dry season (November) when most of the grass has died. The seasonal variation of the combined mass of living grass and litter should not be very high and fluctuated presumably between an estimated 15000 kg ha^{-1} at the end of the dry season to 17000 kg ha^{-1} in February.

The mean vegetation height was estimated visually at 1.5 m in February (maximum 2.5 m), 1.8 m in May, 1.4 m by the end of July and 1.2 m in September 1991. However, the length of 66 individual plants sampled between July 23 and August 10 ranged from 0.79 m to 2.39 m with an average of 1.81(±0.36) m and the visually determined decrease in average height during the dry season must therefore be due to wind lean of the dead grass. The average dry weight of a single plant (including dead leaves) was 7.0(±0.3) g in May (n= 50) and 7.5(±1.1) g by the end of July (n= 66). Stem weight accounted for about 68% of plant weight in May as well as in July. Dead leaves, green leaves and seed plume weights accounted for 10%, 14% and 9% of total plant weight, respectively, in May. The weight of dead leaves increased to 25% by the end of July, coinciding with a decrease in the weight of green leaves to 7% and a total absence of seed plumes. The biomass of each plant component for each height interval was calculated by multiplying the biomass values with the mass fraction of each component for each height interval. Figure 10.1 shows the cumulative distribution of dead leaf, green leaf and stem biomass *versus* height of the vegetation by the end of July. It is clear that by this time fresh leaves were concentrated in the 0.7–1.4 m level and made up only a minor part of the total biomass. At the beginning of September

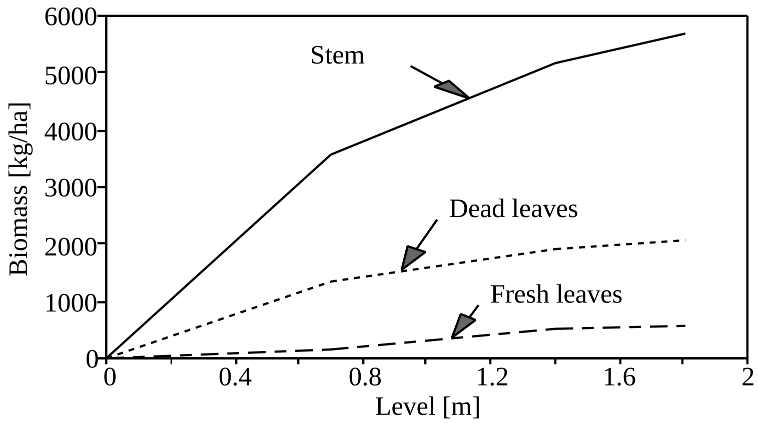

Figure 10.1: *Cumulative biomass of dead leaves, fresh leaves and stem* versus *height of the Nabou grassland vegetation at the end of July 1991.*

Table 10.2: *Estimates of living and dead biomass for the Nabou grassland site at different times of the year and derived estimates of LAI.*

Date **1991**	**Total biomass** kg m-2	**Dead leaves** kg m-2	**Fresh leaves** kg m-2	**Stem** kg m-2	**Seed** kg m-2	**SLA** kg m-2	**LAI** m2 m-2
February 23-28	0.687	-	(0.178)a	(0.508)a	-	(11.4)b	2.0
May 11	0.824	0.081	0.112	0.560	0.071	11.4	1.3
July 23 - August 10	(0.824)c	0.207	0.055	0.561	-	(11.4)b	0.6
September 1	(0.824)c	(0.247)d	0.016	0.561	-	(11.4)b	0.2

a: Dead leaves were assumed absent, grass not yet in flowering stage therefore no seed.
b: Using the SLA as determined on May 11.
c: Total grass biomass assumed to remain constant after May 11.
d: All foliage above 0.7 m dead (visual observation). Fraction of living leaf mass below 0.7 m to total plant mass, as determined between July 23 and August 10, used in the calculation of LAI

all leaves above a height of 0.7 m had died (visual observation) but some green plants were observed below this level. The distribution of biomass between dead leaves, green leaves and stems as well as approximate LAI values at different times of the year are shown in Table 10.2.

Estimates of LAI were obtained by combining the estimated green leaf biomass with the SLA. The SLA of mission grass was estimated at 11.4 m^2 kg^{-1} in May and multiplying this value with the fresh leaf biomass of 1121 kg ha^{-1} yielded an LAI of 1.3 m^2 m^{-2}. An approximation of the LAI for February was made by assuming that all leaves on a plant were green at that time (no moisture stress in the wet season) and that both the leaf to leaf+stem mass ratio and the SLA were similar to those in May. As it unlikely that the SLA will vary much throughout the year, the main error will be associated with the calculated green leaf mass fraction which was estimated at 25% of the total plant mass in February (Table 10.2). No actual leaf biomass and SLA data were available to calculate the LAIs for July, August or September. However, total

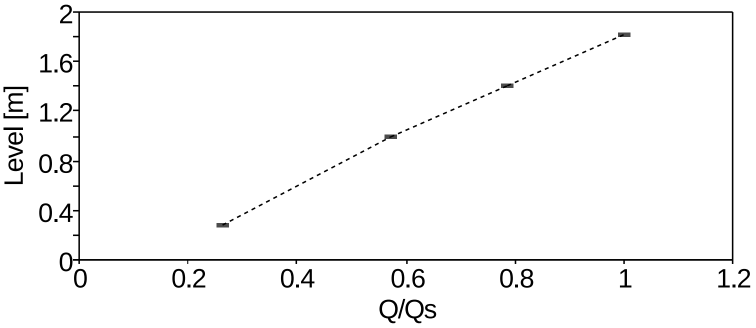

Figure 10.2: *PAR fractions (Q/Q_s) received at several levels within the grass cover.*

biomass for May may be taken as a good approximation as both decomposition and production of biomass are low during the dry season. The distribution of the biomass over the various plant components was determined at the end of July (Section 10.2) and the fresh leaf biomass was obtained by combining the May biomass value with the fraction of fresh leaf mass to total plant mass. Using the SLA value for May the LAI at the end of July was estimated at 0.6 m^2 m^{-2}. On the first of September all leaves above a height of 0.7 m had died and the fresh leaf mass fraction of the 0–0.7 m level (2% of total plant mass), determined between July 23 and August 10, was used to calculate an LAI of 0.2 m^2 m^{-2} from the May biomass and SLA values, which may be considered as the seasonal minimum. This shows that the seasonal variation in grassland LAI is large with a 10-fold difference between the wet season maximum and the dry season minimum. The estimated wet season value of 2.0 m^2 m^{-2} is much higher than the 0.8(±0.3) m^2 m^{-2} found for short grass with a much lower biomass (biomass of grass and litter amounted to 5600 kg ha^{-1}) by McWilliam *et al.* (1993) in a clearing in Amazonia.

The PAR fraction (Q/Q_s) varied from 0.27(±0.15) just above the litter layer to 0.79(±0.11) at 1.4 m as shown in Figure 10.2, with incoming PAR (Q_s) ranging from 860 to 1090 μmol m^{-2} s^{-1}. The canopy gap fraction increased from 35±24% just above the litter layer to 79±16% at 1.0 m and 97±5% at 1.4 m. As shown in more detail in Section 11.2, if the LAI is known the light extinction coefficient (κ) of a canopy can be calculated from the PAR fraction using the Beer-Lambert equation (Pierce and Running, 1988). The extinction coefficient κ is an empirical parameter depending on the geometry of the canopy and ranges from 0.3 to 1.5, with the lower values corresponding with an erectophyl type of canopy (Ross, 1975). Ripley and Redman (1976) found an extinction coefficient of 0.63 for short grass in the temperate zone. Linear interpolation of the derived LAI estimate for May and July-August 1991 resulted in an LAI of 0.8 m^2 m^{-2} on July 10 (*i.e.* the day that the PAR profile of Figure 10.2 was determined). For a measured PAR fraction of 0.27 just above the litter layer, κ would have the very high value of 1.64, which must be attributed to the large amount of PAR intercepted by the grass stems and various kinds of dead material.

Table 10.3: *Concentrations of nutrients in Pennisetum polystachyon grass and litter at the Nabou study site. Macronutrients in %, micronutrients in ppm.*

	N	P	K	Ca	Mg	B	Mn	Zn
Litter	0.497	0.030	0.070	0.359	0.129	20	337	5.5
Mission grass	0.469	0.043	1.328	0.223	0.241	15	284	3.9

Table 10.4: *Total amounts of nutrients (kg ha^{-1}) stored in Pennisetum polystachyon grass and grassland litter at the Nabou study site.*

	N	P	K	Ca	Mg	B	Mn	Zn
February 1991								
Litter standing crop	52.5	3.2	7.4	37.9	13.6	0.058	3.566	0.206
Mission grass	30.4	2.8	86.1	14.4	15.6	0.025	1.842	0.097
Total	*82.9*	*5.9*	*93.5*	*52.4*	*29.2*	*0.083*	*5.408*	*0.304*
May 1991								
Litter standing crop	34.1	2.1	4.8	24.6	8.9	0.037	2.315	0.134
Mission grass	38.6	3.5	109.4	18.3	19.8	0.032	2.340	0.124
Total	*72.7*	*5.6*	*114.2*	*43.0*	*28.7*	*0.070*	*4.655*	*0.258*

10.4 Grassland Nutrient Content

The concentrations of macro- and micronutrients in litter and fresh grass sampled in February 1991 are shown in Table 10.3. The concentrations of N, Ca and the micronutrients were higher in the litter, indicating that these nutrients may be released relatively slowly during decomposition. The concentration of K, on the other hand, was 18-fold higher in living grass than in litter, suggesting that K is easily leached. Concentrations of Mg and P were also higher in living grass but the difference was much less pronounced than for K. Nye and Greenland (1960) provided ranges of 0.29–1.8 for N, 0.05–0.14 for P, 0.54–1.2 for K, 0.17–0.42 for Ca and 0.29–0.35 for Mg. With the exception of K, the concentrations in the Nabou grass were at the lower ends of these ranges.

The amounts of nutrients stored in the grassland vegetation and litter were calculated for February and May, assuming that the concentrations did not change in time (Table 10.4). Amounts of nutrients stored in the litter layer generally exceeded those stored in the living crop in February, with the exception of K, and to a lesser extent Mg, which had a very low concentration in the litter. By the end of the growing season, however, substantial amounts of nutrients (presumably released from the litter layer through decomposition) had been taken up by the vegetation and amounts stored in the living plants exceeded those in the litter layer with the exception, mainly, of Ca. Interestingly, total amounts of nutrients stored in the living crop and litter layer decreased slightly (with the exception of K) as the dry season progressed, despite an overall increase in biomass from 7040 to 8848 kg ha^{-1}. This is thought to reflect the decrease in mass of the litter layer which was larger than the increase in living biomass (*cf.* Table 10.2).

Because the estimated seasonal variation in the combined mass of living grass and litter was not very large and the concentrations of N, P, Ca, B, Mn and Zn in fresh grass were not dramatically different from those in litter the total amounts of these nutrients stored in the vegetation should not show a very large seasonal variation either. However, K, and to a lesser extent Mg, may well show a large seasonal variation with progressively higher concentrations during the growing season, a rapid decline at the end of the growing season coinciding with the dying of the grass, and low levels during the dry season. Further work is necessary to test these assertions.

A rate of litter turnover (K_L) can be calculated as the ratio of the annual litter production to the litter standing crop (Swift *et al.*, 1979; Gunadi, 1993b; Burghouts, 1993). Such an estimate was obtained for the Nabou grassland site using the annual production rate of grass and the seasonal minimum litter standing crop (*cf.* Section 12.4). The grass vegetation is highly seasonal and dies off almost completely during the dry season. The annual production of grass litter can therefore be approximated by the annual grass production, which was estimated at 6646 kg ha^{-1} (Table 10.1). With a seasonal minimum litter standing crop of 6869 kg ha^{-1} as observed in May 1991, a K_L value of 0.97 was obtained. The rate of decomposition was highest during the wet season as indicated by the loss of 3712 kg ha^{-1} of litter between February 28 and May 10. As such most nutrients released from the decomposing grass litter can be used by the growing crop.

Chapter 11

Forest Biomass and Nutrient Content

11.1 Introduction

In this chapter a description will be given of the accumulation of biomass and nutrient content in *Pinus caribaea* plantations over a period of a rotation. Basic information on the structure of the forest at the respective experimental sites has already been presented in Sections 3.2 – 3.4. More detailed information including diameter and height distributions, pre- and post-cyclone growth rates and LAIs will be presented in this chapter to obtain insight into the changes in forest structure during a rotation period, which often involves damage by cyclones.

11.2 Methods and Field Procedures

Tree diameter and height surveys were carried out in the Tulasewa (n= 157), Korokula (n= 100) and Koromani forest plots (n= 100) between January and March 1990 and between July and September 1991. Measurements were also made on 10–15 trees in each plot in June and July 1990 and in January 1991 to obtain growth rates for 1990. An additional 106 trees were measured in the Tulasewa forest plot in July 1990 and 368 trees in Koromani forest in July and August 1991 to obtain information on the forest structure surrounding the meteorological towers (*cf.* Chapter 7). Diameters at breast height (1.35 m) over bark (*Dbhob*) were measured with a diameter tape with a resolution of 0.1 cm. Tree height (*h*) and the height of the lowest branch with green needles (crown depth) were measured with a Haglöf clinometer and a measuring tape. Estimates of the mean tree height, obtained with the clinometer, differed by less than 2% from the actual mean height of 39 trees. However, for individual trees the error in the clinometer estimates could be up to 15%. Estimates of the crown diameter were obtained by measuring dimensions of the projected crown at ground level with a measuring tape within the planting row and perpendicular to it.

In each age class (7, 12 and 16 years in 1991) five trees, with diameters and heights close to the stand averages, were destructively sampled for above-ground biomass estimations. One tree (tree A141) was sampled before the passage of cyclone Sina in

November 1990, the other trees were sampled between March and September 1991. No attempts were made to obtain estimates of below-ground biomass as the stumps of harvested trees are left *in situ* and therefore do not represent a net loss of nutrients. All trees were cut at a height of about 0.2 m with a chainsaw after the diameter, height, crown depth and crown diameters had been measured. The fresh weights of dead and green branches (diameter $\geq$1 cm), twigs (diameter $<$1 cm), needles, cones and male flowers were determined in the field for each two meter section of the living crown. Subsamples of each component were taken at each level to obtain factors for the conversion of fresh weights to dry weights and for chemical analysis. After the tree had been stripped from its crown the stem was cut into one-metre sections and 2 cm thick disks were collected from each section up to slash point (diameter over bark of 7 cm). Separate disks for chemical analysis were collected at the base of the tree, at the point with a diameter over bark (Dob) of 10 cm and at the level where $Dob = (Dob_{base} + Dob_{10cm})/2$. Fresh weight of each disk was recorded and the Dob measured, after which bark was separated from stemwood. Fresh weights of bark and stemwood were recorded and the diameter under bark (Dub) measured. For each trunk section bark weight was calculated from the mean bark to stemwood ratios of the disks collected at the two ends of the section. A rough estimate of the fresh bark and stemwood density was obtained by carefully placing in water and recording the height of the wetted area. The volume of each disk was measured as a function of its diameter and thickness as determined at six points with a calliper (precision 0.05 mm). The total dry weight of each component per tree was calculated by multiplying the total fresh weight of that component by the ratio of dry to fresh weight as determined from subsamples.

Weighed bulk samples were taken from stemwood, bark, dead branches and twigs and green branches and twigs for chemical analysis. Foliage samples were bulked such that representative samples were obtained for the lower, middle and upper levels of the canopy and for dead foliage. As the sample size was small the *Student's t* distribution was used to test whenever average concentrations in tree components differed between sites.

Nutrient concentrations in harvestable timber (wood and bark) for the Oleolega catchment were determined from disks collected from 12 trees according to the method described above. Five representative locations were selected within the catchment and 2–3 trees were sampled at each location in December 1990. The locations, coded A–E, are shown on the map given in Figure 15.3.

All samples were sent to the Forest Research Institute in New Zealand for analysis of N, P, K, Ca, Mg and B, Mn and Zn (foliage only) as described in Section 10.2.

An attempt was made to obtain relationships between available nutrients in the topsoil around the sample trees and corresponding concentrations in stemwood and foliage of those trees. Two soil samples were collected within 50 cm of the stumps immediately after the trees were sampled for biomass. The samples for each depth interval (0–10 and 10–20 cm) were bulked to account for spatial variations. The samples were air dried and analysed for exchangeable Na, K, Mg, Ca, NH_4, 'available' P and soluble NO_3, as well as for pH_{H2O}, pH_{KCl} and loss on ignition as described in Chapter 4. The analytical data are presented in Appendix 26.

Allometric regression equations (Pardé, 1980; Madgwick, 1983) were used to calculate weights of tree components as well as that of whole trees as a function of the stem volume ($Dbhob^2h$). Stand biomass (kg ha^{-1}) was calculated as the sum of the weights of the individual trees or tree components divided by plot area. Nutrient contents (kg ha^{-1}) were calculated as the product of the biomass of each component times the average concentration of the respective nutrient in that component.

The specific leaf area (SLA) was determined on 146 individual needle sets collected in Tulasewa forest and on 90 needle sets collected in Koromani forest (Opdam, 1993). The surface area of each individual set was calculated from needle length (l) and average thickness, as determined at $0.25 * l$ and $0.75 * l$ (Swank and Schroeder, 1974; Kaufmann and Troendle, 1981). Needle sets consisted mostly of three individual needles although sets containing two, four or five needles were not uncommon. When all needles within a set were grouped together a cylindrical shape was formed of which the radius was equal to the thickness of the needle. The surface area of the set was calculated from the length and the radius (r) following Equation 11.1 where n represented the number of needles in a set (3, 4 or 5). The fresh weight of each group of five sets was determined as well as the dry weight of all sets combined together.

$$2\pi rl + 2nrl \tag{11.1}$$

Information on the distribution of weight and moisture content of individual needle sets with height of the crown was obtained by randomly collecting 100 fresh needle sets within each 1 m section of the live crown from 14 trees and recording their fresh and oven-dry weights.

Estimates of pre- and post-cyclone LAIs for each of the study forests were calculated from the SLA, the foliage biomass and the tree density. Independent estimates were obtained using the Decagon Sunfleck ceptometer described earlier according to the method of Pierce and Running (1988). Several transects were made through each forest and at every 3 m along a transect 20 PAR (Q) measurements were made by holding the ceptometer level with arms outstretched and sampling while turning a 360° circle at about 15° increments. Measurements of incoming PAR (Q_s) were made regularly in adjacent grasslands. The Beer-Lambert equation (Equation 11.2) was used to calculate the LAI using an extinction coefficient (κ) of 0.52 as given by Jarvis *et al.* (1976) and confirmed by Pierce and Running (1988) for coniferous forests.

$$LAI = -\frac{\ln(Q/Q_s)}{\kappa} \tag{11.2}$$

Pre-cyclone measurements were made in Tulasewa forest only (July 1990, n= 50), whereas post-cyclone measurements were made in Tulasewa (n= 60), Korokula (n= 105) and in Koromani (n= 74) forests in July 1991. Another 131 measurements were made in the forest surrounding the meteorological tower near the Koromani forest plot. All measurements were made between 11:00 and 14:00 h under clear skies. Canopy gap fractions were determined in the same fashion and using the PAR treshold described in Section 10.2

The above-ground biomass of the undergrowth was measured in Koromani forest on May 5, 1991. All undergrowth vegetation in two squares, covering an area of 25 m^2 each, was cut at ground level and the total fresh weight for each species was recorded. Factors for the conversion of fresh weight to dry weight were obtained from subsamples collected for each species.

11.3 Tree and Forest Characteristics

In this section some background information is given on tree structure, as well as wood and foliage properties of *Pinus caribaea* Morelet var. *hondurensis* grown in Fiji, as obtained from the literature and the present study. The information has been included as some of it may be of importance for forest fire prediction models (pers. comm. Dr. M.E. Alexander) or as future reference for studies on pine plantation forests in Fiji. Furthermore, tree and forest structure have a large influence on the surface roughness parameters used for the calculation of evapotranspiration with various micro-meteorological techniques (Chapter 7).

11.3.1 Tree Structure

Changes in the mass–height distributions of stems, branches, foliage and total biomass during a rotation are shown in Figures 11.1A–D, respectively. Measured weights were converted to t ha^{-1} using the pre-cyclone biomass data presented in Section 11.5.

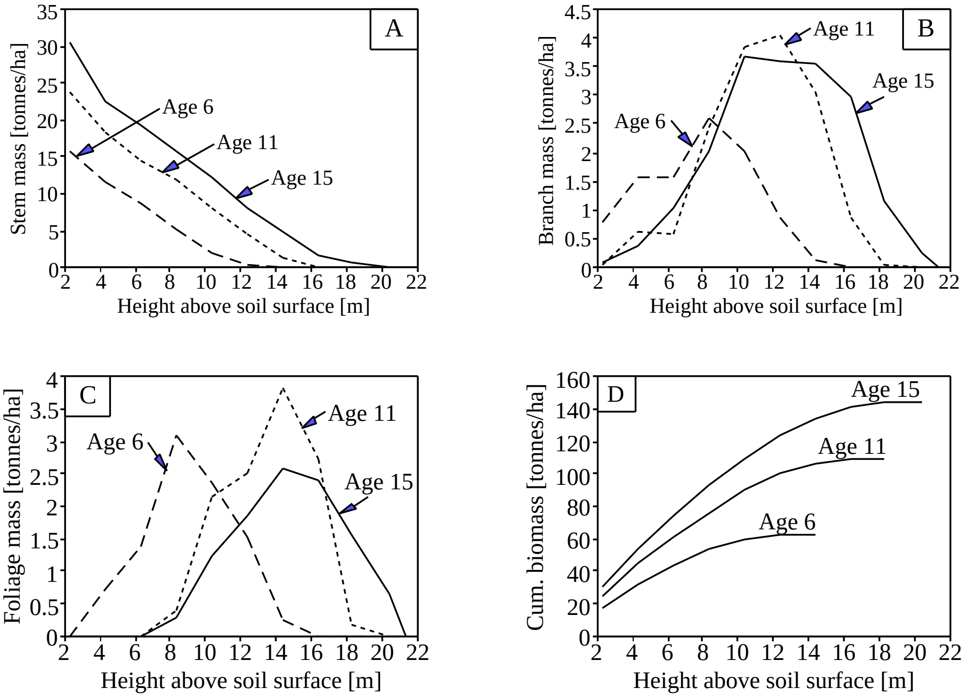

Figure 11.1: *Height distributions of stem biomass (A), branch biomass (B), needle mass (C) and cumulative total mass (D) for each of the forest plots.*

Information on the growth rates of the respective forests is presented in Section 11.3.4 and it suffices to say that annual diameter increments were much higher in the Tulasewa forest plot than in the Korokula and Koromani plots for which similar values were measured. Figure 11.1A shows that a large proportion of the stem biomass is contained in the lower part of the stem. The curves for the respective age classes are roughly parallel indicating that the stem form remains fairly constant throughout the rotation. The stem form can be described by the taper ($Dbhob/h$), which increased slightly with age from 0.0133($\pm$0.002) m m^{-1} at age six (n= 248) to 0.0139($\pm$0.003) m m^{-1} at age 11 (n= 100) and 0.0149($\pm$0.004) m m^{-1} (n= 450) at age 15. Similar values (range 0.0116–0.015 m m^{-2}) for the taper of *Pinus caribaea* were found in plantations in Nigeria (Egunjobi, 1975, 1976; Kadeba, 1991) whereas slightly higher values were observed in Puerto Rico (0.015–0.0175 m m^{-1}; Lugo, 1992).

Figures 11.1B and 11.1C show the development of the crown over a rotation period. Both branch and foliage mass were highest at the mid-crown position for all age classes. The low branch mass at age 6 as compared to those at age 11 and 15 shows that the crown was not yet fully developed at this age, although the foliage mass-height distribution curve was already similar in shape to those of the older forests (Figure 11.1C).

Branch angles were measured at the stem and at a distance of 50 cm from the stem on tree A141 in Tulasewa forest. At the base of the crown (2 m) branches pointed upwards at low angles ranging from 10–20° at the stem to 6–26° at 50 cm from the stem. The angle increased with height in the crown to 39–50° at the stem and 64–76° at 50 cm from the stem at a level of 8.7 m. Branches were near vertical at the top of the tree (11.8 m). In more mature forests, branches at the base of the crown were often near vertical or pointed downwards under a low angle up to distances of 1 m from the stem after which the angle increased to 10–20°, pointing upwards (visual observations).

Figure 11.1D shows that the total mass of the trees increased roughly linearly with the height of the tree until just below the mid-crown position, after which it levelled off.

11.3.2 Wood Properties

Cown *et al.* (1983) provided information on the wood properties of *Pinus caribaea* trees grown in Fiji. The pines in Fiji produced medium to high density wood with an average basic density of 515 kg m^{-3} for trees at age 15 grown in the lowlands. The basic density was positively related to tree age and the largest increase in density was observed between age 5 and 12 (from 340 kg m^{-3} to 470 kg m^{-3}). The basic density showed a negative correlation with site elevation, with 15-year old trees grown above 300 m a.s.l. having an average basic density of 445 kg m^{-3}. The density was highest in stemwood at the base of the tree (540 kg m^{-3} at age 11–15) and dropped below 460 kg m^{-3} above a height of 8 m.

The average dry wood density measured during the present study increased slightly with forest age, from 440(±40) kg m^{-3} in 7 year old pines (n= 5) to 460(±50) kg m^{-3} in 12 (n= 5) and 16-year-old pines (n= 5). The corresponding fresh wood density decreased from 1000(±40) kg m^{-3} at age 7 to 910(±100) kg m^{-3} at age 16. The basic density averaged 470, 526 and 500 kg m^{-3} in stemwood at the base of 7, 12 and 16 year old trees respectively, whereas corresponding densities at the top of the tree averaged 370, 404 and 370 kg m^{-3}.

The mass ratio of dry to fresh stemwood increased with forest age from 0.47(±0.05) (n= 5) at age 7 to 0.51(±0.02) (n= 5) at age 12 and 0.52(±0.07) (n= 5) at age 16. Slightly lower ratios were observed when branches and twigs were included (0.47, 0.50 and 0.51 respectively). Since sampling was restricted to the dry season the presence of a seasonal pattern could not be evaluated.

11.3.3 Properties of Foliage

The average dry weight of individual needle sets was related to height in the canopy but not to age of the tree, as shown in Figure 11.2. The lowest needle weights were observed at the crown base, ranging from 0.13(±0.03) g (n= 5) in Korokula forest

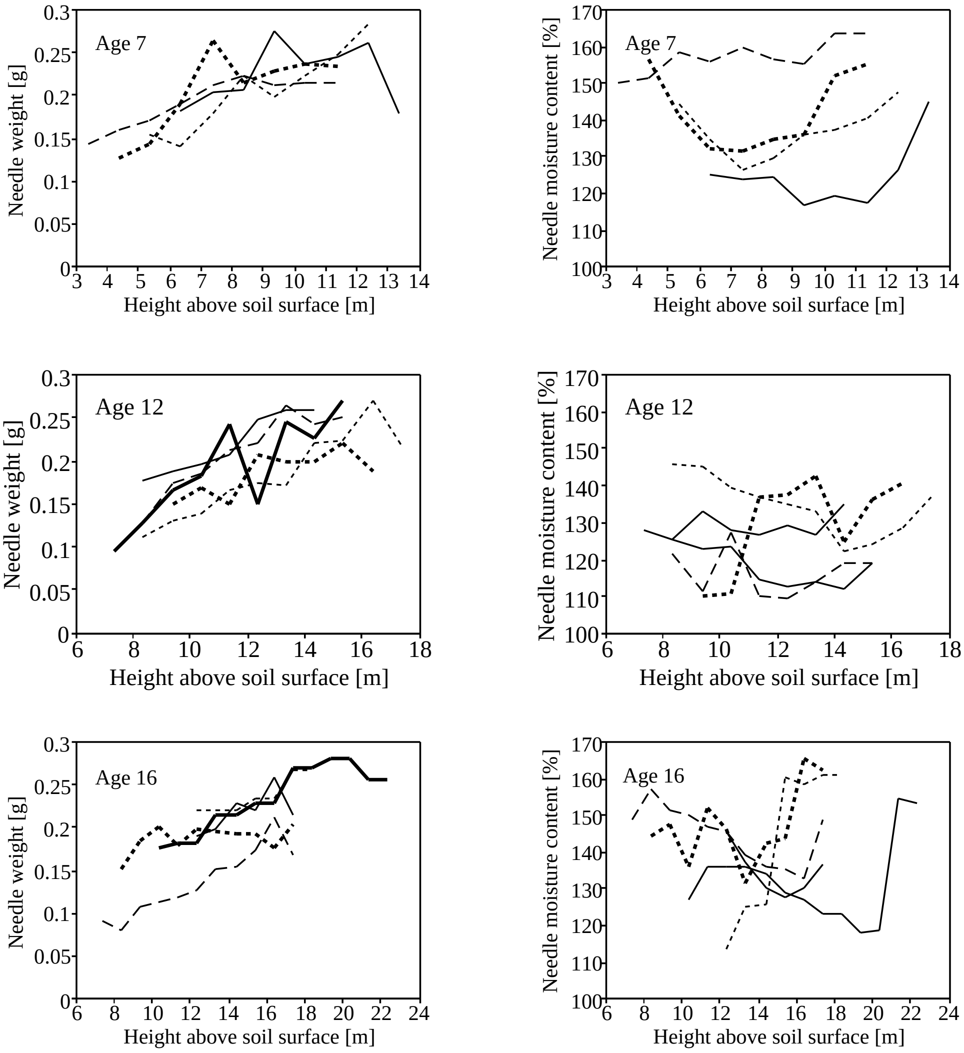

Figure 11.2: *Distribution of average dry weights and foliar moisture contents of individual needle sets (n= 100 needles m^{-1}) with height at age 7 (n= 4 trees), 12 (5 trees) and 16 (5 trees).*

to 0.17(±0.04) g (n= 5) in Koromani and Oleolega forest. Needle weights reached a maximum in the upper levels of the canopy (range 0.25(±0.04) – 0.26(±0.04) g) and decreased slightly at the top of the tree (range 0.222(±0.036) – 0.237(±0.03) g).

Needle moisture contents were related to needle age, as well as to soil moisture status at the time of sampling. Foliar moisture contents measured on 10 trees over a period of two years in a 10-year-old *Pinus caribaea* plantation forest in Toolara, Australia, decreased by 16–31% in old needles compared to the current growth. Similarly, needle moisture contents, measured during the wet season of 1991 in a 19-year-old forest near Darwin, Australia, decreased by 12–29% in old growth as compared to current growth. The moisture content of the current growth in Toolara varied between 137% and 161% over the 2-year period. A similar variation (133%–160%) was observed at the forest near Darwin (pers. comm. Dr. M.E. Alexander). During the present study observed needle moisture contents (Figure 11.2) varied between 110% and 170% of dry weight and were often lowest at the mid-crown position. The large variation observed between trees may partly be related to differences in soil moisture levels during sampling. The higher needle moisture contents observed in the lower levels of the canopy, where the oldest needles are usually found, reflects the regeneration of needles at this level due to improved light conditions following the defoliation by cyclone Sina and is therefore anomalous. The moisture content of the current growth (needles in the upper crown level) in Fiji showed a range similar to those observed in Australia.

Needles sampled in Tulasewa forest had an average length of 24.2(±2.7) cm (n= 146) and a total surface area of 21.05(±4.54) cm^2. The average weight of a dry needle set was 0.301 g resulting in a SLA of 3.55 m^2 kg^{-1}. Standard deviations could not be calculated as the weights of individual needle sets were not measured.

Needles collected at the base (8 m), the middle (13 m) and at the top (17 m) of the crown of tree C92 in Koromani forest were shorter than those collected in Tulasewa forest with average lengths ranging from 19.46(±2.1) cm (n= 30) at crown base to 20.0(±2.6) cm (n= 30) at mid-crown position. The average surface area of the Koromani needle sets increased from 16.1 cm^2 at the base of the crown to 19.0 cm^2 in the upper levels. The corresponding average needle weights increased from 0.15 g to 0.20 g (n= 100). The calculated SLA was 5.31 m^2 kg^{-1} at the base of the crown and decreased to 4.7 m^2 kg^{-1} and 4.9 m^2 kg^{-1} at a level of 13 m and at the top of the crown (17 m) respectively.

Needle lengths varied considerably with the position in the tree (visual observation by the author) but were roughly in the same range for the respective forest sites (*cf.* Figure 11.2) and the data obtained in the Tulasewa and Koromani forest plots were pooled to obtain and an average SLA of 3.77 m^2 kg^{-1}, which was subsequently used to calculate pre- and post-cyclone LAI values for each of the forest plots (Section 11.3.6).

11.3.4 Growth Rates

Tulasewa forest was vigorously growing during the wet season of 1990 with average diameter and height increments of 0.024(±0.007) m yr^{-1} (n= 18) and 2.5(±0.9) m yr^{-1} (n= 10) respectively. The growth slowed down somewhat during the dry season with mean diameter and height increments of 0.010(±0.008) m yr^{-1} (n= 6) and 1.5 m yr^{-1} (n= 8) respectively. This resulted in a pre-cyclone annual diameter increment of 0.018 m yr^{-1} and a height increment of 2.0 m yr^{-1}. The post-cyclone annual diameter increment was slightly lower at 0.014(±0.007) m yr^{-1} (n= 7) and was similar to the mean increments (n= 21) observed in a nearby permanent sample plot of the Fiji Pine Ltd. (0.017 m yr^{-1} and 0.016 m yr^{-1} during 1991 and 1992 respectively; pers. comm.

Dr. J.H.R. Heuch).

Average diameter increments in the Korokula forest plot were much lower than in the Tulasewa forest plot with values of 0.009(±0.005) m yr^{-1} (n= 10) for the wet season and 0.007(±0.004) m yr^{-1} (n= 10) for the dry season of 1990. This resulted in a mean annual pre-cyclone increment of 0.008(±0.003) m yr^{-1}. No increase (-0.001±0.005 m yr^{-1}) was observed between January 1991 and September 1991, *i.e.* after cyclone Sina, indicating that any biomass production was accounted for by regeneration of needles rather than wood production. However, post-cyclone mean annual diameter increments (n= 31) of 0.005 m yr^{-1} and 0.006 m yr^{-1} for 1991 and 1992 respectively were observed in a nearby permanent sample plot (pers. comm. Dr. J.H.R. Heuch).

The average diameter increment in Koromani forest was similar to that in Korokula forest at 0.013(±0.004) m yr^{-1} (n= 15) for the wet season and 0.007(±0.004) m $yr^{-}1$ (n= 15) for the dry season of 1990, resulting in a mean annual pre-cyclone increment of 0.009(±0.003) m yr^{-1}. As in Korokula forest, tree diameters showed no increase (-0.001±0.007 m yr^{-1}) between January 1991 and September 1991, although a post-cyclone annual diameter increment of 0.005 m yr^{-1} (n= 26) was again found in a nearby permanent sample plot of FPL (pers. comm. Dr. J.H.R. Heuch). Such reductions in diameter increment have also been observed to occur after pruning (50–70% of living crown removed) in an 8-year-old *Pinus patula* forest in Malawi (Adlard, 1969).

The increases in tree height fell within the error of measurements during the first six months of 1990, whereas cyclone damage resulted in an average decrease in tree height of 0.7(±1.5) m and 1.0(±1.9) m in Korokula and Koromani forest respectively.

11.3.5 Forest Structure

Table 11.1 provides information on the diameter, height, crown diameters and crown depth of trees in Tulasewa, Korokula and Koromani forests as measured at the start and end of the present study. Mean annual diameter increments (MAI) decreased with age from 0.026 m $year^{-1}$ in Tulasewa forest to 0.019 m yr^{-1} in Korokula forest and 0.014 m $year^{-1}$ in Koromani forest. Corresponding height increments decreased from 1.93 m $year^{-1}$ in Tulasewa forest to 1.34 m $year^{-1}$ and 1.17 m $year^{-1}$ in Korokula and Koromani forest respectively.

Crown depth increased only slightly after canopy closure from 9.1 m in Tulasewa forest to 11.1 m in Koromani forest. As such the living crown base level increased from an average 2.5 m above the soil surface at age 6 to an average 6.4 m above the soil surface at age 15. The crowns of the trees in Tulasewa forest were symmetrical and generally did not interlock although in some places overlap in foliage occurred. In Korokula forest tree crowns were interlocked and the unequal tree spacing resulted in asymmetrical crown shapes as indicated by the crown diameters which were on average 0.8 m larger between planting rows than within them. The tree crowns in Koromani forest were again symmetrical and interlocked in the better stocked areas of the plot. However, asymmetrical crowns were observed on trees along the edges of small gaps where trees had been removed by cyclones.

Changes in the distribution of *Dbhob*, tree height, crown diameter and crown depth over the period of a rotation are shown in Figures 11.3A–D. The frequency distribution curves of *Dbhob* (Figure 11.3A) approached normal distributions of which the mean increases with the age of the forest. The variation around the mean remained fairly constant during the development of the plantation.

In forests not affected by cyclones the shape of the tree height frequency distribution curves (Figure 11.3B) should be similar to that of the *Dbhob*. In the study

Table 11.1: *Averages and standard deviations of diameter, height, crown depth and crown diameter (m) of Pinus caribaea trees in the Tulasewa, Korokula and Koromani forest plots.*

	Average	SD	Maximum	Minimum	n
TULASEWA FOREST (Planted 1984)					
January 1990					
Dbhob	0.156	0.042	0.026	0.253	239
Height	11.6	2.3	15.8	3.6	239
Crown depth	9.1	2.3	14.4	2.1	239
Crown diameter	2.6	0.8	4.6	0.8	225
January 1990, trees planted in 1980					
Dbhob	0.255	0.038	0.182	0.315	15
Height	14.7	3.2	19.7	8.1	15
Crown depth	10.5	2.4	15.1	5.0	15
Crown diameter	3.7	0.9	5.0	2.0	15
September 1991					
Dbhob	0.181	0.044	0.277	0.045	135
Height	13.1	2.6	18	4.2	61
September 1991, trees planted in 1980					
Dbhob	0.272	0.044	0.339	0.185	14
Height	17.9	1.7	20.6	15.7	7
KOROKULA FOREST (Planted 1979)					
January 1990					
Dbhob	0.204	0.036	0.281	0.095	100
Height	14.7	2.6	19.1	6.0	100
Crown depth	9.7	2.2	15.1	4.6	100
Crown diameter (2 m)	3.0	1.2	9.0	0.2	99
Crown diameter (3 m)	3.8	0.9	7.0	1.6	99
September 1991					
Dbhob	0.211	0.038	0.306	0.100	95
KOROMANI FOREST (Planted 1975)					
January 1990					
Dbhob	0.249	0.055	0.461	0.114	100
Height	17.5	2.6	24.3	5.7	100
Crown depth	11.1	2.2	16.5	3.5	100
Crown diameter (3 m)	3.9	1.2	8.0	1.4	99
September 1991					
Dbhob	0.256	0.057	0.479	0.120	100

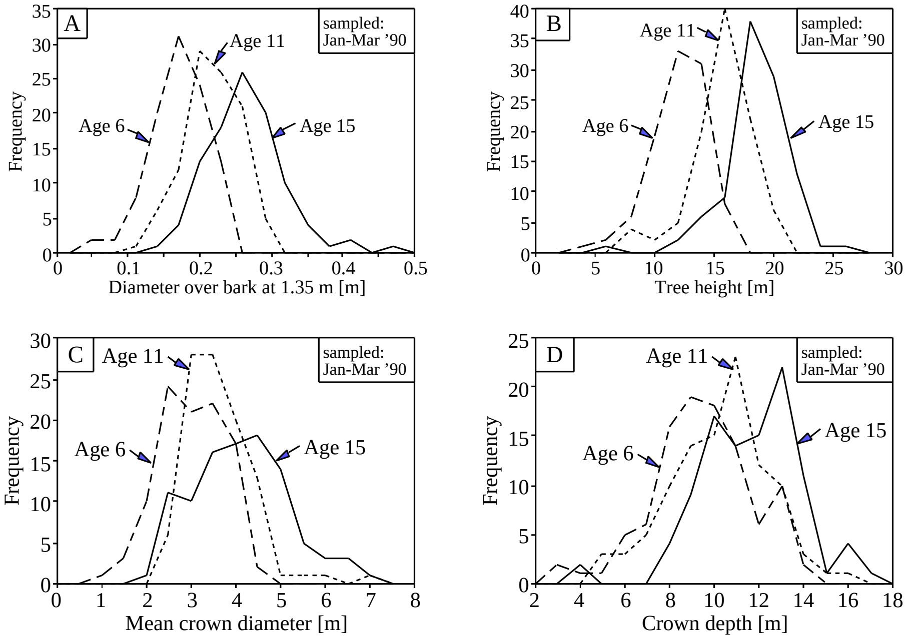

Figure 11.3: *Frequency distributions (n= 100) of the diameter at breast height (A), height (B), crown diameter (C) and crown depth (D) of Pinus caribaea trees at age 6, 11 and 15.*

forests in Fiji, however, the number of trees damaged by cyclones increased with age of the forest (0% in Tulasewa forest in 1990, 35% in Koromani forest). As a result the tree height distribution curves show an increased skewness to the left with increasing forest age (Figure 11.3B).

The crown diameter frequency distribution curves of Tulasewa forest and Koromani forest (Figure 11.3C), which both had been planted at a spacing of 3∗3 m, had a different shape than that of Korokula forest (spacing 2∗3 m), showing the influence of different spacings on crown development. In Koromani forest, and to a much lesser extent in Korokula forest, gaps were created as a result of cyclone damage. Trees at the edge of such gaps usually had larger crown diameters which showed up in the frequency distributions of these forests as a skewness to the right. Figure 11.3D shows the general increase in mean crown depth with forest age. The variation around the mean is high throughout the rotation.

11.3.6 Leaf Area Indices and Canopy Gap Fractions

For each forest plot pre- and post-cyclone LAIs were calculated by combining estimates of foliage biomass (Section 11.5.2) with the SLA (Section 11.3.3). The results are presented in Table 11.2. The pre-cyclone LAI was lowest in Tulasewa forest, whereas the highest value was found for Korokula forest, due to its higher stocking (compared to Koromani forest). Post-cyclone LAIs, measured some 6–9 months after the cyclone event, were significantly lower (α= 0.05) in spite of the regeneration of foliage that

Table 11.2: *Pre- and post-cyclone leaf area indices as obtained from foliage biomass estimates, and from PAR attenuation measurements (κ= 0.52). Standard deviations are given between parentheses, n represents the number of trees (biomass estimates) or the number of sampling locations (ceptometer estimates).*

	Pre-cyclone LAI				**Post-cyclone LAI**			
Location	**Biomass** [m2 m-2]	**n**	**Ceptometer** [m2 m-2]	**n**	**Biomass** [m2 m-2]	**n**	**Ceptometer** [m2 m-2]	**n**
Tulasewa forest	3.5 (0.9)	239	3.7 (1.5)	50	1.7 (0.6)	135	1.5 (1.1)	60
Korokula forest	4.4 (0.7)	100			3.2 (0.7)	95	3.5 (1.4)	105
Koromani forest	4.0 (0.7)	100			3.1 (0.8)	100	2.4 (1.3)	74
Koromani meteosite North							4.0 (1.2)	65
Koromani meteosite South							3.0 (1.4)	66
Koromani meteosite							3.5 (1.4)	131

had occurred in the mean time.

LAI values were also calculated from PAR attenuation measurements (Pierce and Running, 1988) using the Beer-Lambert equation (Section 11.2). Below-canopy PAR values ranged between 3% and 74% of incoming PAR in Tulasewa forest, with an average of 20%. After the forest was damaged by cyclone Sina a larger range of 8%–85% was observed and the PAR within the forest averaged 39% of that outside the forest. Post-cyclone average values of below-canopy PAR in Korokula and Koromani forests ranged from 16–36% of incoming PAR. No pre-cyclone observations were made in these forests.

In Koromani forest post-cyclone ceptometer measurements were made in the forest plot as well as in the area surrounding the meteorological tower (Koromani meteosite). To the north of the road (Figure 3.3) the forest was denser than that to the south of the road which had sustained considerable damage from cyclones. This showed up neatly in the LAI values obtained for the two locations (Table 11.2). The large range in LAI values obtained for Koromani forest reflects the variation in the canopy as a result of cyclone damage.

The LAI values calculated from PAR attenuation measurements using the Beer-Lambert equation were within 25% of those obtained from the biomass and SLA measurements. Extinction coefficients could be calculated for the forest sites by combining the PAR attenuation values with the LAI values derived from biomass measurements. This resulted in κ values of 0.46 and 0.55 for the pre- and post-cyclone forest at Tulasewa, respectively, whereas post-cyclone values of 0.45 and 0.43 were obtained for Korokula and Koromani forests, respectively. These values are close to the average extinction coefficient of 0.52 found for coniferous forests in temperate climates (Jarvis *et al.*, 1976).

Post-cyclone canopy gap fractions ranged from a minimum of 27(±22)% in the forest surrounding the meteorological tower in Koromani to 50(±26)% in Tulasewa forest. The canopy gap fraction measured in Korokula forest was 28(±23)%. Again there was a considerable variation of the canopy gap fraction in Koromani forest with a minimum of 19(±16)% in the forest north of the road and a maximum of 46(±26)% within the plot (*cf.* Section 6.4.1).

Table 11.3: *Regression constants (a, b), standard errors (SE) of the means, coefficients of determination and standard errors of estimate (ERE) for regression analyses using a multiplicative model ($h = a * Dbhob^b$) on two biomass data sets. The number of trees is represented by n.*

Dependent variable	a	SE	b	SE	R-squared	ERE	n
Sound trees	48.2787	1.0276	0.7295	0.0165	0.761	1.156	617
All trees	43.5496	1.0296	0.6832	0.0182	0.634	1.195	811

11.4 Estimations of Above-Ground Biomass

Several studies have been published dealing with the changes in above-ground biomass and nutrient content of *Pinus caribaea* plantation forests at various stages during a rotation. In these studies the whole-tree biomass and the biomass of the tree components (stemwood, stembark, branches and needles) are generally related to tree diameter (Egunjobi and Bada, 1979; Rance *et al.*, 1982; Kadeba, 1991) or volume, expressed as $Dbhob^2h$ (Egunjobi, 1976; , 1983) or as $0.5 * BA * h$, (Russell, 1983) where BA represents basal area (Rance *et al.*, 1982). Allometric regression models of the form $\ln Y = a + b \ln X$, where Y and X represent dependent and independent variables respectively, were used in these studies. Previous work on the determination of biomass of pine plantations in Fiji was carried out by Claeson *et al.* (1984), who compared four regression models on a data set of 18 trees. They found that the logarithmic model relating weight to volume ($Dbhob^2h$) showed the highest correlation coefficients. It is common to relate biomass to *Dbhob* only (Pardé, 1980) because the inclusion of h often does not improve the fit of the regression (Rance *et al.*, 1982; Claeson *et al.*, 1984). However, the inclusion of height in the regression equations does make sense in the Fiji situation, where the forests are often damaged by cyclones which results in a poor correlation between *Dbhob* and h for damaged trees. To illustrate this, diameter-height relations were established using data collected at Tulasewa, Korokula and Koromani forests. The data set consisted of 811 trees of which 194 were damaged by cyclones. Regression analysis was performed on the whole data set, and on a smaller data set containing sound trees only (n= 617). A multiplicative model ($h = a * Dbhob^b$) gave the best fit with a coefficient of determination (r^2) of 0.76 for the sound tree data set. The coefficient of determination decreased to 0.63 when damaged trees were included. The results of the regression analyses and the calculated regression lines are shown in Table 11.3 and Figure 11.4 respectively. The inclusion of cyclone damaged trees resulted in a 6% decrease in predicted tree height.

The tree biomass data collected during the present study in Nabou forest are given in Table 11.4. They were consequently combined with those collected by Claeson *et al.* (1984) (summarized in Table 11.5) to obtain a data set of 32 trees for which expressions were obtained for the total tree biomass and for the mass of the bole, stemwood, stembark and branches. Because Claeson *et al.* (1984) did not make a distinction between branches and twigs, expressions for these components were obtained from the data collected during the present study (15 trees) only.

A logarithmic model ($\ln Y = a + b \ln X$) was used for biomass estimations, where Y represented the weight of the tree or its components and X the volume ($Dbhob^2h$).

Table 11.4: *Biomass data collected during the present study in the Tulasewa (A), Korokula (B) and Koromani forest plots (C), and in the Oleolega (O) catchment. All weights represent oven-dry values.*

Tree	Dbhob [m]	Height [m]	Total [kg]	Stem [kg]	Bole [kg]	Bark [kg]	Branches [kg]	Needles [kg]
A32	0.178	12.0	63.6	47.2	38.9	8.3	8.6	7.7
A47	0.188	12.3	83.0	60.8	50.4	10.4	13.9	8.2
A126	0.197	13.8	108.1	85.0	70.4	14.5	11.8	11.2
A141	0.189	11.8	92.5	55.1	47.5	7.6	19.5	16.4
A221	0.192	11.3	99.4	63.2	53.7	9.4	21.9	12.5
B17	0.206	14.4	125.7	98.3	83.8	14.5	18.2	8.9
B32	0.225	15.7	159.1	123.9	106.6	17.4	24.7	9.5
B59	0.212	16.2	138.4	111.6	100.1	11.5	17.9	8.7
B80	0.206	17.3	162.9	131.6	114.7	17.0	21.3	9.7
B92	0.210	15.8	150.9	113.3	99.9	13.4	26.1	11.4
C20	0.259	17.7	191.3	163.6	135.6	28.0	19.0	8.7
C88	0.270	17.9	225.9	176.5	152.4	24.1	32.9	16.0
C98	0.267	17.8	265.4	208.4	189.6	18.8	40.4	15.7
O13	0.260	18.7	225.5	185.7	163.3	22.4	27.2	12.3
O14	0.264	20.3	377.6	290.0	261.1	28.9	59.8	27.7

Tree	Dbhob [m]	Height [m]	D. branch [kg]	L. branch [kg]	D. twigs [kg]	L. twigs [kg]	Cones [kg]	M. flowers [kg]
A32	0.178	12.0	0.6	6.6	0.38	1.00	0.01	0.00
A47	0.188	12.3	1.8	10.9	0.53	0.71	0.09	0.00
A126	0.197	13.8	1.3	9.0	0.29	1.25	0.08	0.00
A141	0.189	11.8	2.3	14.8	0.56	1.74	1.50	0.00
A221	0.192	11.3	2.6	17.2	0.70	1.35	1.52	0.00
B17	0.206	14.4	3.3	13.7	0.23	0.94	0.16	0.00
B32	0.225	15.7	6.3	15.6	0.44	2.39	0.86	0.01
B59	0.212	16.2	2.9	13.9	0.32	0.74	0.13	0.04
B80	0.206	17.3	5.7	14.4	0.39	0.82	0.09	0.01
B92	0.210	15.8	4.2	18.4	0.81	2.68	0.00	0.00
C20	0.259	17.7	5.3	12.7	0.13	0.83	0.02	0.00
C88	0.270	17.9	2.4	26.4	0.46	3.72	0.15	0.00
C98	0.267	17.8	7.0	30.6	0.75	1.98	0.67	0.03
O13	0.260	18.7	3.5	22.4	0.21	1.12	0.22	0.00
O14	0.264	20.3	4.7	51.7	0.87	2.59	0.13	0.00

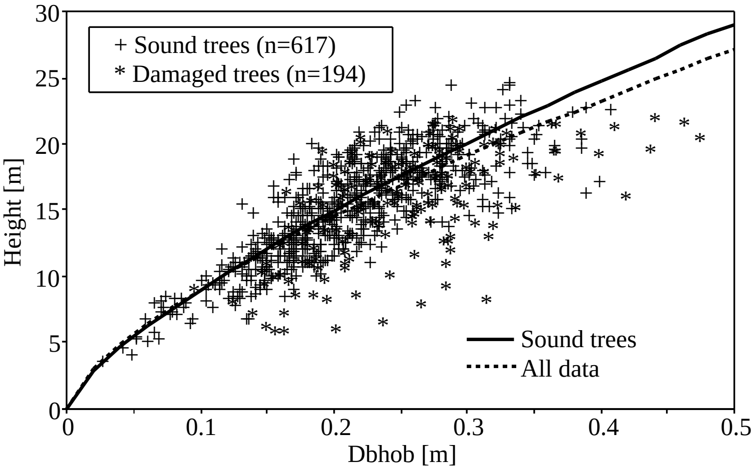

Figure 11.4: *Relationships between diameter at breast height and tree height for two data sets.*

Table 11.5: *Biomass data collected by Claeson* et al. *(1984) in the forests of the Fiji Pine Commission. One small tree ommited as its height (0.9 m) did not correspond with its diameter at breast height (0.04 cm). All weights expressed as oven-dry (105° C) weights.*

Tree	Dbhob [m]	Height [m]	Total [kg]	Stem [kg]	Bole [kg]	Bark [kg]	Branches [kg]	Needles [kg]
F67	0.230	17.2	189.0	145.2	132.4	12.8	18.0	16.7
P70	0.168	15.0	77.5	54.8	47.2	7.6	14.1	8.6
P73A	0.187	13.9	87.9	56.6	44.4	12.2	18.6	12.7
P78A	0.143	7.7	32.3	22.6	18.9	3.7	3.5	6.2
P68A	0.245	18.3	237.0	187.0	153.1	33.9	27.6	22.4
P68B	0.230	16.8	219.0	177.9	152.5	25.4	32.9	8.2
P69	0.179	16.8	140.2	107.3	95.4	11.9	19.5	13.4
P70	0.226	20.1	227.4	184.6	168.8	15.8	27.9	14.9
P71	0.171	10.8	52.9	34.9	28.1	6.8	4.8	13.7
P72	0.197	14.3	110.6	81.5	70.4	11.1	18.1	11.0
P73B	0.165	13.6	93.4	62.4	53.3	9.1	13.2	17.8
P74A	0.205	12.4	96.2	61.8	53.2	8.6	17.4	17.0
P74B	0.204	13.9	125.1	89.5	77.7	11.8	16.6	19.0
P75	0.179	11.6	69.7	49.8	43.1	6.7	7.1	12.8
P76	0.155	8.7	61.8	31.7	26.8	4.9	16.9	13.2
P77	0.125	6.8	37.4	22.6	19.6	3.0	5.4	9.4
P78	0.072	4.6	10.2	3.2	2.5	0.7	2.3	4.7

Table 11.6: *Regression constants (a, b), coefficients of determination (R-squared) and standard errors of estimate (ERE) for equations of the model* $\ln Y = a + b \ln X$ *to predict various biomass components of pinus caribaea trees in Viti Levu. The number of trees used in the regressions is represented by n.*

Dependent variable	a	SE	b	SE	R-squared	ERE	n
Total weight	5.2672	0.0391	0.8449	0.0372	0.945	1.19	32
Bole weight	5.0528	0.0373	1.0414	0.0355	0.966	1.18	32
Stemwood weight	4.9146	0.0419	1.0669	0.0398	0.960	1.20	32
Bark weight	2.9826	0.0427	0.8923	0.0406	0.942	1.21	32
Branch weight	3.2691	0.0799	0.7364	0.0759	0.758	1.42	32
Dead branch weight	1.3909	0.1601	0.9036	0.2927	0.423	1.67	15
Live branch weight	3.0400	0.1083	0.8073	0.1981	0.561	1.41	15
Dead twig weight	-0.9176	0.1754	-0.1302	0.3206	0.013	1.75	15
Live twig weight	0.4659	0.1585	0.4510	0.2898	0.157	1.66	15
Foliage							
Pre-cyclone	2.8143	0.1019	0.3105	0.0768	0.505	1.34234	18
Post-cyclone	2.5472	0.0878	0.4726	0.1698	0.392	1.32416	14

No corrections were made for the small errors resulting from the log-antilog transformation of the variables as these tend to increase the bias (Madgwick, 1983). The regression constants and the coefficients of determination are given in Table 11.6. The correlations between $Dbhob^2h$ and weight were good for total tree mass, bole, stemwood, stembark and combined branch and twig mass, with coefficients of determination ranging between 0.76 and 0.97. Tree biomass and predicted biomass have been plotted against *Dbhob* in Figure 11.5. The coefficients of determination were much lower (0.16–0.56) for the equations predicting biomass of foliage, dead and live branches and live twigs (table 11.6).

Fourteen of the 15 trees in the present data set were sampled within four to ten months after cyclone Sina defoliated the forests. Although fresh needles appeared shortly after the event, regeneration of foliage had not yet been completed at the time of sampling. This is clearly shown in Figure 11.6 where the foliage weights found during the present study and those of Claeson *et al.* (1984) are plotted against *Dbhob*. Separate regression equations were therefore obtained to predict pre-cyclone needle biomass (using the data set of Claeson *et al.* (1984) and tree A141 from the present data set) and post-cyclone needle biomass (using the present data set excluding tree A141) as shown in Figure 11.6. Because cyclones occur regularly in Fiji (*cf.* Section 2.4.4), the forests may be defoliated several times during a rotation and foliage mass may show large variations between trees within an even-aged cyclone damaged stand, as already indicated by the variations in the LAI for Koromani forest (Section 11.3.6).

No correlation with volume was observed for dead twigs ($r^2 = 0.01$) and the average weight of dead twigs on the five trees in each age class was used to calculate the total dead twig biomass for each plot.

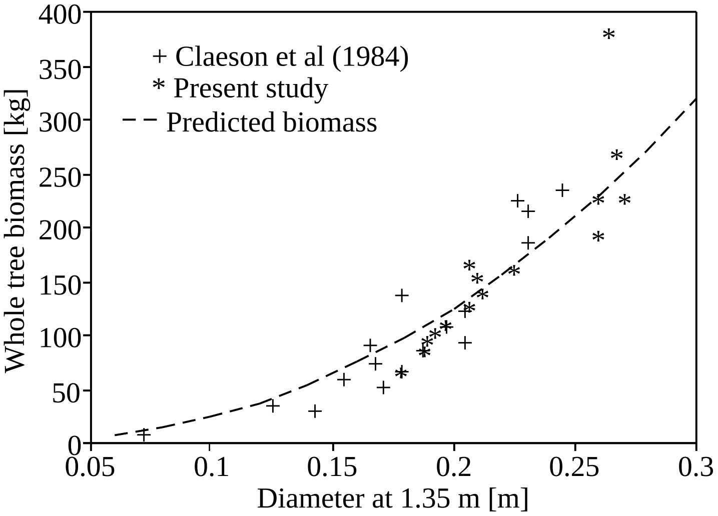

Figure 11.5: *Observed and predicted whole tree biomass as calculated with the logarithmic model. The predicted biomass curve was calculated using heights obtained from the diameter-height expression for the sound tree data set.*

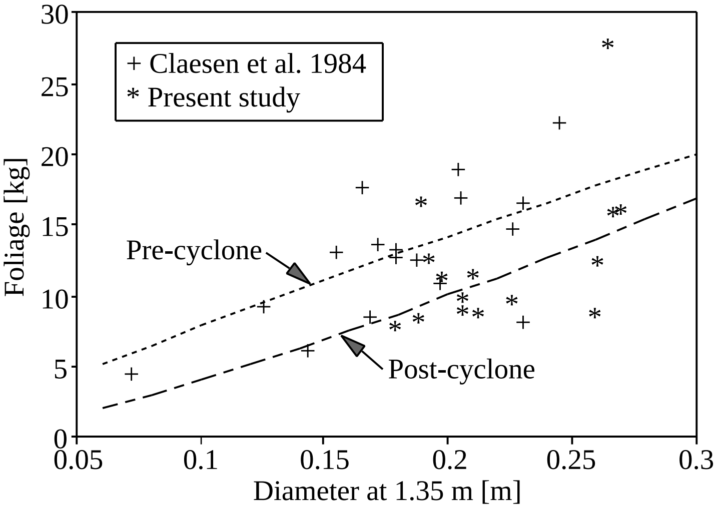

Figure 11.6: *Observed and predicted pre- and post-cyclone foliage biomass.*

11.5 Forest Biomass and Nutrient Content

The rate of nutrient accumulation by a plantation forest is a function of the rate of biomass production, the development stage of the plantation, the availability of nutrients in the soil and the tree species (Miller, 1984). Due to the length of a rotation period (15–20 years) it is usually not feasible to monitor a forest in this respect from planting until harvesting. Alternatively, information on the accumulation of biomass and nutrients may be obtained using a false time series, provided that environmental factors (particularly soils) are similar for each of the study forests (Bruijnzeel, 1983a). This approach has been used during the present study. Therefore the biomass and nutrient accumulation in pine forests of age 6, 11 and 15, representing young, intermediate and mature forest, respectively, were determined.

The research plots were located in relatively well stocked areas within Tulasewa, Korokula and Koromani forests (*cf.* Sections 3.2 – 3.4). The biomass in each of the plots was calculated from the regression equations and growth rates given in the previous sections and results are given in Section 11.5.1. The biomass of the mature forest stand in the Oleolega catchment was calculated from the volume of wood harvested from the catchment between December 1990 and August 1991 and will be discussed separately in Section 15.2.1.

To assess the impact of differences in the soil nutrient status on forest nutrient content an attempt was made to relate nutrient concentrations in foliage and stemwood (Section 11.5.2) to those in the soil around the trees sampled for biomass (Section 11.5.3). The nutrient content and rate of uptake for each forest site will be discussed in Section 11.5.4.

11.5.1 Standing Biomass and Increment Rates

Pine Biomass

Details on the above-ground living pine biomass of the pine trees at the Tulasewa, Korokula and Koromani forest plots, the distribution of biomass within the trees and the productivity of the respective forests are given in Table 11.7. In January 1990 utilisable wood (stemwood and bark) accounted for 70% of the total biomass in Tulasewa forest, with branches and foliage each accounting for 15% of the total biomass. The proportion of needle biomass decreased with forest age to 11% of the pine biomass in the Korokula forest plot and to 7% of that in the Koromani forest plot. This corresponded with an increase in the proportion of utilizable wood to 75% and 80% of the pine biomass in the Korokula and Koromani forest plots, respectively. The proportion of branches and twigs remained more or less constant at 12–13%. Bark accounted for 14% (Tulasewa) to 12% (Koromani) of the total stem mass.

To obtain estimates of pre-cyclone forest productivity and of the loss of biomass after the passage of cyclone Sina, the above-ground biomass for January 1991 was predicted using pre-cyclone *Dbhob* and *h* increments (Section 11.3.4). Biomass predictions were made for sound as well as for cyclone damaged forests using the appropriate regression equations for the prediction of foliar biomass (Table 11.6). The loss of above-ground living biomass resulting from cyclone damage was calculated as the difference between the predicted biomass for the sound forest (using pre-cyclone diameter and height increments given in Section 11.3.4) and that for the damaged forest in January 1991 (based on the decrease in stocking, post-cyclone growth rates, and using the appropriate regression constants for foliage biomass). Tulasewa forest experienced a loss

Table 11.7: *Actual and predicted biomass and annual productivity estimates (MAI up to January 1990) for Tulasewa, Korokula and Koromani forests in kg ha^{-1} dry weight.*

	Total	Stemwood	Stembark	Branches		Twigs		Needles		Cones
				Dead	Live	Dead	Live	Dead	Live	
TULASEWA FOREST, ACTUAL BIOMASS										
Jan '90	62245	37129	6220	1254	7102	407	767		9366	
% of total		59.6	10.0	2.0	11.4	0.7	1.2		15.0	
Sep '91	54522	36329	5621	1139	6171	238	563	73	4460	206
% of total		66.6	10.3	2.1	11.3	0.4	1.0	0.1	8.2	0.4
KOROKULA FOREST, ACTUAL BIOMASS										
Jan '90	109400	71181	10935	2217	11941	360	1050		11715	
% of total		65.1	10.0	2.0	10.9	0.3	1.0		10.7	
Sep '91	103326	69577	10637	2157	11588	342	1009	124	8016	203
% of total		67.3	10.3	2.1	11.2	0.3	1.0	0.1	7.8	0.2
KOROMANI FOREST, ACTUAL BIOMASS										
Jan '90	144800	101579	13980	2855	14485	301	1028		10572	
% of total		70.2	9.7	2.0	10.0	0.2	0.7		7.3	
Sep '91	143283	101993	14013	2862	14508	301	1028	162	8268	148
% of total		71.2	9.8	2.0	10.1	0.2	0.7	0.1	5.8	0.1
TULASEWA FOREST, PREDICTED BIOMASS JAN '91										
Sound forest	84741	53294	8469	1713	9418	407	905		10535	
% of total		62.9	10.0	2.0	11.1	0.5	1.1		12.4	
Cyclone damaged	49697	32761	5152	1043	5703	238	539		4261	
% of total		65.9	10.4	2.1	11.5	0.5	1.1		8.6	
KOROKULA FOREST, PREDICTED BIOMASS JAN '91										
Sound forest	116969	76833	11665	2367	12664	360	1086		11993	
% of total		65.7	10.0	2.0	10.8	0.3	0.9		10.3	
Cyclone damaged	101048	67852.1	10422.9	2113.4	11380	342.2	1000		7937.4	
% of total		67.1	10.3	2.1	11.3	0.3	1.0		7.9	
KOROMANI FOREST, PREDICTED BIOMASS JAN '91										
Sound forest	154392	109030	14849	3034	15305	301	1062		10811	
% of total		70.6	9.6	2.0	9.9	0.2	0.7		7.0	
Cyclone damaged	143903	102645	14112	2882	14612	301	1034		8318	
% of total		71.3	9.8	2.0	10.2	0.2	0.7		5.8	
PRODUCTIVITY OF TULASEWA FOREST										
CAI (1990)	22496	16165	2249	459	2316	0	138		1169	
MAI (1990)	10374	6188	1037	209	1184	68	128		1561	
Loss by cyclone	35044	20533	3317	670	3715	169	366		6274	
PRODUCTIVITY OF KOROKULA FOREST										
CAI (1990)	7569	5651	730	150	723	0	36		278	
MAI (1990)	9945	6471	994	202	1086	33	95		1065	
Loss by cyclone	15921	8981	1242	254	1284	18	86		4056	
PRODUCTIVITY OF KOROMANI FOREST										
CAI (1990)	9592	7451	869	179	820	0	34		239	
MAI (1990)	9653	6772	932	190	966	20	69		705	
Loss by cyclone	10489	6385	737	152	693	0	28		2493	

in living biomass of 35,044 kg ha^{-1} (or 41% of the pre-cyclone above-ground biomass) of which 68% was accounted for by utilisable wood. Defoliation caused a reduction of 60% in the needle biomass of the remaining trees, lowering the proportion of the foliage biomass from 15% of the total in January 1990 to 8% in September 1991. The decrease in stocking from 826 stems ha^{-1} to 485 stems ha^{-1} resulted in a net loss in above-ground tree biomass of 7723 kg ha^{-1} at Tulasewa during the study. The tree biomasses in the Korokula and Koromani forest plots were reduced by 15,921 kg ha^{-1} and 10,489 kg ha^{-1} respectively. In Korokula forest the needle biomass was reduced by 34% causing a decrease in the proportion of needle mass to the total biomass from 11% to 8%. The cyclone caused an estimated reduction of 23% in the needle biomass of Koromani forest.

The stocking in Korokula forest was reduced from 822 stems ha^{-1} to 781 stems ha^{-1} by cyclone Sina and this, in combination with a decrease in average tree height, resulted in a loss in above-ground tree biomass of 6074 kg ha^{-1} during the study. The cyclone defoliated Koromani forest for a large part and afflicted some damage to tree tops but the stocking remained equal at 621 stems ha^{-1}. As the damage was limited to the forest canopy a small net loss in above-ground tree biomass of 1517 kg ha^{-1} was observed during the study.

The mean annual increment (MAI) of total pine biomass decreased slightly with forest age from 10374 kg ha^{-1} in the Tulasewa forest plot to 9653 kg ha^{-1} in the Koromani forest plot. Current annual increases in biomass components (CAI) for 1990 (Table 11.7) were calculated as the difference in above-ground living biomass as measured in January 1990 and predicted (from growth rate measurements given in Section 11.3.4) for sound forest in January 1991. Tulasewa forest was estimated to have accumulated biomass at the highest rate in 1990 with a CAI of 22496 kg ha^{-1} of which 18414 kg ha^{-1}, or 82%, was used for the production of utilisable wood. The CAI of foliage was lower than the MAI, indicating that crown development had peaked at an earlier age. The converse was true for the production of woody material for which the CAI was 2–2.6 times as large as the MAI. The CAI values for all tree components in the Korokula and Koromani forest plots were lower than the corresponding MAI values, indicating that maximum biomass production had occurred earlier in the rotation. Harvestable wood production accounted for 84% and 87% of the CAI in Korokula and Koromani forests respectively.

Undergrowth Biomass

No attempt was made to measure biomass of the living undergrowth directly in Tulasewa forest due to its large seasonal variation (grass). However, a rough estimate was obtained by multiplying the amount of undergrowth litter present on the forest floor in the Tulasewa forest plot (Section 12.5) times the mean ratio (1.23) of grass biomass to grass litter standing crop at the Nabou grassland site grassland (1.20, May 1991) and in Koromani forest (1.26, May 1991). This resulted in an estimated undergrowth biomass of 8066 kg ha^{-1}, which is comparable to that observed in the grassland (Section 10.3).

The undergrowth biomass of Korokula forest was estimated in a similar fashion, resulting in a low value of 1550 kg ha^{-1}. This value may be caused by the low amounts of light penetrating the forest, as indicated by the low canopy gap fractions obtained earlier for this forest (Section 11.3.6).

The undergrowth biomass in the Koromani forest plot was measured and amounted to 3296(±736) kg ha^{-1}, of which some 43% consisted of non-seasonal scrubs (*e.g. Psid-*

Table 11.8: *Average nutrient concentrations and standard deviations (SD) in various tree components in Tulasewa forest. Concentrations of macronutrients are in % and those of micronutrients are in ppm.*

Nutrient	Stemwood	Stembark	Branches		Twigs		Needles					Whole Tree
			Dead	Live	Dead	Live	Dead	Lower	Middle	Upper	Avg	
N	0.095	0.181	0.082	0.178	0.138	0.373	0.306	0.832	0.897	0.995	0.908	0.218
SD	*0.029*	*0.065*	*0.018*	*0.033*	*0.026*	*0.059*	*0.029*	*0.134*	*0.062*	*0.147*	*0.084*	*0.046*
P	0.015	0.020	0.007	0.027	0.011	0.089	0.024	0.078	0.092	0.112	0.094	0.026
SD	*0.001*	*0.007*	*0.002*	*0.003*	*0.005*	*0.035*	*0.008*	*0.011*	*0.020*	*0.024*	*0.015*	*0.003*
K	0.067	0.098	0.027	0.146	0.032	0.367	0.108	0.384	0.425	0.594	0.454	0.130
SD	*0.018*	*0.024*	*0.013*	*0.022*	*0.022*	*0.089*	*0.021*	*0.078*	*0.080*	*0.137*	*0.060*	*0.020*
Ca	0.048	0.052	0.144	0.113	0.186	0.178	0.732	0.699	0.518	0.292	0.507	0.127
SD	*0.004*	*0.010*	*0.015*	*0.024*	*0.015*	*0.021*	*0.215*	*0.122*	*0.146*	*0.110*	*0.093*	*0.029*
Mg	0.022	0.040	0.048	0.067	0.083	0.120	0.218	0.233	0.210	0.185	0.208	0.056
SD	*0.004*	*0.005*	*0.010*	*0.012*	*0.016*	*0.014*	*0.065*	*0.052*	*0.033*	*0.029*	*0.031*	*0.008*
B							10.7	10.5	8.4	8.1	9.0	
SD							*1.7*	*2.3*	*1.8*	*2.3*	*1.6*	
Mn							801	586	591	410	558	
SD							*391*	*282*	*132*	*176*	*107*	
Zn							30	33	34	32	33	
SD							*7*	*6*	*10*	*16*	*9*	

ium guajava, 36%) and young trees (*e.g. Commersonia echinata*, 7%). Grasses (*e.g. Pennisetum polystachyon*) accounted for only 37%, indicating that the undergrowth composition had changed considerably during a rotation.

Increased litter production by the undergrowth after the cyclone event in November 1990 (Section 12.3.1) in the Tulasewa and Korokula forest plots suggested that the improved light conditions within the stands (Section 11.3.6) caused an increase in productivity of the undergrowth. No such increase was observed in the Koromani forest plot.

11.5.2 Nutrient Concentrations of Pine Trees

Average nutrient concentrations and standard deviations (n= 5) for tree components and whole trees in Tulasewa and Korokula forests are given in Tables 11.8 and 11.9 respectively. Because there were no significant differences (α= 0.05) between concentrations in the components of trees sampled in the Koromani forest plot (n= 3) and in the Oleolega catchment (n= 2) the data were pooled and the results are shown in Table 11.10. There was considerable variation in nutrient concentrations between tree components. Concentrations of N, P and K generally increased in the following order: stemwood, dead branches, dead twigs < live branches, bark < dead needles, live twigs < live needles, whereas the concentrations of Ca and Mg showed a different pattern and increased in the order stemwood, bark < dead branches, live branches < dead twigs, live twigs < live needles < dead needles.

Even within an even-aged stand considerable variation was observed in the nutrient concentrations of all components. The largest variations were generally observed for P and K. Such variations in nutrient concentrations were also observed within even-aged *Pinus patula* stands in Tanzania (Lundgren, 1978).

Table 11.9: *Average nutrient concentrations and standard deviations (SD) in various tree components in the Korokula forest plot. Concentrations of macronutrients are in % and those of micronutrients are in ppm.*

Nutrient	Stemwood	Stembark	Branches		Twigs		Needles					Whole Tree
			Dead	Live	Dead	Live	Dead	Lower	Middle	Upper	Avg	
N	0.072	0.156	0.086	0.141	0.156	0.508	0.491	0.882	0.980	1.054	0.965	0.150
SD	*0.020*	*0.031*	*0.012*	*0.020*	*0.032*	*0.219*	*0.055*	*0.079*	*0.089*	*0.158*	*0.097*	*0.020*
P	0.016	0.069	0.016	0.019	0.020	0.080	0.031	0.065	0.069	0.073	0.068	0.026
SD	*0.010*	*0.064*	*0.019*	*0.019*	*0.005*	*0.046*	*0.007*	*0.009*	*0.003*	*0.007*	*0.005*	*0.007*
K	0.039	0.051	0.022	0.077	0.025	0.318	0.082	0.340	0.323	0.366	0.338	0.066
SD	*0.007*	*0.016*	*0.005*	*0.004*	*0.015*	*0.109*	*0.025*	*0.081*	*0.069*	*0.129*	*0.073*	*0.012*
Ca	0.052	0.073	0.138	0.120	0.236	0.231	0.642	0.553	0.423	0.274	0.414	0.091
SD	*0.008*	*0.038*	*0.040*	*0.056*	*0.033*	*0.091*	*0.184*	*0.287*	*0.146*	*0.057*	*0.198*	*0.019*
Mg	0.024	0.047	0.047	0.062	0.085	0.176	0.305	0.296	0.283	0.274	0.291	0.049
SD	*0.003*	*0.012*	*0.009*	*0.017*	*0.011*	*0.106*	*0.082*	*0.095*	*0.079*	*0.071*	*0.068*	*0.006*
B							13.8	12.6	11.6	12.1	12.2	
SD							*2.6*	*2.9*	*1.9*	*4.6*	*2.4*	
Mn							357	358	289	211	298	
SD							*57*	*105*	*25*	*20*	*51*	
Zn							23	25	29	34	29	
SD							*9*	*11*	*8*	*9*	*8*	

Table 11.10: *Average nutrient concentrations and standard deviations (SD) in various tree components in the Koromani forest plot and in the Oleolega catchment. Concentrations of macronutrients are in % and those of micronutrients are in ppm.*

Nutrient	Stemwood	Stembark	Branches		Twigs		Needles					Whole Tree
			Dead	Live	Dead	Live	Dead	Lower	Middle	Upper	Avg	
N	0.073	0.171	0.104	0.134	0.150	0.435	0.411	1.017	1.027	1.093	1.041	0.151
SD	*0.017*	*0.042*	*0.027*	*0.014*	*0.018*	*0.042*	*0.070*	*0.121*	*0.109*	*0.128*	*0.106*	*0.023*
P	0.010	0.014	0.008	0.015	0.009	0.058	0.029	0.066	0.067	0.077	0.070	0.014
SD	*0.004*	*0.006*	*0.004*	*0.001*	*0.004*	*0.008*	*0.014*	*0.008*	*0.011*	*0.017*	*0.010*	*0.003*
K	0.049	0.088	0.039	0.097	0.038	0.347	0.095	0.405	0.412	0.667	0.488	0.087
SD	*0.008*	*0.045*	*0.006*	*0.019*	*0.024*	*0.082*	*0.018*	*0.062*	*0.098*	*0.270*	*0.116*	*0.020*
Ca	0.061	0.114	0.160	0.154	0.291	0.320	0.761	0.690	0.578	0.331	0.533	0.108
SD	*0.012*	*0.060*	*0.046*	*0.059*	*0.033*	*0.100*	*0.050*	*0.163*	*0.135*	*0.099*	*0.117*	*0.019*
Mg	0.020	0.038	0.033	0.046	0.058	0.123	0.178	0.173	0.162	0.161	0.173	0.038
SD	*0.003*	*0.014*	*0.005*	*0.009*	*0.006*	*0.030*	*0.044*	*0.033*	*0.045*	*0.043*	*0.041*	*0.012*
B							14.7	16.0	13.6	14.9	14.8	
SD							*1.3*	*3.4*	*2.3*	*4.3*	*2.6*	
Mn							486	872	827	482	741	
SD							*200*	*703*	*786*	*613*	*608*	
Zn							26	29	32	35	32	
SD							*4*	*6*	*7*	*9*	*7*	

Foliar nutrient levels varied with position in the crown. Concentrations of N, P, K and Zn increased with height and were lowest in dead needles, indicating that retranslocation of these nutrients into living tissue may occur prior to abscission. Concentrations of Ca, Mg, B and Mn decreased with height (needle age) and were highest in dead foliage indicating accumulation of these nutrients in litterfall. Micronutrients were not analyzed in woody components and estimates of the amount of micronutrients in stem biomass were therefore made using the average concentrations of B, Mn and Zn observed in 12 stems sampled in the Oleolega drainage basin (Table 15.2).

Significance levels for the differences in average nutrient concentrations between sites are shown in Table 11.11. Significant differences between the sites were observed for all nutrients except Zn (in foliage only). Egunjobi and Bada (1979) observed little variation in nutrient concentrations in *Pinus caribaea* tree components between two stands of age 6 and 10 planted on soils with similar chemical characteristics in Nigeria. This suggests that the presently observed differences in nutrient concentrations between the sites may be related to differences in soils rather than to changes with forest age. Therefore, an attempt is made in Section 11.5.3 to relate differences in nutrient concentrations of tree components to differences in soil nutrient status. The impact of inter-site differences in nutrient concentrations in the major nutrients sinks (such as stemwood and foliage) on the prediction of nutrient accumulation during a rotation period will be discussed in Section 11.5.4.

11.5.3 Plant–Soil Relations

The nutrient content of a forest depends on the accumulation of biomass and the nutrient concentrations in the various tree components, which are both in some way related to soil properties.

It is unlikely that the first rotation forests in the Nabou Estate have experienced nutrient or water stress for long periods of time. Therefore the impact of differences in soil type on biomass accumulation may be considered relatively small when compared to the impact of cyclones. However, differences in chemical properties of the soils in Tulasewa, Korokula and Koromani forests (Chapter 4) may well have influenced concentrations of nutrients in the various tree components (Mead, 1984), and thereby overall forest nutrient content.

To complicate the matter, the uptake of any specific nutrient often not only depends on the availability of that nutrient in the soil but also on a range of other factors like soil pH, the presence of other nutrients or complexes which interact with the nutrient under consideration, soil environmental conditions (*e.g.* moisture conditions, structure) and biotic factors (*e.g.* presence of fungi, distribution of roots) (Mead, 1984; Turner and Lambert, 1986). As such it is difficult to predict how variations in soil nutrient status will affect the total nutrient content of a forest at the end of the rotation.

Linear regression analysis was used to see whether stemwood and foliar nutrient levels (weighted averages) of the 15 trees sampled for biomass could be related to corresponding nutrient levels and pH_{H2O} in the 0–20 cm layer of soil around each of these trees. No attempts were made to relate nutrient levels in bark and branches to those in the soil as these tree components contained only a minor part of the total tree nutrient content (Tables 11.14 – 11.16). The regression equations used were of the form $Y = a_1X_1 + a_2X_2 + b$ where Y represented the levels of N, P, K, Ca, Mg in the tree components, and X_1 and X_2 those of corresponding nutrients in the soil and, whenever included in the regression, pH_{H2O}. No data were available for the micronutrient

Table 11.11: *Significance levels for differences in average nutrient concentrations in tree components per site. A= Tulasewa forest, B= Korokula forest, CO= Koromani/Oleolega forest.*

Difference	**Stem**		**Branches**		**Twigs**		**Foliage**			
in means	wood	bark	Dead	Live	Dead	Live	Dead	Low	Mid	High
NITROGEN										
A<>B	ns	ns	ns	>*	ns	ns	<***	ns	<*	ns
A<>CO	ns	ns	ns	>**	ns	<*	<**	<**	<**	ns
B<>CO	ns	ns	ns	ns	ns	ns	>*	<*	ns	ns
PHOSPHORUS										
A<>B	ns	<*	ns	>**	ns	ns	ns	>**	>**	>***
A<>CO	ns	<*	>*	>*	>***	ns	>*	>**	>**	>**
B<>CO	>*	ns	ns	ns	ns	ns	ns	ns	ns	ns
POTASSIUM										
A<>B	>***	>***	ns	>***	ns	ns	ns	ns	>**	>**
A<>CO	>*	ns	<*	>***	ns	ns	ns	ns	ns	ns
B<>CO	<*	<*	<***	<*	ns	ns	ns	ns	<*	<**
CALCIUM										
A<>B	ns	ns	ns	ns	<*	ns	ns	ns	ns	ns
A<>CO	<**	<**	ns	<**	<***	<**	ns	ns	ns	ns
B<>CO	ns	ns	ns	<*	ns	ns	ns	ns	<*	ns
MAGNESIUM										
A<>B	ns	ns	ns	ns	ns	ns	ns	ns	<*	<**
A<>CO	ns	ns	>**	>**	>***	ns	ns	>**	>*	ns
B<>CO	>*	ns	>**	>**	>**	ns	>**	>**	>**	>**
ZINC										
A<>B							ns	ns	ns	ns
A<>CO							ns	ns	ns	ns
B<>CO							ns	ns	ns	ns
MANGANESE										
A<>B							>**	>*	>***	>**
A<>CO							ns	ns	ns	ns
B<>CO							ns	<*	ns	ns
BORON										
A<>B							<*	ns	<**	<*
A<>CO							<**	<**	<***	<**
B<>CO							ns	<*	ns	ns

ns: not significant; *: significance level 0.10; **: significance level 0.05; ***: significance level 0.01

Table 11.12: *Regression constants (a_1, a_2 and b) and coefficients of determination for regression equations relating foliage and stem nutrient concentrations (%) to corresponding exchangeable nutrient concentrations in the soil (meq 100 g^{-1} soil) and pH_{H2O}.*

Dependent	Independent		Regression constants			CD	n
Y	X1	X2	a1	a2	b		
Stemwood							
K	K		0.243		0.031	0.341	15
K	K	pH	0.219	-0.017	0.126	0.385	15
P	pH		0.012		-0.048	0.128	15
P	P-Bray		0.257		0.008	0.586	3
Ca	pH		-0.015		0.135	0.100	15
Mg	pH		0.005		-0.006	0.107	15
Foliage							
K	K		1.288		0.316	0.204	15
K	K	pH	1.045	-0.176	1.275	0.301	15
N	pH		-0.179		1.924	0.102	15
P	P-Bray		-0.501		0.087	0.254	3
P	pH		-0.028		0.226	0.116	15
Ca	pH		-0.307		2.127	0.159	15
Mg	pH		0.167		-0.667	0.223	15
Mn	pH		-1004		5897	0.243	15

concentrations in the soil and concentrations of these elements in the vegetation were therefore related to soil pH$_{H2O}$ only. Regressions for which the coefficients of determination were higher than 0.1 are shown in Table 11.12. Not surprisingly, none of the regression equations was significant, with F-ratios lower than 3. The results indicated that the concentration of K in stemwood and foliage was positively related to that of exchangeble K in the soil, with coefficients of determination of 0.34 and 0.20 respectively. Inclusion of the pH$_{H2O}$ resulted in slightly higher coefficients of determination (0.39 and 0.30 respectively), with K inversely related to soil pH$_{H2O}$. No significant relations could be established for exchangeable Mg and Ca nor for 'available' N and P in the soil, and those in stemwood or foliage, with coefficients of determination all below 0.05.

The present method of P extraction employed a fairly weak extractant (Ca-lactate) and this undoubtedly resulted in the underestimation of 'available' P over longer periods of time. The Bray II extraction method, which was applied to the samples collected in the soil pits at the various study sites was more agressive (Dr. V.J.G. Houba, pers. comm.) and may have provided more realistic estimates in the case of trees (Sanchez, 1976). Regressions were therefore also calculated with the Bray-II P concentration in the 0-10 cm layer as independent and the average P content in foliage and stems as dependent parameters. The results showed that the P concentration in stems were positively related to Bray-II 'available' P in topsoil, whereas P in foliage showed a negative relationship to that in the soil.

Concentrations of P and Mg in stemwood were positively related to pH with coefficients of determination of 0.13 and 0.11 respectively, whereas Ca showed an inverse relationship with a coefficient of determination of 0.10 only. The concentration of Mg in foliage was positively related to pH whereas the concentrations of N, P and Ca showed an inverse relationship with soil pH.

A foliar nutrient status guide was developed for *Pinus caribaea* in Queensland by Bevege and Humphreys (1978) and this was used to determine whether any of the forest sites was likely to have nutrient deficiencies at the time of sampling (Table 11.13). The critical level for a nutrient also depends on other nutrients being adequately supplied (Mead, 1984) and deficiencies in one of the nutrients may alter the critical levels of other nutrients (Bevege, 1978). Critical levels are known to vary with forest age (Miller *et al.*, 1981) and tree provenance (Goddard and Hollis, 1984). There is also some uncertainty whether critical levels derived for a species in a specific region may be applied to the same species in other regions due to the dependency of the critical levels on environmental conditions (*e.g.* temperature, rainfall) (Mead, 1984). The foliar nutrient concentrations observed in Tulasewa, Korokula, Koromani and Oleolega forests were well above the adequacy levels as given by Bevege and Humphreys (1978), with the exception of B in Tulasewa forest (Table 11.13). This confirms the visual observation that the forests presently studied did not show any signs of nutrient stress. Boron levels in the foliage of Nabou and Ra forests (and to a lesser extent in Bua and Lololo forests) were below the suggested deficiency levels, which may cause problems similar to those observed in second rotation forests in the Lololo Estate (*e.g.* shoots without needles; Dr. J.H.R. Heuch, pers. comm.). Similarly the low N levels in the foliage collected in the Ra Estate indicate that deficiencies may occur in future rotations.

The foliar nutrient levels given in Table 11.13 show considerable variation both within and between regions, presumably reflecting differences in soil nutrient status, climate and possibly tree provenance. Furthermore, foliar nutrient levels are known to show a seasonal variation (Leaf, 1973; van den Driessche, 1974; Lamb, 1976) which may also explain part of the variation.

Foliar nutrient levels below the critical level as given by Bevege and Humphreys (1978) were observed, but this did not necessarily result in a low biomass production, as shown by the Nigerian forests which were productive (Table 11.9), in spite of very low foliar P levels. As such care should be taken when applying critical levels to predict nutrient deficiencies.

11.5.4 Forest Nutrient Content

Nutrient Content of Pines

As nutrient concentrations vary between component parts of trees (Tables 11.8 – 11.10) the pattern of nutrient accumulation will differ from that of the biomass itself. As such the largest accumulation of nutrients may be expected to occurr early in the rotation during the development of the nutrient-rich crown. After canopy closure the demand for nutrients becomes less as nutrient uptake is primarily for the production of nutrient-poor wood (Bruijnzeel, 1983a; Miller, 1984; Gholz *et al.*, 1985).

The nutrient contents of the above-ground living biomass and the within-tree distribution of nutrients for Tulasewa, Korokula and Koromani forests are given in Tables 11.14, 11.15 and 11.16 respectively. Relatively large proportions of macronutrients were observed in foliage. The foliage in Tulasewa forest accounted for 15% of the total pine biomass but the associated macronutrient content varied between 48% (P) and 59% (Ca) of the total. Due to the low concentrations in wood as compared to those in needles the nutrient content of harvestable wood, which accounted for 70% of the

Table 11.13: *Foliar nutrient status guide, average foliar nutrient concentrations and standard deviations (SD) for needles collected during the present study and in several other forest estates of Fiji Pine Ltd. on Viti Levu and Vanua Levu (Source: Fiji Pine Limited), and foliar nutrient concentrations observed in plantation forests in other tropical countries. Concentrations of macronutrients in % and those of micronutrients in ppm.*

Forest	Age	N	P	K	Ca	Mg	B	Mn	Zn	Cu
Nutrient status guide (Bevege & Humphreys, 1978)										
Adequacy		0.900	0.068	0.350	0.110	0.080	12	35	25	2
Deficiency		0.800	0.060	0.280	0.090	0.050	8	25	18	1.8
VITI LEVU										
Nabou (n=15)	Mixed	0.895	0.159	0.856	0.199	0.160	6.4	139	22	3.5
SD		0.082	0.033	0.103	0.030	0.020	1.3	36	3	0.3
Nabou, present study										
Tulasewa (n=5)	*7*	*0.995*	*0.112*	*0.594*	*0.292*	*0.185*	*8.1*	*410*	*32*	
SD		*0.132*	*0.022*	*0.122*	*0.098*	*0.026*	*2*	*158*	*14*	
Korokula (n=5)	*11*	*1.054*	*0.073*	*0.366*	*0.274*	*0.274*	*12.1*	*211*	*34*	
SD		*0.141*	*0.007*	*0.115*	*0.051*	*0.063*	*4.1*	*18*	*8*	
Koromani (n=3)	*16*	*1.064*	*0.080*	*0.657*	*0.321*	*0.160*	*12.9*	*228*	*32*	
SD		*0.009*	*0.017*	*0.298*	*0.018*	*0.018*	*3.4*	*56*	*6*	
Oleolega (n=2)	*16*	*1.137*	*0.073*	*0.683*	*0.346*	*0.164*	*17.9*	*863*	*40*	
SD		*0.171*	*0.012*	*0.110*	*0.136*	*0.056*	*2.1*	*711*	*9*	
Lololo (n=46)	Mixed	0.866	0.101	0.653	0.209	0.130	8.2	683	20	3.7
SD		0.090	0.023	0.225	0.085	0.029	1.9	674	4	0.8
Ra (n=3)	Mixed	0.738	0.146	0.593	0.252	0.192	6.7	131	21	3.2
SD		0.129	0.043	0.119	0.103	0.049	0.5	61	5	1.3
VANUA LEVU										
Bua (n=71)	Mixed	1.074	0.096	0.516	0.259	0.152	7.8	441	18	2.9
SD		0.225	0.033	0.244	0.136	0.047	7.5	307	8	0.7
BRAZIL (1)	6	2.51	0.30	0.74	0.71	0.30		50		
	5.5	1.21	0.14	0.18	0.69	0.08				
BRAZIL (2)	9.5	0.74	0.05	0.26	0.55	0.14				
SURINAM (1)	5.5	0.99	0.07	0.21	0.89	0.28				
	8.5	1.05	0.06	0.33	0.54	0.13				
	15.5	0.98	0.07	0.62	0.46	0.09				
NIGERIA (3)	6	0.94	0.04	0.72	0.33	0.17				
	10	0.87	0.03	0.75	0.35	0.18				
PUERTO RICO (4)	5	1.31	0.07	0.18						
	19.5	1.44	0.07	0.46						

(1) Chijoke, 1980; (2) Russel, 1983; (3) Egunjobi and Bada, 1979; (4) Lugo, 1992

Table 11.14: *Total nutrient content of pine trees and undergrowth, and within tree distribution of nutrients in Tulasewa forest in kg ha*$^{-1}$ *dry weight in January 1990.*

Nutrient	Total (pine)	Stemwood	Stembark	Branches		Twigs		Needles		Under-growth
				Dead	Live	Dead	Live	Dead	Live	
N	148.7	35.3	11.3	1.0	12.6	0.6	2.9		85.0	37.8
Standard deviation		*9.7*	*3.7*	*0.2*	*1.7*	*0.1*	*0.4*		*7.9*	
% of total		*23.7*	*7.6*	*0.7*	*8.5*	*0.4*	*1.9*		*57.2*	
P	18.4	5.6	1.2	0.1	1.9	0.0	0.7		8.8	3.5
Standard deviation		*0.4*	*0.4*	*0.0*	*0.3*	*0.0*	*0.2*		*1.4*	
% of total		*30.4*	*6.8*	*0.5*	*10.5*	*0.2*	*3.7*		*48.0*	
K	87.1	24.9	6.1	0.3	10.4	0.1	2.8		42.5	107.1
Standard deviation		*5.9*	*1.4*	*0.2*	*1.4*	*0.1*	*0.6*		*5.6*	
% of total		*28.6*	*7.0*	*0.4*	*11.9*	*0.1*	*3.2*		*48.8*	
Ca	80.5	17.8	3.2	1.8	8.0	0.8	1.4		47.5	18.0
Standard deviation		*1.5*	*0.6*	*0.2*	*0.9*	*0.1*	*0.2*		*8.7*	
% of total		*22.1*	*4.0*	*2.2*	*10.0*	*0.9*	*1.7*		*59.0*	
Mg	36.8	8.2	2.5	0.6	4.8	0.3	0.9		19.5	19.4
Standard deviation		*1.1*	*0.3*	*0.1*	*1.1*	*0.0*	*0.1*		*2.9*	
% of total		*22.2*	*6.8*	*1.6*	*13.0*	*0.9*	*2.5*		*53.0*	
B	0.136	0.05	0.01						0.08	0.12
Standard deviation		*0.01*	*0.00*						*0.02*	
% of total		*33.1*	*5.1*						*61.8*	
Mn	7.697	2.12	0.36						5.23	2.29
Standard deviation		*1.00*	*0.17*						*1.00*	
% of total		*27.5*	*4.6*						*67.9*	
Zn	0.786	0.41	0.07						0.31	0.03
Standard deviation		*0.26*	*0.04*						*0.08*	
% of total		*51.9*	*8.7*						*39.3*	

Table 11.15: *Total nutrient content of pine trees and undergrowth, and within tree distribution of nutrients in Korokula forest in kg ha^{-1} dry weight in January 1990.*

Nutrient	Total	Stemwood	Stembark	Branches		Twigs		Needles		Under-growth
				Dead	Live	Dead	Live	Dead	Live	
N	205.7	51.2	17.0	1.9	16.8	0.6	5.3		112.9	7.3
Standard deviation		*12.8*	*3.1*	*0.2*	*3.3*	*0.1*	*2.1*		*11.3*	
% of total		*24.9*	*8.3*	*0.9*	*8.2*	*0.3*	*2.6*		*54.9*	
P	30.4	11.4	7.5	0.4	2.3	0.1	0.8		8.0	0.7
Standard deviation		*6.4*	*6.2*	*0.4*	*0.6*	*0.1*	*0.4*		*0.6*	
% of total		*37.4*	*24.8*	*1.2*	*7.5*	*0.2*	*2.8*		*26.2*	
K	85.9	27.7	5.6	0.5	9.2	0.1	3.3		39.5	20.6
Standard deviation		*5.0*	*1.5*	*0.1*	*1.5*	*0.0*	*1.0*		*8.5*	
% of total		*32.3*	*6.5*	*0.6*	*10.7*	*0.1*	*3.9*		*46.0*	
Ca	114.0	37.0	8.0	3.1	14.3	0.9	2.4		48.4	3.5
Standard deviation		*5.0*	*3.7*	*0.8*	*3.6*	*0.2*	*0.8*		*23.2*	
% of total		*32.4*	*7.0*	*2.7*	*12.5*	*0.7*	*2.1*		*42.5*	
Mg	66.8	17.1	5.1	1.0	7.4	0.3	1.8		34.0	3.7
Standard deviation		*1.4*	*1.2*	*0.2*	*1.2*	*0.1*	*1.0*		*8.0*	
% of total		*25.5*	*7.7*	*1.6*	*11.1*	*0.5*	*2.8*		*51.0*	
B	0.241	0.09	0.01						0.14	0.02
Standard deviation		*0.02*	*0.00*						*0.03*	
% of total		*35.3*	*5.4*						*59.3*	
Mn	8.172	4.06	0.62						3.49	0.44
Standard deviation		*1.92*	*0.30*						*0.60*	
% of total		*49.6*	*7.6*						*42.7*	
Zn	1.243	0.78	0.12						0.34	0.01
Standard deviation		*0.50*	*0.08*						*0.09*	
% of total		*63.0*	*9.7*						*27.3*	

total biomass, was low ranging from 26% (Ca) to 37% (P) of the total. In Korokula forest the foliage, accounting for 11% of the total biomass, contained between 26% (P) and 55% (N) of the total nutrient content, whereas the harvestable wood (75% of the total biomass) contained between 25% (N) to 37% (P) of the total. Similar values were obtained for Koromani forest where the macronutrient content of the foliage (7% of biomass) varied between 33% (P) and 47% (N) of the total and harvestable wood (80% of biomass) contained 42% (N) to 54% (P) of the total. Similar patterns have been reported for a range of tropical forest plantations, both hardwood (George, 1977; Bruijnzeel, 1983a; Hase and Fölster, 1982) and coniferous ones (Lundgren, 1978; Chijioke, 1980; Bruijnzeel, 1984).

The micronutrients Mn and B showed patterns that were similar to those of the macronutrients. However, harvestable wood contained a larger proportion of the total Zn content (61%, 63% and 79% in the Tulasewa, Korokula and Koromani forest plots respectively) as a result of the relatively high concentration in the stem (11±7 ppm; Table 15.2).

The total nutrient contents of the Tulasewa, Korokula and Koromani stands in January, 1990, and in September, 1991, as well as that predicted for January 1991 (sound and damaged forest) are given in Table 11.17. Mean annual and current rates of uptake plus predicted returns of nutrients to the forest floor by cyclone Sina are shown as well. Not surprisingly, the current annual nutrient uptake was highest in

Table 11.16: *Total nutrient content and within-tree distribution of nutrients in kg* ha^{-1} *dry weight in Koromani forest (January 1990).*

Nutrient	Total	Stemwood	Stembark	Branche		Twigs		Needles		Under-growth
				Dead	Live	Dead	Live	Dead	Live	
N	235.4	74.2	23.9	3.0	19.4	0.5	4.5		110.1	15.4
Standard deviation		*15.2*	*5.3*	*0.7*	*2.3*	*0.0*	*0.4*		*11.2*	
% of total		*31.5*	*10.2*	*1.3*	*8.2*	*0.2*	*1.9*		*46.8*	
P	22.5	10.2	2.0	0.2	2.2	0.0	0.6		7.4	1.4
Standard deviation		*3.1*	*0.8*	*0.1*	*0.6*	*0.0*	*0.1*		*1.1*	
% of total		*45.1*	*8.7*	*1.0*	*9.6*	*0.1*	*2.6*		*32.8*	
K	132.5	49.8	12.3	1.1	14.1	0.1	3.6		51.6	43.8
Standard deviation		*7.1*	*5.6*	*0.1*	*3.0*	*0.1*	*0.8*		*12.3*	
% of total		*37.6*	*9.3*	*0.8*	*10.6*	*0.1*	*2.7*		*38.9*	
Ca	165.3	62.0	15.9	4.6	22.3	0.9	3.3		56.4	7.3
Standard deviation		*10.2*	*7.4*	*1.2*	*4.4*	*0.2*	*0.9*		*12.4*	
% of total		*37.5*	*9.6*	*2.8*	*13.5*	*0.5*	*2.0*		*34.1*	
Mg	53.0	20.3	5.3	0.9	6.7	0.2	1.3		18.3	7.9
Standard deviation		*3.0*	*1.8*	*0.1*	*0.7*	*0.0*	*0.3*		*4.3*	
% of total		*38.4*	*10.0*	*1.8*	*12.6*	*0.3*	*2.4*		*34.5*	
B	0.295	0.12	0.02						0.16	0.02
Standard deviation		*0.03*	*0.00*						*0.03*	
% of total		*41.3*	*5.7*						*52.9*	
Mn	14.421	5.79	0.80						7.83	0.93
Standard deviation		*2.74*	*0.38*						*6.43*	
% of total		*40.1*	*5.5*						*54.3*	
Zn	1.609	1.12	0.15						0.34	0.05
Standard deviation		*0.71*	*0.10*						*0.07*	
% of total		*69.4*	*9.6*						*21.0*	

Table 11.17: *Total nutrient content of above-ground living tree biomass in Tulasewa, Korokula and Koromani forests at various stages during the study plus estimated annual rates of uptake as well as amounts of nutrients released by cyclone Sina. Micronutrients in the stem (wood+bark) were calculated from concentrations obtained for trees in the Oleolega drainage basin. Amounts in kg ha^{-1} dry weight.*

						In stem and foliage			In foliage		
	N	P	K	Ca	Mg	B	Mn	Zn	B	Mn	Zn
TULASEWA FOREST, Planted 1984											
Jan ’90	148.66	18.35	87.14	80.49	36.75	0.136	7.70	0.79	0.084	5.23	0.31
Sep ’91	99.53	13.04	61.56	53.03	25.07	0.090	4.88	0.61	0.040	2.49	0.15
Jan ’91, predicted											
Sound forest	183.72	23.10	109.50	98.87	45.58	0.169	9.40	1.03	0.095	5.88	0.35
Cyclone damaged	92.48	12.07	57.01	49.35	23.30	0.084	4.54	0.56	0.038	2.38	0.14
Actual uptake	-49.13	-5.31	-25.58	-27.46	-11.68	-0.046	-2.82	-0.18	-0.044	-2.74	-0.16
Mean annual uptake	24.78	3.06	14.52	13.42	6.13	0.023	1.28	0.13	0.014	0.87	0.05
Uptake in 1990	35.06	4.75	22.36	18.38	8.83	0.033	1.70	0.24	0.011	0.65	0.04
Cyclone release	91.24	11.03	52.49	49.52	22.28	0.085	4.86	0.47	0.057	3.50	0.21
KOROKULA FOREST, Planted 1979											
Jan ’90	206.00	30.44	86.05	114.16	66.91	0.241	8.17	1.24	0.143	3.49	0.34
Sep ’91	167.89	27.35	72.34	97.15	55.29	0.194	6.96	1.12	0.098	2.39	0.23
Jan ’91, predicted											
Sound forest	215.22	32.22	90.27	119.94	70.01	0.253	8.62	1.32	0.146	3.57	0.35
Cyclone damaged	165.19	26.81	71.10	95.44	54.38	0.191	6.83	1.09	0.097	2.37	0.23
Actual uptake	-38.10	-3.09	-13.70	-17.01	-11.63	-0.047	-1.21	-0.13	-0.045	-1.10	-0.11
Mean annual uptake	18.73	2.77	7.82	10.38	6.08	0.022	0.74	0.11	0.013	0.32	0.03
Uptake in 1990	9.22	1.79	4.22	5.78	3.09	0.012	0.45	0.08	0.003	0.08	0.01
Cyclone release	50.04	5.41	19.17	24.50	15.62	0.062	1.79	0.23	0.049	1.21	0.12
KOROMANI FOREST, Planted 1975											
Jan ’90	235.42	22.54	132.52	165.29	52.96	0.295	14.42	1.61	0.156	7.83	0.34
Sep ’91	211.83	20.98	121.53	153.35	49.08	0.261	12.74	1.54	0.122	6.13	0.26
Jan ’91, Predicted											
Sound forest	246.26	23.73	139.08	173.76	55.67	0.309	15.07	1.71	0.160	8.01	0.35
Cyclone damaged	213.17	21.11	122.30	154.33	49.40	0.263	12.82	1.55	0.123	6.16	0.27
Actual uptake	-23.59	-1.56	-10.99	-11.94	-3.88	-0.034	-1.68	-0.07	-0.034	-1.70	-0.08
Mean annual uptake	15.69	1.50	8.83	11.02	3.53	0.020	0.96	0.11	0.010	0.52	0.02
Uptake in 1990	10.84	1.19	6.56	8.47	2.71	0.014	0.65	0.10	0.004	0.18	0.01
Cyclone release	33.09	2.62	16.78	19.43	6.27	0.045	2.25	0.16	0.037	1.85	0.08

Tulasewa forest and exceeded the mean annual uptake. The converse was true for the other sites, which indicates that nutrient requirements are largest between age 6 and 10. This is consistent with the high CAI for nutrient-rich foliage biomass observed for Tulasewa (Table 11.7).

On the basis of predictions suggested by Table 11.17 cyclone Sina released 50%, 21% and 12% of the nutrients stored in the above-ground living biomass of Tulasewa, Korokula and Koromani forests respectively. This resulted in reductions of respectively 31%, 15% and 8% in the nutrient content of the above-ground pine biomass in September, 1991, as compared to those in January, 1990. Even larger reductions were observed in the Luquillo Experimental Forest in Puerto Rico, where hurricane Hugo in 1989 reduced the above-ground biomass of natural rain forest by 50%, with associated decreases in the nutrient content of 45% (N), 46% (P) and 48% (K, Ca, Mg) of pre-hurricane values (Scatena *et al.*, 1993).

Nutrient Content of Undergrowth

No direct estimates were made of the amounts of nutrients stored in the undergrowth of the respective study sites as the uptake of nutrients during the growing season is likely to be balanced by their release during the dry season (*cf.* Section 10.3). In Tulasewa forest the pre-cyclone undergrowth was dominated by *Pennisetum polystachyon* and its nutrient content was therefore assumed to be similar to the values given in Table 10.4. On this basis the pre-cyclone nutrient content of the undergrowth at Tulasewa will have amounted to 16–30% of that of the pines for N, P, Ca, B, Mn and Zn, about 54% of that of the pines for Mg, whereas the K content of the undergrowth may have exceeded that of the pines by a factor of 1.26 (Table 11.14). The large reduction in the undergrowth biomass between age 6 and 11 will therefore result in the release of significant amounts of nutrients (particularly K) potentially for uptake by the pine trees. The undergrowth grew vigorously after the reduction in stand density caused by cyclone Sina and the proportion of nutrients in the undergrowth will therefore have been considerably higher than the values presented above.

Rough estimates of the pre-cyclone nutrient contents of the undergrowth in Korokula and Koromani forests were obtained by multiplying the concentrations of nutrients in mission grass times the estimated undergrowth biomass in these forests (Section 11.5.1) and these are presented in Tables 11.15 and 11.16, respectively. As the composition of the undergrowth vegetation in Korokula and Koromani forests was different from that of grassland, a substantial error may have been introduced in this way. However, because the estimated amounts of nutrients in the undergrowth were low compared to those in the pines (<6% for N, P, and Ca, 6–15% for Mg and 24–33% for K) the associated error in the overall nutrient budget was considered small. In the Korokula and Koromani stands large changes were not observed between the pre- and post-cyclone undergrowth, and the proportion of nutrients in the undergrowth may have been only slightly higher than the values presented above in September 1991.

11.6 Forest Development and Nutrient Accumulation

Plantation Development

Naturally, the development of pine plantations in Fiji is strongly affected by the frequency of cyclone occurrence during a rotation. Cyclone damage had considerably reduced the stocking of the study forests compared to that at planting. In November 1990 cyclone Sina effectively wrecked Tulasewa forest and to a lesser extent the Ole-olega forest, whereas Korokula and Koromani forests were defoliated. This created additional gaps and caused an increase in the variation of the LAI (*cf.* Sections 6.4.1 and 11.3.6). Pre-cyclone diameter increments were high, but decreased after cyclone Sina, presumably as a result of the need to regenerate foliage that had been blown away by the cyclone (Section 11.4). Tree heights also varied widely in the forests as a result of previous cyclone damage to the crowns (*e.g.* stem snap). Crown interlock occurred between age 6 and 10, at a stocking of 820–830 trees ha^{-1}.

Pinus caribaea plantation forests have been established succesfully in countries with distinctly different climates (*i.e.* in terms of rainfall amounts and distribution) and soils (Evans, 1992). Some backgound information on these forests is provided in Table 11.18 for comparison with the forests presently under consideration. Due to the large variation in stocking between the various plantations it is difficult to generalize on the effects of climate or geology on diameter and height increments. Comparison with forests of comparable stocking and age revealed that tree growth in Tulasewa forest was much better than that of the Nigerian forest at Kaduna (Kadeba, 1991), possibly as a result of the lesser amounts of rainfall and of site fertility. Similarly, the growth of Koromani forest was comparable to that of a mature pine forest in Puerto Rico, another area with volcanically derived soils and occasional cyclones (Lugo, 1992).

Biomass Accumulation

Comparison between the grassland and forest sites showed that the total living biomass increased from an initial maximum of 8000 kg ha^{-1} for grassland during the wet season (Section 10.3) to about 150 t ha^{-1} for a mature plantation forest (*e.g.* Koromani forest, Section 11.5.1). Carden (1979) reported a biomass of 185 t ha^{-1} for a 'typical' 15-year-old plantation forest in Fiji with a stocking of 832 trees ha^{-1}. This compares well with the present study, considering the difference in stocking between Koromani forest (620 trees ha^{-1}) and that of Carden (1979). Figure 11.7 shows the changes in tree biomass, mass of utilizable wood, foliage and undergrowth over a rotation period as obtained from the biomass data collected during the present study.

The observed increase in pine biomass was largest during the first 10 years after plantation establishment. However, the lower productivity of the older forest could be fully explained by the loss of production as a result of cyclone damage, which reduced the stocking by 26% in Koromani forest compared to that of Tulasewa forest (pre-cyclone situation). As shown in Figure 11.7 the mass of utilizable wood increased at a fairly uniform rate throughout the rotation period, whereas crown development slowed down between age 6–11. The accumulation of above-ground pine plus undergrowth biomass (M_f, in kg ha^{-1}) with increasing forest age (A_f, in years) could be described by the regression equation:

$$M_f = 9227(\pm 335) \cdot A_f + 10633(\pm 3759)$$

Table 11.18: *Site and forest characteristics of Pinus caribaea var. hondurensis plantation forests in various tropical countries.*

Location	**Rock type**	**Height** [m]	**Rainfall** [mm]	**Dry months**	**Age** [years]	**Stocking** [trees/ha]	**Dbh** [cm]	**H** [m]	**Reference**
FIJI									
Tulasewa	AV	116	1800	6	6	826	15.6	11.6	Present study
Korokula	AV	50			11	822	20.4	14.7	
Koromani	AV	90			15	621	24.9	17.5	
BRAZIL									
Jari Florestal	S	50	2300	5	6	981			Chijioke (1980)
Jari Florestal	S	50	2300	5	9.5	1033	23.6	18.2	Russel (1983)
NIGERIA									
Kaduna	IM	610	1250	5	5	842	10.5	8.8	Kadeba (1991)
					7	1036	14.4	9.6	
					9	1100	15.8	11.6	
					11	999	17.9	13.8	
					15	1201	20.1	17.4	
Ibadan	IM	230	1330	5	6	2634	12.2	10.3	Egunjobi (1975)
					8	2390	10.5		
					9	2767	12.6		
					10	2866	14		
AUSTRALIA									
Beerburrum	S	20	1100	5	5	1153			Richards and Bevege (1967)
PUERTO RICO									
Luquillo	AV	350	3360	0	11	1400	17.5		Cuevas et al. (1991)
Luquillo	AV	220	3900	0	4	1290	14	8	Lugo (1992)
		580			18.5	850	27.8	18	

AV: Acid volcanic; S: Sedimentary; IM: Igneous/metamorph

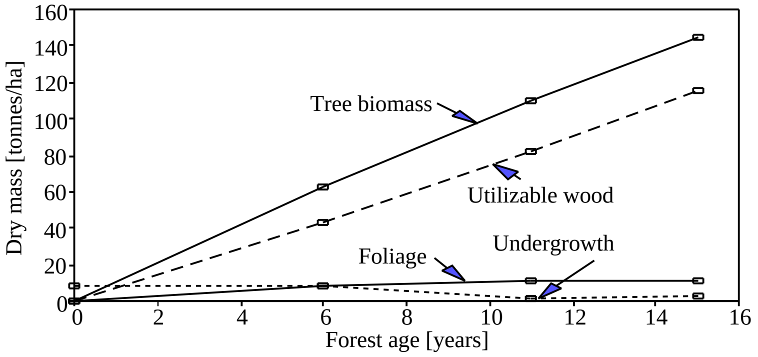

Figure 11.7: *Changes in tree biomass, mass of utilizable wood, foliage biomass and undergrowth biomass over a rotation period.*

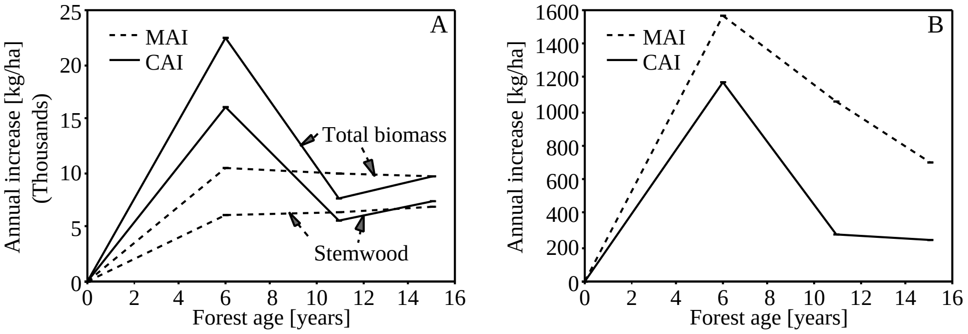

Figure 11.8: *Changes in CAI and MAI (kg ha^{-1}) over a rotation for (A) total stemwood, biomass and (B) foliage.*

$$\text{n}= 4,\ r^2 = 1.00 \tag{11.3}$$

Similarly, the following expression was obtained for the accumulation of above-ground pine biomass with stand age:

$$M_f = 9813(\pm 128) \cdot A_f$$
$$\text{n}= 4,\ r^2 = 1.00 \tag{11.4}$$

where the regression constant b was forced to zero to avoid a finite pine biomass at zero forest age.

At the current spacings of 2∗3 m or 3∗3 m crown interlock occurred shortly after age 6 when the foliage biomass production levelled off. This coincided with a change in undergrowth biomass, which decreased from about 8000 kg ha^{-1} to 1500–3000 kg ha^{-1} at the end of the wet season, as well as with a change in the undergrowth composition. The proportion of mission grass decreased from 93% of the total in grassland to 37% in the 15-year-old forest, where bushes and young native trees reappeared. The decrease in undergrowth biomass may is likely to be the result of reduced light conditions below the closed canopy (Section 11.3.6), whereas the change in composition could be attributed to the protection of the forests from fire, which allowed the survival of seedlings which would normally die during regular burns.

The changes in the MAI and CAI of total biomass and stemwood with forest age are shown in Figure 11.8A, whereas those for foliage are shown separately in Figure 11.8B. The MAI of total biomass decreased slightly after age 6, which may partly be due to the decrease in stocking in the older stands (*e.g.* Koromani forest) related to cyclone damage. However, the MAI of stemwood increased from 6188 kg ha^{-1} in Tulasewa forest to 6772 kg ha^{-1} in Koromani forest, with a corresponding decrease in the MAI for needles from 1500 kg ha^{-1} to 700 kg ha^{-1}. As such there is a shift towards wood production once the crown has been fully developed. The CAI for total biomass in Tulasewa forest was some 200% higher than the MAI, indicating that the forest at age six was producing biomass at a much higher rate than during the previous years. The CAI was similar to the MAI for the older forests suggesting that biomass production had peaked at age 6 or shortly thereafter. The current productivity of Korokula forest (age 11) was lower than that during previous years as the CAI was lower than the MAI, which may be related to the relatively poor quality of the soil at this site (Chapter 4).

Table 11.19: *Total and stem biomass and mean annual increments for Pinus caribaea plantations in Fiji and other tropical countries.*

Location	Elevation [m]	Age [years]	Biomass (tonnes/ha)			MAI (tonnes/ha)		Reference
			Tree	Stem	Foliage	Tree	Stem	
FIJI								
Tulasewa	116	6	62.2	43.3	9.4	10.4	7.2	Present study
Korokula	50	11	109.4	82.1	11.7	9.9	7.5	
Koromani	90	15	144.8	115.6	10.6	9.7	7.1	
BRAZIL								
Jari Florestal	50	6	66.0	53.7	7.2	11.0	9.0	Chijioke (1980)
Jari Florestal	50	9.5	212.1	161.0	28.1	22.3	16.9	Russell (1983)
NIGERIA								
Kaduna	610	5	18.1	12.1	3.4	3.6	2.4	Kadeba (1991)
		7	50.6	36.3	8.1	7.2	5.2	
		9	78.0	56.2	12.0	8.7	6.2	
		11	105.2	78.5	14.4	9.6	7.1	
		15	161.2	126.9	18.3	10.7	8.5	
Ibadan	230	6	68.3	47.4	11.5	11.4	7.9	Egunjobi (1975)
Ibadan	230	6	62.0	43.9	9.8	12.9	7.3	Egunjobi and Bada (1979)
		8	57.7	42.2	9.1	9.0	5.3	
		9	108.0	80.0	15.7	14.8	8.9	
		10	144.4	97.4	20.2	17.9	9.7	
AUSTRALIA								
Beerburrum	20	5	58.7			11.7		Richards and Bevege (1967)
PUERTO RICO								
Luquillo	350	11	94.9			9.5		Cuevas et al. (1991)
Luquillo	220	4	38	27*	11	9.5		Lugo (1992)
	580	18.5	166	131*	35	9.0		

*: Branches included

A comparison of the total biomass, stemwood biomass and MAI for the forests in Fiji and those of plantation forests in various other tropical countries is presented in Table 11.19. Data on annual rainfall, stocking, tree diameter and height for the respective forests have already been presented in Table 11.18. The relationship of stem biomass *versus* forest age is given in Figure 11.9. The biomass production of the forests in Fiji was comparable to those of the forests elsewhere, in spite of the relatively low stocking. The large variation in annual rainfall amounts and soils between sites therefore seems to have little effect on biomass production. For instance, the production of the dry Nigerian forests was similar to those of forests in the more humid areas of Fiji, Brazil and Puerto Rico. The biomass of a 9.5-year-old *Pinus caribaea* plantation in Jari Florestal, Brazil, (Russell, 1983) was exceptionally high when compared to that of a 6-year-old plantation of similar stocking in the same area (Chijioke, 1980). However, Russell (1983) obtained his value for a very small plot (0.03 ha, 31 trees), which may have affected the result as the spatial variation in biomass may not have been covered adequately.

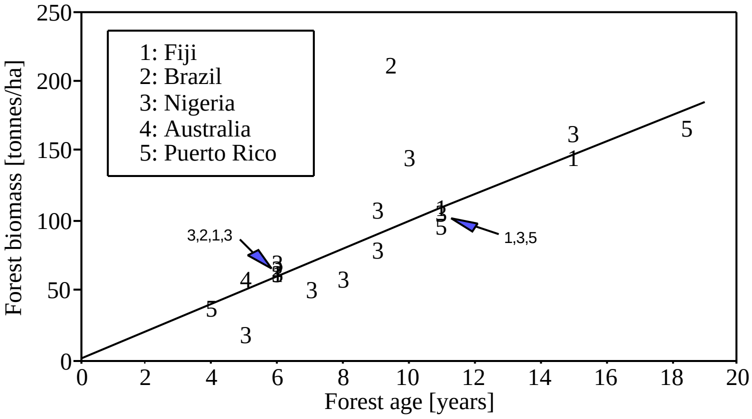

Figure 11.9: *Above-ground biomass* versus *forest age for Pinus caribaea plantation forests in various tropical countries. The solid line describes the accumulation of biomass with forest age for the Fiji plantations.*

Nutrient Accumulation in Biomass

As indicated earlier, the false time series approach may describe accumulation of the biomass and biomass nutrient content during a rotation period accurately, provided that the pre-planting soil conditions, and other environmental circumstances at the various forests are similar (Hase and Fölster, 1982; Bruijnzeel, 1983a). Although the soils in the grassland and forest plots were typical for those in the Nabou Forest Estate area, significant differences were observed in their nutrient status and physical characteristics (Chapter 4). This will almost certainly have affected the forest nutrient content (*cf.* Section 11.5.3), and possibly also the biomass accumulation, rendering the false time series approach more or less invalid. The approach was further complicated by the large spatial variation in stocking, and therefore biomass, within older stands due to differences in damage by cyclones. However, this may be viewed as typical for the Fijian situation and a reduction in biomass over the period of a rotation due to cyclone damage cannot be avoided.

The accumulation of macronutrients with increasing forest age is shown in Figure 11.10. As indicated earlier, the nutrient uptake of Tulasewa forest in 1990 was higher than the mean annual uptake, whereas the converse was true for the older forests. As such the maximum annual nutrient uptake occurs somewhere between age 6 and 11, coinciding with the development of the crown. Large fluctuations were observed for the accumulation of K. These are most likely to be caused by differences of exchangeable K in the soils (Chapter 4), which was shown to affect concentrations of this nutrient in stemwood as well as in foliage (Section 11.5.3). Although this illustrated the limitations of the false time series in predicting the accumulation of K, better results were obtained for the other macronutrients which were less influenced by differences in the site quality (Figure 11.10). Taking the respective figures at face value Tulasewa forest contained 2.6 (Mg) to 4.4 (P) times the amount of nutrients in grassland vegetation and litter at the end of the wet season (Table 10.4). After the canopy had been fully developed nutrient uptake decreased somewhat and Koromani forest contained 3.0 (Mg) to 6.0 (Ca) times the amounts present in grassland biomass

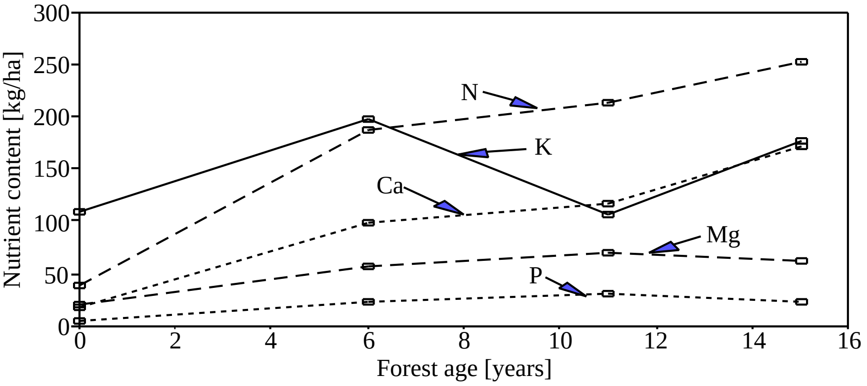

Figure 11.10: *Accumulation of N, P, K, Ca and Mg in pine trees and undergrowth during a rotation period.*

Table 11.20: *Linear regression constants, standard errors (between brackets) and coefficients of determination for expressions describing the changes in nutrient content (kg* ha^{-1}*) of the above-ground forest biomass (including undergrowth) with increasing forest age (years). Lines were fitted through four data points representing age 0, 6, 11 and 15 years.*

Nutrient	a	b	r2	Nutrient	a	b	r2
N	2.47(0.07)	34.62 (0.76)	1.00	**Mg**	1.42 (0.57)	10.20 (6.42)	0.75
P	0.05 (0.01)	2.17 (0.11)	0.94	**Mn**	0.21 (0.09)	1.65 (0.98)	0.75
K	0.34 (0.25)	5.97 (2.82)	0.48	**B**	0.0048 (0.0026)	0.0284 (0.0296)	0.62
Ca	4.35 (0.64)	23.22 (7.22)	0.96	**Zn**	0.0004 (0.0022)	0.1180 (0.0252)	0.01

at the end of the wet season, although these values may have been influenced by the rather low soil nutrient status of the Koromani site. Similar accumulation patterns were observed for Mn, B and Zn of which the amounts at the end of the rotation were 4.4, 5.8 and 6.9 times those observed in grassland respectively (*cf.* Tables 10.4 and 11.17).

Linear regression equations ($Y = a \cdot X + b$) were calculated to describe nutrient accumulation in pine biomass (Y) as a function of forest age (X). The resulting regression constants and the coefficients of determination are given in Table 11.20. The regression coeffient a represents the mean annual increase in the content of the nutrient under consideration. Not surprisingly, a low coefficient of determination was found for K due to the low value of this nutrient in Korokula forest (Table 11.10).

A large part of the variation caused by differences in site quality disappears when the nutrient content of a tree component (including K) is expressed as a fraction of total forest nutrient content (including undergrowth and litter standing crop). This is shown in Figure 11.11 where the accumulations of macronutrients and Zn in merchantable wood are expressed as a fraction of the total. Zn had not been analysed in branches and twigs and the total therefore consisted of Zn in stems, foliage, undergrowth and needle

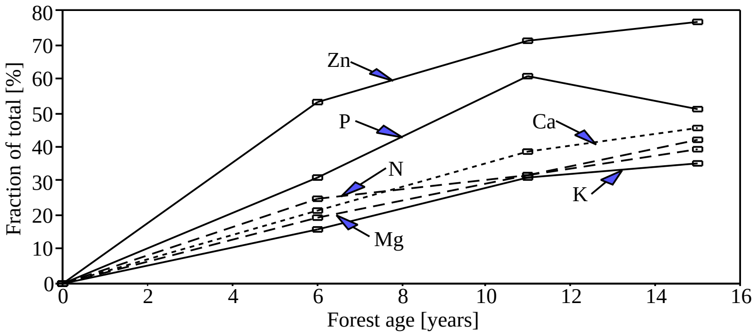

Figure 11.11: *Accumulation of macronutrients and Zn in merchantable wood over the period of a rotation expressed as a fraction of the total in trees, undergrowth and litter.*

litter. The values presented for Zn in Figure 11.11 are therefore slightly overestimated. The figure shows that 35–45% of the total N, K, Ca and Mg contents of the vegetation is removed at the end of a rotation when tree stems are harvested. These percentages are much higher for P (up to 60%) and Zn (up to 77%). Because 'available' P is fairly low in the soils under study (Chapter 4) deficiencies of P, and possibly Zn, may occur in future rotations. Fractions of Mn and B removed in merchantable timber wood are not shown but were similar to those of N, K, Ca and Mg. Since amounts of available micronutrients in the soil were not determined the potential for depletion of these nutrients by harvesting could not be evaluated, and further research is necessary on this subject.

The nutrient contents of *Pinus caribaea* plantation forests in Brazil, Nigeria and Puerto Rico are shown in Table 11.21 together with the results of the present study. The nutrient contents for forests of similar age varied considerably. Very high values for all nutrients were obtained by Russell (1983), which may partly be due to the exceptionally high biomass derived for this site (Table 11.19). The values published for Puerto Rico (Lugo, 1992) included nutrients in pines as well as in other overstory species growing in the plantation, which may explain the high nitrogen contents. The Fiji forests seem to contain somewhat lower amounts of N than most other plantations elsewhere but occupy intermediate positions with respect to some other macronutrients.

Table 11.21: *Nutrient contents of Pinus caribaea plantation forests at various locations in the tropics. All amounts are in kg ha^{-1} dry weight.*

Location	Elevation [m]	Age [years]	Forest Nutrient Content [kg/ha] N	P	K	Ca	Mg	Reference
FIJI								
Tulasewa	116	6	149	18	87	81	37	Present study
Korokula	50	11	206	30	86	114	67	
Koromani	90	15	235	23	133	165	53	
BRAZIL								
Jari Florestal	50	6	197	33	46	78	25	Chijioke (1980)
Jari Florestal+	50	9.5	673	51	218	392	136	Russell (1983)
NIGERIA								
Ibadan	230	6	221	10	126	98	40	Egunjobi and Bada (1979)
		10	374	18	258	187	74	
PUERTO RICO								
Luquillo*	220	4	342	12	36			Lugo (1992)
	580	18.5	1359	22	441			

*: includes nutrients in pines as well as in other overstory trees

Chapter 12

Litter Dynamics and Associated Nutrient Fluxes

12.1 Introduction

This chapter deals with the amounts of nutrients returned to the forest floor in litterfall, the rate of litter decomposition, and the accumulation of organic matter and nutrients on the forest floor. The object of the study was to provide an answer to the question to what extent immobilization of nutrients occurs in the litter layer, as frequently observed under pines in temperate (Will, 1967; Ballard and Will, 1981; Carey *et al.*, 1982; Gholz *et al.*, 1985) and tropical climates (Egunjobi and Bada, 1979; Chijioke, 1980; Cuevas *et al.*, 1991; Lugo, 1992; Gunadi, 1993b).

Nutrients returned to the forest floor in litterfall and subsequently released by decomposition constitute an important component of the internal nutrient cycle of a forest ecosystem. Litterfall is generally low during the first few years after establishment of a plantation (canopy development phase) and consists mainly of foliage, whereas later on in the rotation woody litterfall (*e.g.* branches, cones) becomes increasingly more important (Gholz *et al.*, 1985). Amounts of litter production generally depend on species (deciduous, coniferous), climate (*e.g.* rainfall, wind speed), soil (water holding capacity, nutrient status) and forest characteristics (*e.g.* stocking, age) (Bray and Gorham, 1964).

Few studies have been made of litterfall in *Pinus caribaea* plantation forests. The only data available are those of plantations in Nigeria (Egunjobi and Fasehun, 1972; Egunjobi, 1975; Kadeba and Aduayi, 1985; Kadeba, 1991) and in Puerto Rico (Cuevas *et al.* 1991; Lugo, 1992), which grow under rather different rainfall regimes than in Fiji. A comparison with amounts of litter production and nutrient returns at these sites will be made at the end of Section 12.6.

If the rate of decomposition is lower than that of litter production, accumulation of organic matter on the soil surface will occur, with associated immobilization of nutrients which in turn can lead to nutrient deficiencies on poor soils and reduced growth of the vegetation (Lutz and Chandler, 1946). The rate of decomposition depends on the interaction of biological (presence of soil fauna, fungi and bacteria), physical (temperature, litter layer moisture content) and chemical (soil nutrient status and litter quality) factors (Swift *et al.*, 1979). Although it is often claimed that decomposition proceeds at faster rates in the tropics (*cf.* Jordan, 1989), others (*e.g.* Anderson *et al.*, 1983; Anderson and Swift, 1983) have suggested otherwise.

The rate and patterns of release of the various nutrients from coniferous litter vary considerably in the temperate zone, where most of the research on litter decomposition has been conducted. Potassium and phosphorus seem to be very mobile with sharp drops in concentrations shortly after incubation and relatively stable levels afterwards (Burgess, 1956; Will, 1967). However, the rapid initial release of these nutrients is caused by leaching rather than by decomposition as this process has hardly begun within the first three months (Will, 1967). Nitrogen levels on the other hand generally increase until the N concentration is high enough (critical N concentration) to satisfy the requirements of the decomposer population (Berg and Staaf, 1981) after which N levels remain stable. Therefore N is immobilized until the critical concentration is reached and then released at the rate of weight loss (Gosz, 1984). Because carbon levels remain fairly stable during decomposition the C/N ratio decreases from a high initial level to a stable lower level at which N and C are released at similar rates. Ca and Mg are generally released more slowly (Burgess, 1956; Will, 1967) and often accumulate in the litter layer during the growth of a forest.

The ratio (K_L) of annual litter production to amount of litter on the forest floor is often used as an indication of the turnover rate of litter under steady state (*i.e.* non-seasonal) conditions (Swift *et al.*, 1979). Kimmins (1987) reported an annual K_L-value of 0.28 for temperate evergreen coniferous forests. However, differences in decomposition rates (read: K_L) among locations or forest types are often difficult to interprete, partly because turnover rates only represent net dissapearance rates from the litter layer and do not explicitly refer to the processes involved, such as mineralization of elements, their uptake by roots within the litter layer, or their translocation of into the soil (Burghouts, 1993). This is illustrated by a comparison of K_L values obtained for *Pinus caribaea* plantations growing under rather different climatic conditions. Egunjobi and Onweluzo (1979) and Kadeba and Aduayi (1985) reported very low annual K_L-values (0.28–0.31) for *Pinus caribaea* litter in 7–10 year old plantation forests in the dry zone of Nigeria (annual rainfall 1330 mm), where the wet season constituted the most active period of decomposition. The low turnover rate resulted in an increase of the amount of litter on the forest floor from 3700 kg ha^{-1} at age 6 to 19710 kg ha^{-1} at age 10 (Egunjobi and Bada, 1979). In contrast, Cuevas *et al.* (1991) and Lugo (1992) found high annual K_L-values (0.9–1.5) in 11–20 year old *Pinus caribaea* plantations on a mountain slope in Puerto Rico (annual rainfall: 3800 mm) where amounts of litter on the forest floor reached values of 10.5–18.9 t ha^{-1}. The range of K_L may therefore be large (0.3–1.5) for a single species and local factors (*e.g.* climate, soil) seem very important in the decomposition process.

On the other hand various investigators working in stands of *Pinus merkusii* planted on volcanic soils in Central Java, Indonesia, have reported reasonably similar values for K_L (0.66; Bruijnzeel, 1983a; Sutjahjo, 1975) Gunadi (1993a) reported low needle litter turnover rates in the very wet season (K_L= 0.2) and higher rates during the dry season (K_L= 0.8) with and annual value of 0.50 for a rather open 32 year old *Pinus merkusii* plantation (annual rainfall 3450 mm) on sandier soils in the same area. Lundgren (1978) reported the very low value of 0.2 for a 20-year-old plantation of *Pinus patula* growing on volcanic soils in upland Tanzania where the low raionfall (1060 mm year^{-1}) may have been limiting decomposition.

Amounts and nutrient contents of litter on the forest floor at the study sites will be discussed in Section 12.5.

12.2 Methods and Instrumentation

Monthly amounts of litterfall in the study sites were determined in each plot using 8 litter traps (0.25 m^2) from December 1989 (Tulasewa) and February 1990 (Koromani) until June 1990, and 12 from July 1990 until October, 1991. The traps were emptied once a month during the dry season and twice a month during the wet season to avoid losses of nutrients (Proctor, 1983) by decomposition and leaching (particularly K). The litter was dried and the weights of pine needles, woody parts (stemwood, bark, twigs and branches), male flowers, cones, seeds and undergrowth were determined separately. For each study site, bulked monthly needle litter samples were sent to FRI, New Zealand, for chemical analysis. The nutrient concentrations in woody litter, male flowers and undergrowth litter were obtained from single bulk samples of each component prepared at the end of the study for each site.

Litter decomposition rates were measured using the meshbag technique (Will, 1967). All litter bags were made from chemically inert wire mesh (1 mm mesh) and measured 15*20 cm. Openings on the sides, where the top and bottom of the bags were stitched together, permitted entry to soil fauna whereas the loss of needles through these openings was avoided. Each bag contained a dead twig and 15 grammes of air-dry green–yellow needles stripped from the lower branches of several trees in each of the stands. Initial subsamples of the air dry twigs and needles were dried at 70 °C to obtain conversion factors from air-dry to oven-dry weights. In each forest 25–30 litter bags were placed on the litter layer and covered with a thin layer of fresh needle litter to avoid detection and theft. The rate of decomposition was estimated by regularly (at three-month intervals) removing increasing numbers of bags (3–7) at a time in each forest plot and recording the air-dry and oven-dry weights of their contents (Will, 1967). For each forest the needle litter was bulked and sent to FRI for chemical analysis (N, P, K, Ca, Mg). No chemical analyses were done on twigs. The analytical procedures at FRI, New Zealand, have been discussed in Section 10.2

Litter standing crop was determined by sampling the litter layer (L+F layer) once every month from January 1990 until September 1990 (8 samples at a time) and once every three months (12 samples at a time) until September, 1991. Samples were collected by randomly placing a 500 cm^2 metal plate on the litter layer and sampling everything below the plate after cutting the litter layer around the plate with scissors. The field-moist weight of each sample was determined shortly after sampling after which the sample was dried at 70 °C (see Section 11.2). The total dry weight was determined as well as the respective weights of needles, woody parts (downed stemwood after cyclone Sina, bark, branches, twigs) male flowers, cones, seeds and undergrowth material. The nutrient concentrations in needle litter (and undergrowth litter in Tulasewa forest) were determined at FRI, New Zealand, for each sampling occassion, whereas those in woody litter, male flowers and undergrowth litter were determined on bulk samples prepared from the total sample for each plot at the end of the study.

The carbon and nitrogen contents of freshly fallen needles and strongly decomposed needles, both sampled from the litter and fermentation layers in Korokula forest in September 1991, were determined to obtain C/N ratios for each of these layers. The analytical procedures have been given in Section 4.2.

Due to the limited number of samples the *"Student's"* *t* distribution (Spiegel, 1972) was used to decide whether observed differences in measured values between sites were statistically significant.

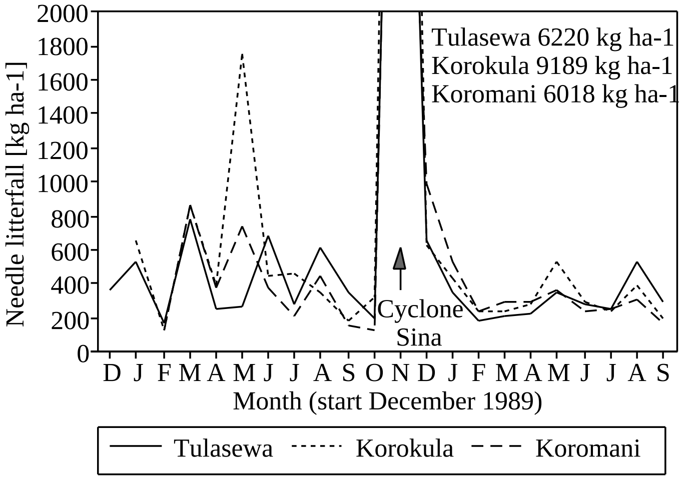

Figure 12.1: *Monthly amounts of needle fall (kg ha^{-1}) in Tulasewa, Korokula and Koromani forests. Amounts produced during the passage of cyclone Sina in November 1990 indicated in the upper right hand corner.*

12.3 Litterfall and Nutrient Content

12.3.1 Litter Production

The passage of cyclone Sina had a major impact on amounts, as well as nutrient concentrations of litterfall. Therefore pre-cyclone, cyclone and post-cyclone litterfalls will be discussed separately. The pre-cyclone data set spanned 9 (Koromani) to 11 months (Tulasewa), which of course is rather short in view of the seasonal climate. The same holds for the post-cyclone data set (9 months).

Total monthly pre-cyclone pine litterfall in the Tulasewa forest plot averaged 404(±200) kg ha^{-1} (range 167–790 kg ha^{-1}). The average monthly total measured at the Korokula forest plot was significantly higher ($\alpha = 0.05$) at 774(±432) kg ha^{-1} (range 151–1760 kg ha^{-1}) whereas the average for the Koromani forest plot (447(±261) kg ha^{-1}, range 155–970 kg ha^{-1}) was not significantly different from that of Tulasewa forest but significantly lower ($\alpha = 0.05$) than that in Korokula forest. Monthly amounts of needle fall in Tulasewa, Korokula and Koromani forests are shown in Figure 12.1, whereas the actual amounts are listed in Appendix 28.1. The proportion of needle fall to the total decreased with forest age from 96% in Tulasewa forest to 72% and 85% in Korokula and Koromani forests, respectively. The passage of Cyclone Rae south of Viti Levu in March 1990 did not afflict much damage to the forest but the moderately strong winds removed dead needles formerly suspended in the canopies resulting in a peak in the needle fall (Figure 12.1). The production of litter in Tulasewa and Koromani forests remained relatively low during the dry season of 1990, indicating that these forests did not experience any water stress even after several dry weeks in April and May. However, litterfall in the Korokula forest plot peaked strongly in May 1990, suggesting that the forest experienced water stress during this dry period (Section 6.5). This difference in litter production during prolonged dry spells between forests illustrates the impact of soil properties (*e.g.* soil depth, water holding capacity) on the litter production.

The spatial variation in pre-cyclone litterfall was large as indicated by large standard deviations for monthly totals of litterfall which ranged between 41% (Koromani) and 58% (Korokula) of the average. The standard deviations for needle fall were relatively low (37–47% of average needle fall), whereas those for branches and cones were high, often exceeding the average by a factor 2–3. Therefore some confidence can be placed in the average amounts of needle fall, but the values for the other components should be treated with caution as these could be seriously in error.

No clear seasonal trends could be established from the pre-cyclone data for needle fall. However, the production of male flowers, seeds and possibly cones was strongly seasonal. Seeds were exclusively produced during the wet season, reaching a peak in March–April, whereas male flower litter production peaked during the dry season (July–August). A peak in the production of cone litter was observed during the dry season in Korokula forest, but not in Koromani forest where cone litter production was low anyway. Because cone production does not start before canopy development is completed only few trees in Tulasewa forest produced cones, which explains the low amounts observed in both pre-cyclone and cyclone litterfall.

Estimates of the annual litterfall and the relative contributions of the various components based on pre-cyclone observations are presented in Table 12.1. Annual pre-cyclone litterfall was highest in Korokula forest as a result of high production rates for woody litter as well as for needle litter during dry periods. The relatively high woody litterfall in Korokula forest may be related to the rather dense tree spacing (2*3 m) which caused interference of tree crowns within the rows of planting (asymmetric crowns) and also reduced the light conditions in the lower canopy levels compared to those in the other two forests which had different spacings (see also Section 11.3.6). The number of dead branches/twigs on the trees in Korokula forest during the pre-cyclone period was therefore higher (visual observation by the author). The high production of cone litter in Korokula forest as compared to that in Koromani forest further increased the difference in litter production. In spite of the difference in age, and therefore development phase, similar litterfall totals were observed in the Koromani and Tulasewa forest plots, probably because of the relatively low tree density in the former (Chapter 3). When litter production rates were expressed in kg tree^{-1}, however, total litter and needle litter production were lowest in the Tulasewa forest plot and highest in the Korokula forest plot.

As expected, cyclone Sina had a large impact on litter production at all sites. Amounts recorded in November 1990 were 2–4 times higher than the estimated annual pre-cyclone totals, whereas cyclone-induced needle fall exceeded estimated annual needle fall by a factor 1.5 (Table 12.1). The standard deviations for cyclone needle fall (32–46% of the average value) were similar to those of the average pre-cyclone values and the measured amounts are therefore thought to be reasonably accurate. The values obtained for the other litter components could again be seriously in error due to the large spatial variation observed for these components. This was particularly true for woody litter fall (which included parts of tree stems!) of which the standard deviations were 0.8–2.5 times the average.

Cyclone needle fall in Tulasewa forest compared well with the predicted loss of foliage from the biomass pre- and post-cyclone predictions for January 1991 (Table 11.7). In the Korokula and Koromani forest plots, where the stand density was less affected by the cyclone, measured amounts of needle fall were larger than those predicted from biomass estimations. However, because the regression equations for post-cyclone fo-

Table 12.1: *Pre-cyclone, cyclone and post-cyclone production of litterfall and its respective components in Tulasewa, Korokula and Koromani forests. Annual rates were obtained by extrapolation on a time basis which is thought to produce realistic values as clear seasonal trends were not observed for the largest litterfall component (needles). All amounts in kg* ha^{-1} *dry weight.*

	Needles	**Wood**	**M. flowers**	**Cones**	**Seed**	**Total**	**Undergrowth**
TULASEWA FOREST							
Pre-cyclone litter fall	4441.4	42.2	88.0	9.5	13.1	4594.2	254.3
% of total	*96.7*	*0.9*	*1.9*	*0.2*	*0.3*		
Cyclone litter fall	6874.9	14469.3	5.4	471.0	0.0	21820.6	230.8
% of total	*31.5*	*66.3*	*0.0*	*2.2*	*0.0*		
Post-cyclone litter fall	2676.7	3.6	20.1	0.0	0.0	2700.4	460.9
% of total	*99.1*	*0.1*	*0.7*	*0.0*	*0.0*		
Pre-cyclone annual total	**4845.2**	**46.0**	**96.0**	**10.4**	**14.3**	**5011.9**	**277.4**
Post-cyclone annual total	**3568.9**	**4.8**	**26.8**	**0.0**	**0.0**	**3600.5**	**614.5**
KOROKULA FOREST							
Pre-cyclone litter fall	5555.8	681.3	571.6	901.7	26.2	7736.6	127.9
% of total	*71.8*	*8.8*	*7.4*	*11.7*	*0.3*		
Cyclone litter fall	9821.7	5270.9	51.2	2948.6	0.0	18092.4	101.7
% of total	*54.3*	*29.1*	*0.3*	*16.3*	*0.0*		
Post-cyclone litter fall	2835.8	43.5	143.7	0.0	1.0	3024.0	296.4
% of total	*93.8*	*1.4*	*4.8*	*0.0*	*0.0*		
Pre-cyclone annual total	**6667.0**	**817.6**	**685.9**	**1082.0**	**31.4**	**9283.9**	**153.5**
Post-cyclone annual total	**3781.1**	**58.0**	**191.6**	**0.0**	**1.3**	**4032.0**	**395.2**
KOROMANI FOREST							
Pre-cyclone litterfall	3435.6	99.1	375.9	95.5	15.0	4021.1	544.7
% of total	*85.4*	*2.5*	*9.3*	*2.4*	*0.4*		
Cyclone litterfall	7012.3	9352.4	106.2	1390.6	0.0	17861.5	817.3
% of total	*39.3*	*52.4*	*0.6*	*7.8*	*0.0*		
Post-cyclone litterfall	2678.8	17.4	115.1	1.0	2.7	2815.0	466.4
% of total	*95.2*	*0.6*	*4.1*	*0.0*	*0.1*		
Pre-cyclone annual total	**4580.8**	**132.1**	**501.2**	**127.3**	**20.0**	**5361.5**	**726.3**
Post-cyclone annual total	**3571.7**	**23.2**	**153.5**	**1.3**	**3.6**	**3753.3**	**621.9**

liage biomass were based on data collected several months after the passage of the cyclone (Section 11.4), the difference may be explained by the rapid regeneration of needles in the intermediate period, which resulted in overestimation of the predicted pre-cyclone foliage biomass for January 1991 (Table 11.7). The loss of needles associated with the passage of cyclone Sina formed 73%, 84% and 65% of the pre-cyclone needle biomass in the Tulasewa, Korokula and Koromani forest plots, respectively (Table 11.7), illustrating the severe damage afflicted to the forest canopies by the cyclone (Lodge *et al.*, 1991). Measured amounts of woody litterfall in Tulasewa and Korokula forests were lower than those predicted from the biomass estimations, whereas measured amounts were similar to predicted amounts for Koromani forest.

Post-cyclone annual totals are presented in Table 12.1. Because the pine trees were rapidly generating new foliage and because needle biomass was very low anyway, post-cyclone monthly averages of litterfall were much lower than the corresponding pre-cyclone averages. Post-cyclone monthly amounts of litterfall were not significantly different between the Tulasewa, Korokula and Koromani forest plots at 297(±98), 336(±112) and 313(±97) kg ha^{-1}, respectively. The litterfall composition had also changed with the proportion of needle fall increasing to 95–99% of the total, with corresponding decreases in the proportions of other components. Most of the cones and dead branches had been removed from the canopy during the cyclone, reducing woody and cone litterfall to almost zero (Table 12.1).

The litterfall produced by the undergrowth in the three forest plots consisted for a large part of grass leaves and seeds and the actual litter production by the undergrowth was severely underestimated because dead grass stalks often remained erect and did not end up in the littertraps. Pre-cyclone litter production by the undergrowth in the Tulasewa forest plot, which was heavily dominated by *Pennisetum polystachyon* grass may be approximated by the production rates for grass presented in Table 10.1, *i.e.* about 6.5 t ha^{-1}. Taking the latter value at face value this would imply that production of litter by the undergrowth at this site was at least as high as that by the tree storey for the pre-cyclone period. The improved light conditions within the forest after the cyclone event in November 1990 caused a two-fold increase in measured litter production of the undergrowth, and the actual production may well have been much higher than that of the forest. Due to the low undergrowth biomass in the Korokula forest plot, and the low proportion of grass in the undergrowth at Koromani forest, the underestimates presented for these forests should not lead to serious errors in the overall forest nutrient budgets. A more than two-fold increase in undergrowth litterfall was also observed in the Korokula forest plot after cyclone Sina, but not in Koromani forest which already had a more open character due to previous cyclone damage (Section 3.4).

12.3.2 Nutrient Concentrations in Litterfall

Average nutrient concentrations in needle fall and in bulk samples of woody litterfall (stemwood, branches, twigs and cones), male flower litterfall (if present) and undergrowth litterfall in Tulasewa, Korokula and Koromani forests are presented in Table 12.2, whereas monthly needle fall concentrations are given in Appendix 28.1. Concentrations in needle fall were fairly similar to those of dead and yellow needles collected from within the crowns of trees sampled for biomass (Tables 11.8, 11.9 and 11.10), which suggests that losses of nutrients in the period between needle fall and sampling were negligible. However, concentrations of P in needle fall in Korokula forest were much higher than in dead needles collected from within the crowns.

Fluctuations in needle fall nutrient levels showed no distinct seasonal patterns, although Mg levels reached a maximum at the end of the wet season (April–May) in both the Korokula and Koromani forest plots (Appendix 28.1).

Monthly concentrations of N, K and Ca in needle fall in Tulasewa forest are shown in Figure 12.2. Trends for P and Zn were similar to that of N, whereas the trends for Mg, B and Mn were similar to that of Ca, although less pronounced. Seasonal variations in needle fall nutrient levels in Korokula and Koromani forests were comparable to those shown for Tulasewa forest (see Appendix 28.1). Clearly, cyclone Sina had a much larger impact on needle fall nutrient levels than any seasonal trend might have had. Ca levels in post-cyclone needle fall were lower than those in pre-cyclone needle fall, whereas N, P, K, Mg, Mn and Zn levels were all higher than in pre-cyclone needle fall until four months after the event when nutrient concentrations returned to pre-cyclone levels (Figure 12.2). These changes in concentrations suggest that during this period relatively young needles died and fell without complete retranslocation of

Table 12.2: *Average nutrient concentrations in pre-cyclone, cyclone needle fall and post-cyclone needle fall, and in bulk samples of woody litter fall, male flower and undergrowth litterfall in Tulasewa, Korokula and Koromani forests. Concentrations for macro- and micronutrients in % and ppm respectively.*

	N	P	K	Ca	Mg	B	Mn	Zn
TULASEWA FOREST								
Dec'89-Oct'90, pre-cyclone needle fall								
Weighted average	0.389	0.016	0.092	0.887	0.200	9.4	563	26
Arithmetric mean (n=11)	0.387	0.016	0.096	0.878	0.200	9.5	581	27
Standard deviation	0.039	0.004	0.024	0.064	0.012	0.9	69	3
Nov'90-Dec'90, cyclone needle fall								
Weighted average (n=2)	0.670	0.069	0.314	0.610	0.193	8.0	487	24
Jan'91-Sep'91, post-cyclone needle fall								
Weighted average (n=9)	0.436	0.035	0.106	0.823	0.223	10.1	647	30
Arithmetic mean	0.444	0.035	0.107	0.828	0.224	10.1	636	30
Standard deviation	0.107	0.011	0.035	0.070	0.015	0.8	7	3
Woody litter fall (bulk)	0.199	0.028	0.172	0.163	0.061			
Undergrowth litter fall (bulk)	0.668	0.050	0.579	0.305	0.252			
KOROKULA FOREST								
Jan'90-Oct'90, pre-cyclone needle fall								
Weighted average	0.312	0.012	0.074	0.780	0.327	13.6	378	14
Arithmetic mean (n=10)	0.321	0.013	0.072	0.784	0.317	13.8	392	14
Standard deviation	*0.043*	*0.006*	*0.022*	*0.069*	*0.021*	*1.6*	*44*	*2*
Nov'90-Dec'90, cyclone needle fall								
Weighted average (n=2)	0.772	0.049	0.226	0.562	0.309	14.9	380	16
Jan'91-Sep'91, post-cyclone needle fall								
Weighted average	0.482	0.096	0.084	0.690	0.340	14.4	381	21
Arithmetic mean (n=9)	0.471	0.091	0.082	0.694	0.338	14.4	400	21
Standard deviation	*0.131*	*0.040*	*0.015*	*0.042*	*0.015*	*0.6*	*100*	*3*
Woody litter fall (bulk)	0.394	0.033	0.156	0.200	0.101			
Male flower fall (bulk)	0.851	0.064	0.141	0.161	0.147			
Undergrowth litter fall (bulk)	1.092	0.082	0.790	0.993	0.622			
KOROMANI FOREST								
Feb'90-Oct'90, pre-cyclone needle fall								
Weighted average	0.342	0.011	0.099	0.684	0.206	10.2	607	16
Arithmetic mean (n=9)	0.334	0.011	0.095	0.683	0.201	10.7	624	19
Standard deviation	*0.043*	*0.002*	*0.014*	*0.050*	*0.021*	*1.9*	*66*	*9*
Nov'90-Dec'90, cyclone needle fall								
Weighted average (n=2)	0.807	0.048	0.268	0.518	0.184	10.9	612	21
Jan'91-Sep'91, post-cyclone needle fall								
Weighted average	0.520	0.021	0.110	0.658	0.185	11.3	735	25
Arithmetic mean (n=9)	0.506	0.020	0.105	0.656	0.184	11.6	748	25
Standard deviation	*0.119*	*0.008*	*0.021*	*0.036*	*0.007*	*1.1*	*66*	*6*
Woody litterfall	0.314	0.029	0.121	0.324	0.093			
Male flower fall (bulk)	0.813	0.057	0.126	0.186	0.133			
Undergrowth litter fall	1.030	0.048	0.269	1.203	0.515			

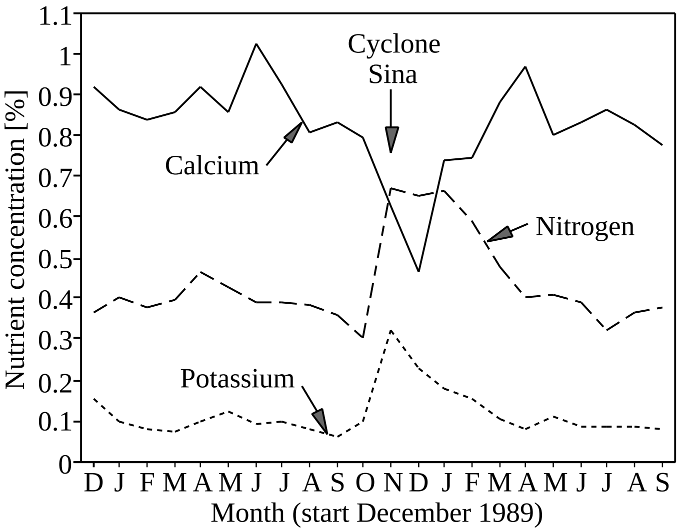

Figure 12.2: *Concentrations of N, K and Ca in monthly samples of needle fall in Tulasewa forest.*

their nutrients. The differences in means of pre- and post-cyclone concentrations in needle fall for each site are shown in Table 12.3 together with their significance levels.

Similar changes in needle fall nutrient concentrations were observed in a *Pinus caribaea* plantation forest at Humpty Doo, Queensland, after a wildfire defoliated the stand in 1978 (Maggs, 1981).

Significant differences were observed between sites (Table 12.3), possibly reflecting differences in site quality. Pre-cyclone levels of N, P, Ca and Zn were highest in the Tulasewa forest plot whereas Mg and B levels were highest in Korokula forest. K and Mn concentrations were highest in the Tulasewa and Koromani forest plots, respectively. No significant differences were found for the N concentrations in needle fall between the sites in the post-cyclone period. Ca and Zn levels in needle fall were again highest in the Tulasewa forest plot, whereas P, Mg and B levels were highest in the Korokula forest plot and Mn was highest in the Koromani forest plot.

12.3.3 Nutrient Returns to the Forest Floor via Litterfall

Amounts of nutrients deposited onto the forest floor in litterfall in the Tulasewa, Korokula and Koromani forest plots during the study are given in Tables 12.4 – 12.6, respectively. Needle fall accounted for 97.4% of the total return of K to the forest floor in the Tulasewa forest plot, and for 99.7% of that for Ca with intermediate values for N, P and Mg. In the older forests where woody litterfall formed a larger fraction of total litterfall (Table 12.1), needle fall still accounted for a large proportion of the annual return of nutrients to the forest floor. In the Korokula forest plot needle fall accounted for 43% of the annual return of P and for 91% of that for Ca with intermediate values for N (61%), K (56%) and Mg (88%). Similar values were observed in Koromani forest where needle fall accounted for 58% of the pre-cyclone annual return of P and for 91%

Table 12.3: *Significance levels for within- and between-site differences in mean nutrient concentrations in pre- and post-cyclone needle litterfall.*

Difference in means of needle fall	N	P	K	Ca	Mg	B	Mn	Zn
Tulasewa pre- <> post-cyclone	<*	<***	ns	>*	<***	<*	<**	<**
Korokula pre- <> post-cyclone	<**	<***	ns	>***	<***	<**	ns	<***
Koromani pre- <> post-cyclone	<***	<***	ns	ns	>**	ns	<***	<*
Pre-cyclone Tulasewa <> Korokula	>***	>*	>**	>***	<***	<***	>***	>***
Pre-cyclone Tulasewa <> Koromani	>***	>***	ns	>***	ns	<*	ns	>**
Pre-cyclone Korokula <> Koromani	ns	ns	<***	>***	>***	>***	<***	<*
Post-cyclone Tulasewa <> Korokula	ns	<***	>**	>***	<***	<***	>***	>***
Post-cyclone Tulasewa <> Koromani	ns	>***	ns	>***	>***	<***	<***	>**
Post-cyclone Korokula <> Koromani	ns	>***	<***	>**	>***	>***	<***	<**

ns: not significant; *: significance level 0.10; **: significance level 0.05; ***: significance level 0.01

Table 12.4: *Amounts of nutrients (kg ha^{-1}) returned to the forest floor in litterfall in the Tulasewa forest plot.*

	N	P	K	Ca	Mg	B	Mn	Zn
Dec’89-Oct’90, pre-cyclone needle fall	17.27	0.69	4.09	39.38	8.86	0.04	2.50	0.12
Nov’90-Dec’90, cyclone needle fall	46.07	4.78	21.60	41.93	13.29	0.05	3.35	0.17
Jan’91-Sep’91, post-cyclone needle fall	11.68	0.93	2.83	22.03	5.98	0.03	1.73	0.08
Dec’89-Oct’90, pre-cyclone woody litter fall	0.13	0.02	0.11	0.11	0.04			
Nov’90-Dec’90, cyclone woody litter fall	29.73	4.18	25.70	24.35	9.11			
Jan’91-Sep’91, post-cyclone woody litter fall	0.01	0.00	0.01	0.01	0.00			
Total in pine litter fall	**104.89**	**10.60**	**54.33**	**127.81**	**37.28**			
Total in cyclone pine litter fall	**75.80**	**8.96**	**47.29**	**66.29**	**22.40**			
Pre-cyclone annual total pine litter fall	**18.98**	**0.78**	**4.58**	**43.08**	**9.71**			
Dec’89-Oct’90, pre-cyclone undergrowth litter fall	1.70	0.13	1.47	0.78	0.64			
Nov’90-Dec’90, cyclone undergrowth litter fall	1.54	0.12	1.34	0.70	0.58			
Jan’91-Sep’91, post-cyclone undergrowth litter fall	3.08	0.23	2.67	1.41	1.16			
Total in undergrowth litter fall	**6.32**	**0.47**	**5.48**	**2.89**	**2.38**			
Pre-cyclone annual total	**1.85**	**0.14**	**1.61**	**0.85**	**0.70**			

Table 12.5: *Amounts of nutrients (kg ha^{-1}) returned to the forest floor in litterfall in the Korokula forest plot.*

	N	P	K	Ca	Mg	B	Mn	Zn
Jan'90-Oct'90, pre-cyclone needle fall	17.36	0.66	4.11	43.34	18.15	0.08	2.10	0.08
Nov'90-Dec'90, cyclone needle fall	75.81	4.79	22.16	55.16	30.34	0.15	3.73	0.15
Jan'91-Sep'91, post-cyclone needle fall	13.66	2.73	2.39	19.57	9.65	0.04	1.08	0.06
Jan'90-Oct'90, pre-cyclone woody litter fall	6.24	0.52	2.47	3.17	1.60			
Nov'90-Dec'90, cyclone woody litter fall	32.38	2.71	12.82	16.44	8.30			
Jan'91-Sep'91, post-cyclone woody litter fall	0.17	0.01	0.07	0.09	0.04			
Jan'90-Oct'90, pre-cyclone male flower fall	4.86	0.37	0.81	0.92	0.84			
Nov'90-Dec'90, cyclone male flower fall	0.44	0.03	0.07	0.08	0.08			
Jan'91-Sep'91, post-cyclone male flower fall	1.22	0.09	0.20	0.23	0.21			
Total in pine litter fall	**152.14**	**11.91**	**45.11**	**139.00**	**69.21**			
Total in cyclone pine litter fall	**108.63**	**7.53**	**35.06**	**71.68**	**38.72**			
Pre-cyclone annual total pine litter fall	**34.15**	**1.85**	**8.86**	**56.92**	**24.70**			
Jan'90-Oct'90, pre-cyclone undergrowth litter fall	1.40	0.10	1.01	1.27	0.80			
Nov'90-Dec'90, cyclone undergrowth litter fall	1.11	0.08	0.80	1.01	0.63			
Jan'91-Sep'91, post-cyclone undergrowth litter fall	3.24	0.24	2.34	2.94	1.84			
Total in undergrowth litter fall	**5.74**	**0.43**	**4.16**	**5.22**	**3.27**			
Pre-cyclone annual total	**1.68**	**0.13**	**1.21**	**1.52**	**0.95**			

of that for Mg with intermediate values for Ca (71%), N (75%) and K (83%).

The estimated annual returns of N, P and K in pre-cyclone litterfall were much smaller (9–25%, 25–31% and 13–23% in Tulasewa, Korokula and Koromani forests respectively) than the corresponding amounts released in cyclone induced litterfall. Estimated annual returns of Ca in pre-cyclone litterfall in the three forests were 65%, 79% and 46% of those in the litterfall associated with cyclone Sina, respectively, with corresponding values of 43%, 64% 45% for Mg. In Puerto Rico, nutrient returns in litterfall during the passage of hurricane Hugo also equalled or exceeded the mean annual nutrient returns in litterfall in natural rain forests for years without hurricanes (Lodge *et al.*, 1991). Because cyclones of the intensity of cyclone Sina pass regularly over the forests in Viti Levu (once every 2–3 years, Section 2.4.4) the amounts of N, P and K, and to a lesser extent of Mg and Ca, in litterfall during a cyclone event may well be similar to the return of the total amounts recorded during the period between two cyclones. However, not all forests will be equally affected by the same cyclone due to differences in exposure to the wind field (Walker, 1991), and it is therefore difficult to predict the total return of nutrients to the forest floor over a rotation period for the Fijian situation.

As indicated, the return of nutrients to the forest floor in undergrowth litter was underestimated in all plots. However, as the undergrowth biomass in the forests plots did not show a major change during the present study (visual observation), amounts of nutrients released from undergrowth litter are likely to be used by the undergrowth during the following wet season. The undergrowth biomass showed a sharp decrease after canopy closure, somewhere between age 6 and 11 (Figure 11.7). During this period the release of nutrients from undergrowth litter may be expected to exceed the uptake.

Table 12.6: *Amounts of nutrients (kg ha^{-1}) returned to the forest floor in litterfall in the Koromani forest plot.*

	N	P	K	Ca	Mg	B	Mn	Zn
Feb'90-Oct'90, pre-cyclone needle fall	11.75	0.37	3.41	23.48	7.09	0.03	2.09	0.06
Nov'90-Dec'90, cyclone needle fall	56.61	3.35	18.82	36.30	12.91	0.08	4.29	0.15
Jan'91-Sep'91, post-cyclone needle fall	13.93	0.57	2.94	17.61	4.94	0.03	1.97	0.07
Feb'90-Oct'90, pre-cyclone woody litter fall	0.61	0.06	0.24	0.63	0.18			
Nov'90-Dec'90, cyclone woody litter fall	33.73	3.12	13.00	34.81	9.99			
Jan'91-Sep'91, post-cyclone woody litter fall	0.06	0.01	0.02	0.06	0.02			
Feb'90-Oct'90, pre-cyclone male flower fall	3.06	0.21	0.47	0.70	0.50			
Nov'90-Dec'90, cyclone male flower fall	0.86	0.06	0.13	0.20	0.14			
Jan'91-Sep'91, post-cyclone male flower fall	0.94	0.07	0.15	0.21	0.15			
0.0								
Total in pine litter fall	**121.54**	**7.80**	**39.18**	**114.00**	**35.93**			
Total in cyclone pine litter fall	**91.21**	**6.52**	**31.96**	**71.30**	**23.05**			
Pre-cyclone annual total pine litter fall	**20.55**	**0.85**	**5.49**	**33.09**	**10.36**			
Feb'90-Oct'90, pre-cyclone undergrowth litter fall	5.61	0.26	1.47	6.55	2.81			
Nov'90-Dec'90, cyclone undergrowth litter fall	8.42	0.39	2.20	9.83	4.21			
Jan'91-Sep'91, post-cyclone undergrowth litter fall	4.80	0.22	1.25	5.61	2.40			
Total in undergrowth litter fall	**18.83**	**0.88**	**4.92**	**22.00**	**9.42**			
Pre-cyclone annual total	**7.48**	**0.35**	**1.95**	**8.74**	**3.74**			

12.4 Litter Decomposition

Decomposition rates of needles and twigs and the release of nutrients from decomposing needles were studied in the Tulasewa, Korokula and Koromani forest plots using the mesh-bag technique. In addition, litter turnover rates (fractional loss weights, K_L) were calculated as the ratio of pre-cyclone needle litterfall (Table 12.1) to corresponding amounts of needle litter on the forest floor (Table 12.7) for the older forests where the litter layer had presumably reached a steady state, This resulted in pre-cyclone K_L-values of 0.62 and 0.41 for needle litter in the Korokula and Koromani forest plots respectively. These values lie in between those obtained by Egunjobi and Onweluzo (1979; K_L about 0.3) and Cuevas *et al.* (1991; K_L= 0.9–1.5) for *Pinus caribaea* litter in stands in Nigeria and Puerto Rico, respectively.

Total C decreased from 52.5% in freshly fallen needles in the L-layer to 49.9% in severely decomposed needles in the underlying F-layer in the Korokula forest plot. Corresponding N levels increased from 0.50% to 0.97%, implying a decrease in C/N ratio from 105 in fresh needle litter to 52 in heavily decomposed needles.

The rates and patterns of decomposition of both needles and twigs were roughly similar between sites. Needle decomposition rates were highest during the wet season of 1990, shortly after incubation, with observed mass losses of about 20% of the initial mass within two months after incubation. Decomposition slowed down somewhat during the following dry season but increased again during the wet season of 1991 (Figure 12.3).

Needle decomposition rates were similar in the Tulasewa and Korokula forest plots with equal first year mass losses of 48% and slightly lower in Koromani forest where 43% of the initial mass was lost after one year. At 600 days after incubation 28(±7)% of

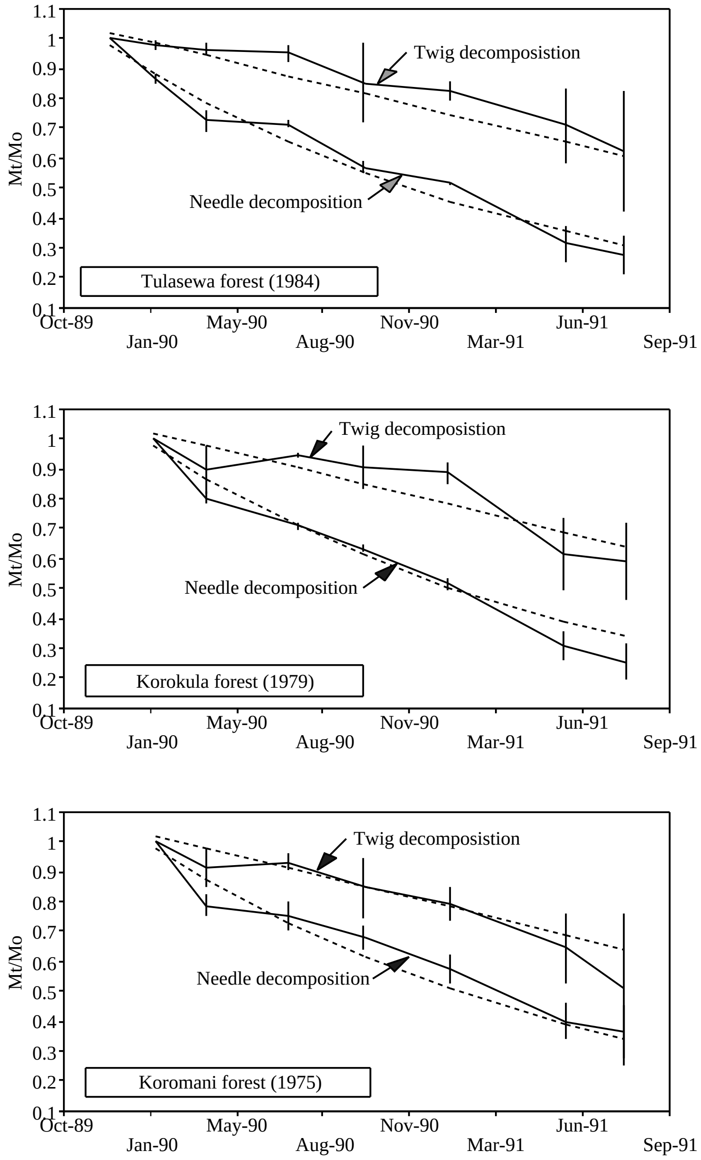

Figure 12.3: *Needle and twig decomposition rates in the Tulasewa, Korokula and Koromani forest plots, expresssed as the ratio of mass at time t after incubation (M_t) to that at incubation (M_0). Dotted line represents a fitted curve using an exponential decay function.*

the initial needle mass was left on the forest floor in the Tulasewa forest plot, whereas in the Korokula and Koromani forest plots, respectively, 25(±6)% and 37(±9)% of the initial needle mass was left after 550 days. These differences must be attributed to differences in soils, as the climatic conditions and needle litter quality were fairly similar at all sites. The first year mass losses observed during this study were similar to those found in by Gunadi and Verhoef (1993) in stands of *Pinus merkusii* in Central Java.

Twig decomposition was much slower than that of needles (Figure 12.3) and exhibited a different pattern with little mass loss during the first year after incubation (11–21%) and increased losses in the following period (20–30%) mass loss in 7 months.

An exponential decay model (Witkamp and Olson, 1963):

$$M_t/M_0 = a \exp^{-b \cdot t} \tag{12.1}$$

was fitted to the grouped needle decomposition data (n=22) where M_t/M_0 represented the needle mass fraction remaining at time t (in months) after incubation. Non-linear regression analysis on the needle decomposition data for all plots (n=22) resulted in values of 0.976(±0.022) and 0.059(±0.003) for a and b respectively, with a coefficient of determination of 0.96. The exponential decay model did not describe the decay of twigs accurately so a linear model ($M_t/M_0 = a + b \cdot t$) was used instead. Linear regression analysis gave values of 1.020(±7.952) and -0.021(±0.000) for the intercept and slope respectively with a coefficient of determination of 0.85. The predicted decomposition rates have been shown in Figure 12.3) as dotted lines.

The corresponding changes in nutrient concentrations (C_t) and contents over the duration of the study are shown in Figure 12.4. Concentrations of K, and to a lesser extent P, showed a sharp drop in the first 2–3 months after incubation, possibly as a result of leaching, and remained fairly constant afterwards (Figure 12.4A,B and C), indicating that these nutrients are then removed parallel to the mass loss. At the end of the study 84–93% of K and 44%–76% of P had been released, with the lower values observed for the Koromani forest plot.

At the Tulasewa and Korokula forest plots N concentrations increased steadily from initial levels of 0.8% and 0.9% to a critical value of 1.6–1.7% after 16 months, and showed a slight decrease thereafter (Figure 12.4A and B). Total N increased throughout the study in Koromani forest from an initial level of 1.0% to a critical N concentration of 1.9% at the end of the study when the increase levelled off (Figure 12.4C). The corresponding C/N ratio was calculated assuming that the concentration of total C remained constant at 50% during the decomposition. This would result in a decrease of the C/N ratio from initial values ranging between 50 and 64 to values ranging between 27 and 32 at the end of the study (Figure 12.5). Figures 12.4D–F show that N remained immobilized, with the release amounting to less than 20% of the initial N content during the first year, until the critical concentration was reached and N was released at a higher rate. Some 32% (Koromani forest) to 56% (Korokula forest) of N had been released by August 1991.

Concentrations of Mg decreased slightly in the first months (Figures 12.4A–C), possibly as a result of leaching, and increased from then onwards to 150% of their initial concentration (0.25–0.32%). As such Mg became increasingly immobilized during the process and some 45–62% of the total Mg content was released over the 550–600 day period. A similar pattern was observed for the concentration of Ca in the needle litter, which showed a 167% (Tulasewa) to 195% (Koromani) increase compared to the initial concentration (0.7–1.1%) over the 18 months. The release of Ca after

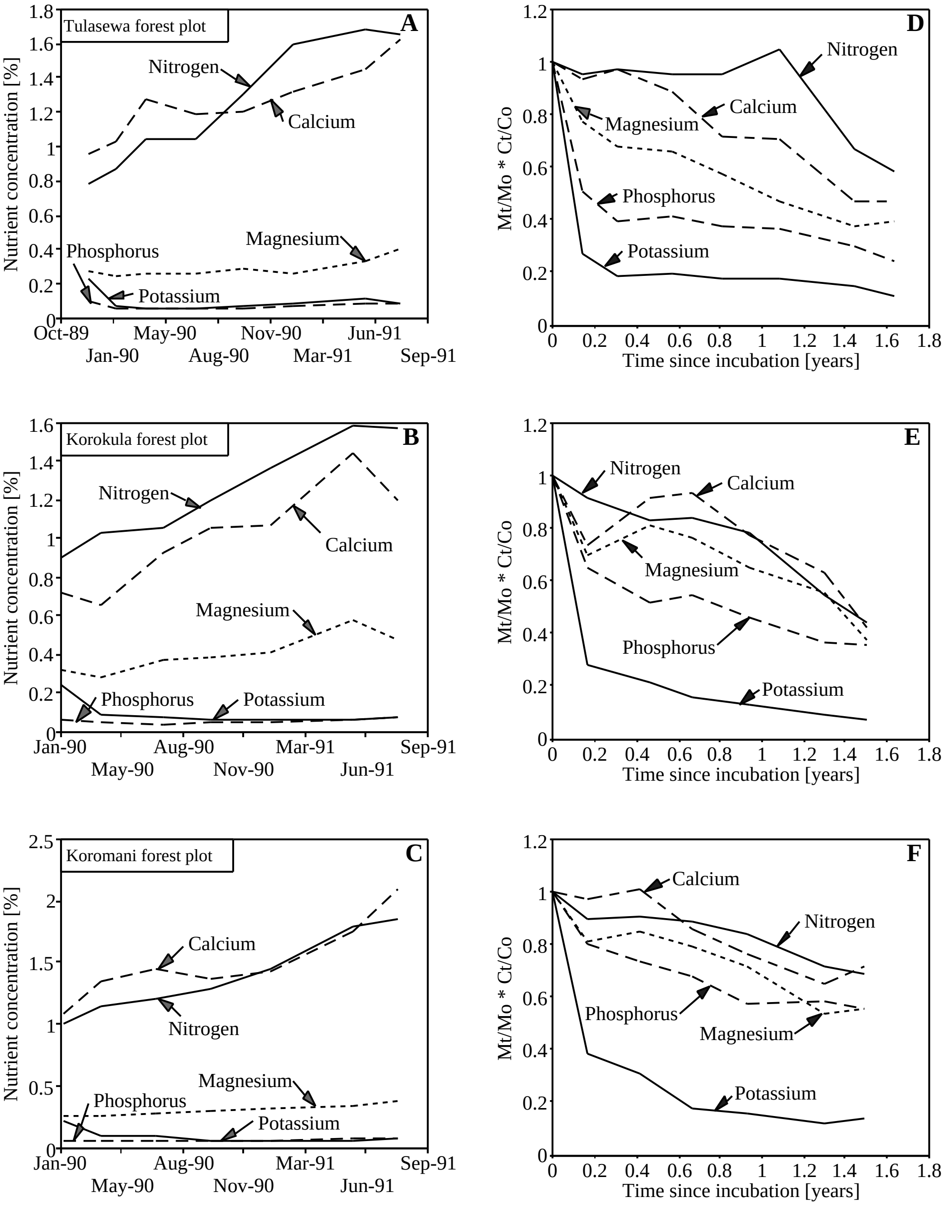

Figure 12.4: *(A,B,C) Changes in needle litter nutrient concentrations and (D,E,F) relative nutrient contents, expressed as a fraction of the initial nutrient content, during the decomposition study in the Tulasewa, Korokula and Koromani forest plots.*

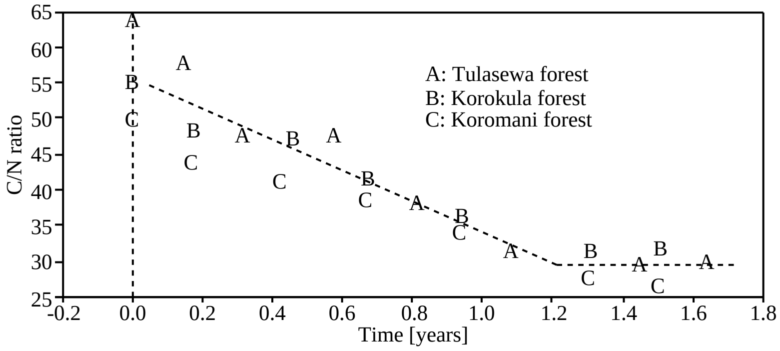

Figure 12.5: *Changes in C/N ratio during decomposition of pine needle litter assuming a constant value of 50% for the concentration of total C.*

18 months was much higher in the Tulasewa and Korokula forest plots than in the Koromani forest plot with 53–58% released at the former and only 29% released at the latter (Figures 12.4D–F).

The concentrations of N, P and K in the green–yellow needles sampled from within the lower parts of the tree crowns (*i.e.* before natural abscission) for the litter decomposition experiment were higher than those observed in pre-cyclone needle fall (see Table 12.2), whereas Ca and Mg concentrations were slightly lower. This indicated that retranslocation (N, P, K) had not finished before needles were sampled. The lower concentrations of N, P and K in needle fall may also have arisen from the fact that abscissed needles are often intercepted lower down in the tree crowns and undergrowth vegetation and may remain suspended for considerable periods of time during which time it is likely that some changes in nutrient concentrations will occur (*e.g.* leaching of K, P and possibly N), before the needles finally reach the forest floor. The higher N concentration in the above samples may also have influenced the release of this element during the decomposition experiment as the initial C/N ratio was much lower (52–64) than that in needle litterfall (129–160). However, the C/N ratio in decomposed needles sampled from the fermentation layer in Korokula forest was also higher (52) than that of needle litter at the end of the decomposition experiment (30) suggesting that the critical N concentration may depend on the initial nutrient concentrations in the needle litter. As such it would be possible to apply the results of the present study to litter with lower initial concentrations. The concentrations of N, P and K in cyclone needle fall were similar to those of needles sampled for the litter decomposition experiment and the results of the experiment will therefore certainly be representative for post-cyclone needle decomposition.

12.5 Litter Standing Crop

12.5.1 Mass and Composition of the Litter Layer

The amount of litter on the forest floor depends on the interplay between litter production and the decomposition both of which have been discussed in the previous sections. The temporal variations in litter standing crop at the Tulasewa, Korokula

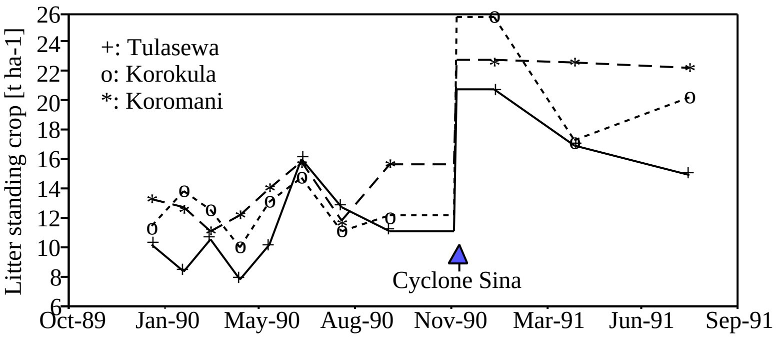

Figure 12.6: *Litter standing crop in the Tulasewa, Korokula and Koromani forest plots.*

and Koromani forest plots are shown in Figure 12.6. Seasonal patterns were fairly similar for the three plots with relatively low amounts during the wet season, coinciding with high decomposition rates (Section 12.4), and higher amounts during the dry season, when decomposition slowed down.

The litter layer mass during the wet season of 1990 in the Tulasewa forest plot was comparable to that in the Nabou grassland plot (Section 10.3) and ranged between 7725(±2686) and 10550(±3582) kg ha^{-1}. The mass increased at the start of the dry season, reaching a maximum of 16065(±9124) kg ha^{-1} after two dry months in June 1990, and decreased again gradually during the wetter months of August and September to 11055(±2222) kg ha^{-1}. Amounts of litter on the forest floor were significantly higher in the Korokula (α= 0.10) and Koromani (α= 0.05) forest plots (Figure 11.7), with no significant differences between the latter two. During the wet season of 1990 litter layer mass ranged from 9955(±1741) kg ha^{-1} to 13863(±2356) kg ha^{-1}) in the Korokula forest plot and from 11050(±3388) kg ha^{-1} to 13245(±4293) kg ha^{-1} in the Koromani forest plot. Litter standing crop peaked at 14778(±2380) kg ha^{-1}) in June at the Korokula forest plot, followed by a gradual decrease during the dry season to 10483(±1734) kg ha^{-1} in September. Similarly, a maximum of 15715(±7553) kg ha^{-1} was observed in June at the Koromani forest plot (Figure 12.6). Measured amounts of needle litter and undergrowth litter (Tulasewa forest only) are listed in Appendix 28.2.

After the passage of cyclone Sina in November 1990 amounts of litter standing crop at the Tulasewa, Korokula and Koromani forest plots increased dramatically to 20702(±5339) (excluding fallen trees), 25750(±7103) and 22688(±4882) kg ha^{-1}, respectively. Decomposition of the freshly fallen needles reduced the needle mass with 2900 (Tulasewa) to 4800 kg ha^{-1} (Koromani) in the period January–August 1991. Average amounts of pre- and post-cyclone litter standing crop in the three plot are given in Table 12.7. It was not possible to include fallen tree stems in the Tulasewa forest plot after the cyclone event and the post-cyclone amounts of litter on the forest floor therefore reflect amounts of needles and small woody components (*e.g.* branches, twigs and cones) only. The actual amount of total litter (including stems) was estimated at 30000–45000 kg ha^{-1} in December 1990 using the equations from Section 11.4.

The composition of the litter layer changed between age 6 and 11, reflecting the sharp decrease in undergrowth biomass. The litter layer in the Tulasewa forest plot consisted for 62% of grass litter, whereas needles accounted for 28% of the total, ranging from 1250(±1297) kg ha^{-1} in February to 5451(±1779) kg ha^{-1} in June 1990. Severely decomposed and burned tree stems of the forest that was destroyed and burned in 1983 were still present at the start of the study and formed the bulk of woody material in the litter layer. This material was included in the litter layer samples collected.

The proportion of undergrowth litter was much lower in the older forests, ranging from 10% of the total in the Korokula forest plot to 19% in Koromani forest plot (Table 12.7). This corresponded with an increase in the proportion of needles to 72% of the total in Korokula forest and 62% in Koromani forest. The pre-cyclone forest floor needle mass in the Korokula and Koromani forest plots varied between 7138(±1201)–11033(±1976) and 7217(±3225)–10679(±1527) kg ha^{-1}, respectively.

The high litterfall associated with cyclone Sina caused an increase in the proportion of needles from 28% before the event to 43% of the total in the post-cyclone litter layer (excluding downed stemwood) in the Tulasewa forest plot, with a corresponding decrease in the proportion of undergrowth to 34% of the total. The proportions of needles in the post-cyclone litter layers in Korokula and Koromani forest plots decreased respectively to 55% and 48%, with corresponding increases in woody litter (branches, twigs and cones) from 15% and 16% to 36% and 32% of the total.

12.5.2 Nutrient Concentrations of Litter

Average pre- and post-cyclone concentrations of nutrient in the various components of the litter layers (needles, undergrowth material, branches, cones, male flowers) in the Tulasewa, Korokula and Koromani forest plots are given in Table 12.8, whereas the analytical data is listed in Appendix 28.2. Concentrations of N, P, K and Mg were highest in undergrowth litter and male flowers, followed by those in needles, cones and wood. The concentration of Ca was highest in needles and lowest in cones and wood.

Differences in mean pre- and post-cyclone concentrations in needle litter for each site are shown in Table 12.9 together with their significance levels. Significant increases were observed in the concentrations of N and P at all sites after the passage of cyclone Sina, whereas concentrations of Mg and B remained fairly unchanged. The Ca concentration decreased significantly in the Tulasewa forest plot, but not in the other forest plots, whereas K concentrations increased in both the Tulasewa and Koromani forest plots. As shown in Table 12.9 there were significant differences between the sites. Pre-cyclone levels of N, Mg and B were highest in the Korokula forest plot, the concentration of K was highest in the Koromani forest plot and those of Ca and Zn were highest in the Tulasewa forest plot. P levels were lowest in the Koromani forest plot whereas Mn levels were lowest in Korokula forest. Post-cyclone levels of N and K in needle litter were not significantly different between sites.

Linear regression analysis was used to see whether the quality of pre-cyclone needle fall influenced the quality of the litter layer. The results indicated that average pre-cyclone concentrations of K, Ca, Mg B, Mn and Zn in needle fall were positively correlated with those in needle litter with coefficients of determination between 0.90 (K) and 1.00 (Zn), whereas the N concentration in needle fall was negatively correlated with that in needle litter with a coefficient of determination of 0.92. The concentration of P in needle fall was poorly correlated with that in needle litter with a coefficient of determination of 0.25.

Table 12.7: *Pre- and post-cyclone amounts and distribution of litter on the forest floors (kg ha^{-1}) in the Tulasewa, Korokula and Koromani forest plots.*

	Total	Needles	Wood	M. flowers	Cones	Seed	Undergrowth
TULASEWA FOREST (Planted 1984)							
Jan'90-Sep'90							
Pre-cyclone mean (n=7)	10561	2951	607	52	389	3.2	6558
Standard deviation	2504	1230	666	44	954	5.5	882
% of total		27.9	5.7	0.5	3.7	0.0	62.1
Jan'91-Jul'91							
Post-cyclone mean (n=3)	17494	7437	2967	47	1100	5.0	5938
Standard deviation	2407	1208	1035	29	457	7.1	1591
% of total		42.5	17.0	0.3	6.3	0.0	33.9
KOROKULA FOREST (Planted 1979)							
Jan'90-Sep'90							
Pre-cyclone mean (n=7)	12493	9030	704	315	1184	2.1	1257
Standard deviation	*1482*	*1284*	*368*	*84*	*483*	*3.6*	*700*
% of total		*72.3*	*5.6*	*2.5*	*9.5*	*0.0*	*10.1*
Jan'91-Jul'91							
Post-cyclone mean (n=3)	21097	11539	4185	111	3352	2.2	1908
Standard deviation	*3519*	*2369*	*855*	*64*	*1005*	*2.1*	*552*
% of total		*54.7*	*19.8*	*0.5*	*15.9*	*0.0*	*9.0*
KOROMANI FOREST (Planted 1975)							
Jan'90-Sep'90							
Pre-cyclone mean (n=7)	13511	8434	1268	249	943	0.4	2617
Standard deviation	*1626*	*1078*	*922*	*48*	*575*	*0.9*	*1014*
% of total		*62.4*	*9.4*	*1.8*	*7.0*	*0.0*	*19.4*
Jan'91-Jul'91							
Post-cyclone mean (n=3)	22531	10871	4670	141	2604	4.4	4241
Standard deviation	*193*	*1966*	*2157*	*61*	*1725*	*5.2*	*1134*
% of total		*48.2*	*20.7*	*0.6*	*11.6*	*0.0*	*18.8*

As the undergrowth vegetation in Tulasewa forest was similar to the grassland vegetation, pre-cyclone concentrations in undergrowth litter (Table 12.8) were comparable to those observed in grassland litter (Table 10.3). Concentrations of all macronutrients in the undergrowth litter of the Tulasewa forest plot increased after the cyclone event. The reason for this is obscure, but it is suggested that the large amounts of nutrients returned to the forest floor in the pine litterfall increased the availability of nutrients for the grass, resulting in a lower need for retranslocation of nutrients before dieback.

12.5.3 Nutrient Content of Litter

The immobilization of nutrients in the litter layer reflects both differences in the litter layer mass and composition as well as nutrient concentrations of the respective components. Average pre- and post-cyclone nutrient contents of the litter layers in the Tulasewa, Korokula and Koromani forest plots are given in Tables 12.10–12.12, respectively. In Tulasewa forest N, P, K and Mg in undergrowth litter accounted for 58–69% of total pre-cyclone litter layer nutrient content, whereas Ca accounted for 34% of the total. In the older forests most of the nutrients were stored in needle litter. However, in spite of the low undergrowth biomass (compared to that of

Table 12.8: *Averages and standard deviations (foliage only) of pre- and post-cyclone nutrient concentrations in the various components of the litter layers Tulasewa, Korokula and Koromani forests. Concentrations in % for macronutrients and in ppm for micronutrients.*

	N	P	K	Ca	Mg	B	Mn	Zn
TULASEWA FOREST (Planted 1984)								
Needles Jan'90-Sep'90								
Pre-cyclone mean (n=7)	0.409	0.019	0.068	0.901	0.212	9.4	610	31
Standard deviation	*0.017*	*0.001*	*0.011*	*0.034*	*0.015*	*0.8*	*67*	*2*
Needles Jan'91-Jul'91								
Post-cyclone mean (n=3)	0.877	0.056	0.141	0.794	0.213	9.2	680	32
Standard deviation	*0.045*	*0.004*	*0.051*	*0.002*	*0.007*	*0.5*	*42*	*0*
Woody parts	0.306	0.036	0.148	0.147	0.088			
Male flowers	0.853	0.060	0.109	0.298	0.227			
Undergrowth Jan'90-Sep'90								
Pre-cyclone mean (n=7)	0.528	0.026	0.112	0.235	0.157			
Standard deviation	*0.003*	*0.001*	*0.006*	*0.037*	*0.011*			
Undergrowth Jan'91-Jul'91								
Post-cyclone mean (n=3)	0.857	0.051	0.131	0.580	0.236			
Standard deviation	*0.106*	*0.008*	*0.038*	*0.125*	*0.029*			
KOROKULA FOREST (Planted 1979)								
Needles Jan'90-Sep'90								
Pre-cyclone mean (n=7)	0.478	0.021	0.049	0.763	0.298	12.5	443	14
Standard deviation	*0.036*	*0.004*	*0.004*	*0.050*	*0.017*	*1.8*	*24*	*2*
Needles Jan'91-Jul'91								
Post-cyclone mean (n=3)	0.783	0.037	0.088	0.731	0.285	11.3	445	21
Standard deviation	*0.085*	*0.002*	*0.011*	*0.017*	*0.035*	*0.4*	*24*	*2*
Branches/twigs	0.240	0.015	0.055	0.203	0.090			
Cones	0.430	0.020	0.077	0.068	0.113			
Male flowers	0.793	0.035	0.057	0.314	0.236			
Undergrowth	0.761	0.036	0.119	0.551	0.294			
KOROMANI FOREST (Planted 1975)								
Needles Jan'90-Sep'90								
Pre-cyclone mean (n=7)	0.434	0.011	0.092	0.709	0.210	10.2	632	16
Standard deviation	*0.050*	*0.003*	*0.018*	*0.038*	*0.016*	*1.2*	*62*	*2*
Needles Jan'91-Jul'91								
Post-cyclone mean (n=3)	0.802	0.046	0.102	0.705	0.215	11.5	764	22
Standard deviation	*0.060*	*0.003*	*0.034*	*0.009*	*0.009*	*1.0*	*33*	*1*
Woody parts	0.379	0.027	0.071	0.244	0.102			
Male flowers	0.817	0.044	0.059	0.345	0.172			
Undergrowth	0.933	0.049	0.083	0.733	0.235			

Table 12.9: *Significance levels for within- and between-site differences in mean nutrient concentrations in pre- and post-cyclone needle litter.*

Difference in means of needle litter	N	P	K	Ca	Mg	B	Mn	Zn
Tulasewa pre- <> post-cyclone	<***	<***	<***	>***	ns	ns	<*	ns
Korokula pre- <> post-cyclone	<***	<***	<***	ns	ns	ns	ns	<***
Koromani pre- <> post-cyclone	<***	<***	ns	ns	ns	<*	<***	<***
Pre-cyclone Tulasewa <> Korokula	<***	ns	>***	>***	<***	<***	>***	>***
Pre-cyclone Tulasewa <> Koromani	ns	>***	<***	>***	ns	ns	ns	>***
Pre-cyclone Korokula <> Koromani	>*	>***	<***	>**	>***	>**	<***	ns
Post-cyclone Tulasewa <> Korokula	ns	>***	ns	>***	<**	<***	>***	>***
Post-cyclone Tulasewa <> Koromani	ns	>**	ns	>***	ns	<**	<**	>***
Post-cyclone Korokula <> Koromani	ns	<***	ns	>*	>**	ns	<***	ns

ns: not significant; *: significance level 0.10; **: significance level 0.05; ***: significance level 0.01

Table 12.10: *Average pre- and post-cyclone nutrient content (kg ha^{-1}) of litter standing crop in the Tulasewa forest plot.*

	N	P	K	Ca	Mg	B	Mn	Zn
Pre-cyclone needle litter	12.0	0.6	2.1	26.8	6.3	0.03	1.8	0.09
Standard deviation	*4.9*	*0.2*	*1.1*	*11.8*	*2.6*	*0.01*	*0.9*	*0.04*
Post-cyclone needle litter	64.7	4.2	10.7	59.0	15.8	0.07	5.0	0.24
Standard deviation	*7.6*	*0.7*	*4.9*	*9.5*	*2.1*	*0.01*	*0.6*	*0.04*
Pre-cyclone woody litter	3.0	0.4	1.5	1.5	0.9			
Standard deviation	*4.9*	*0.6*	*2.4*	*2.4*	*1.4*			
Post-cyclone woody litter	12.4	1.5	6.0	6.0	3.6			
Standard deviation	*1.8*	*0.2*	*0.9*	*0.9*	*0.5*			
Pre-cyclone male flower litter	0.4	0.0	0.1	0.2	0.1			
Standard deviation	*0.4*	*0.0*	*0.0*	*0.1*	*0.1*			
Post-cyclone male flower litter	0.4	0.0	0.1	0.1	0.1			
Standard deviation	*0.3*	*0.0*	*0.0*	*0.1*	*0.1*			
Pre-cyclone undergrowth litter	34.6	1.7	7.4	15.2	10.3			
Standard deviation	*4.7*	*0.2*	*1.2*	*2.2*	*1.7*			
Post-cyclone undergrowth litter	49.3	2.9	7.4	32.5	13.6			
Standard deviation	*6.9*	*0.3*	*1.3*	*1.0*	*1.8*			
Pre-cyclone total	**50.2**	**2.6**	**11.0**	**43.6**	**17.6**			
Post-cyclone total	**126.9**	**8.6**	**24.2**	**97.6**	**33.0**			

Table 12.11: *Average pre-cyclone and post-cyclone nutrient content (kg ha*$^{-1}$ *of litter standing crop in the Korokula forest plot.*

	N	P	K	Ca	Mg	B	Mn	Zn
Pre-cyclone needle litter	43.3	1.9	4.4	68.6	26.8	0.11	4.0	0.13
Standard deviation	*7.6*	*0.5*	*0.8*	*8.5*	*3.5*	*0.03*	*0.7*	*0.03*
Post-cyclone needle litter	88.5	4.2	10.4	84.0	33.3	0.13	5.1	0.23
Standard deviation	*8.9*	*0.6*	*3.6*	*15.1*	*9.3*	*0.03*	*0.8*	*0.03*
Pre-cyclone branch/twig litter	1.7	0.1	0.4	1.4	0.6			
Standard deviation	*0.9*	*0.1*	*0.2*	*0.7*	*0.3*			
Post-cyclone branch/twig litter	10.0	0.6	2.3	8.5	3.8			
Standard deviation	*2.1*	*0.1*	*0.5*	*1.7*	*0.8*			
Pre-cyclone male flower litter	2.5	0.1	0.2	1.0	0.7			
Standard deviation	*0.7*	*0.0*	*0.0*	*0.3*	*0.2*			
Post-cyclone male flower litter	0.9	0.0	0.1	0.3	0.3			
Standard deviation	*0.5*	*0.0*	*0.0*	*0.2*	*0.2*			
Pre-cyclone cone litter	5.1	0.2	0.9	0.8	1.3			
Standard deviation	*2.1*	*0.1*	*0.4*	*0.3*	*0.5*			
Post-cyclone cone litter	14.4	0.7	2.6	2.3	3.8			
Standard deviation	*4.3*	*0.2*	*0.8*	*0.7*	*1.1*			
Pre-cyclone undergrowth litter	9.6	0.5	1.5	6.9	3.7			
Standard deviation	*5.3*	*0.3*	*0.8*	*3.9*	*2.1*			
Post-cyclone undergrowth litter	14.5	0.7	2.3	10.5	5.6			
Standard deviation	*4.2*	*0.2*	*0.7*	*3.0*	*1.6*			
Pre-cyclone total	**62.1**	**2.8**	**7.4**	**78.7**	**33.2**			
Post-cyclone total	**128.4**	**6.2**	**17.6**	**105.6**	**46.7**			

the pines; Table 12.7) the contributions of macronutrients in undergrowth litter were considerable, ranging between 15–34% for N, 16–44% for P, 19–20% for K, 9–23% for Ca and 11–23% of the total for Mg, with the lower values observed in the Korokula forest plot. The high litterfall resulting from cyclone interference caused a decrease in the proportions of macronutrients in undergrowth litter to 33–41%, 10–13% and 17–26% of the respective totals in the Tulasewa, Korokula and Koromani forest plots (Tables 12.10–12.12).

12.6 Litter Dynamics in *Pinus caribaea* Plantations

Due to the large (and unpredictable) impact of cyclones on litterfall, and because of the effects of differences in soil type and forest stocking on litter fall, accurate predictions for changes in litter production during a rotation period are difficult to make for the Fijian case. However, the pre-cyclone averages obtained during the present study may be used as a first estimate since high litterfall after the passage of a cyclone will be more or less compensated by below average litterfall in the subsequent regeneration phase (*cf.* Table 12.1).

Comparison of pre-cyclone litter production in the Fijian forests with those of forests in Nigeria and Puerto Rico revealed that the variation in litter production for forests of similar age can be considerable (Table 12.13). Annual amounts of litterfall

Table 12.12: *Average pre-cyclone and post-cyclone nutrient content (kg ha*$^{-1}$ *of litter standing crop in the Koromani forest plot.*

	N	P	K	Ca	Mg	B	Mn	Zn
Pre-cyclone needle litter	36.4	0.9	7.7	59.6	17.6	0.09	5.3	0.13
Standard deviation	*4.5*	*0.2*	*1.3*	*7.0*	*2.3*	*0.01*	*0.5*	*0.01*
Post-cyclone needle litter	86.0	4.9	11.7	76.6	23.2	0.13	8.3	0.24
Standard deviation	*9.3*	*0.6*	*5.9*	*13.7*	*3.4*	*0.03*	*1.6*	*0.04*
Pre-cyclone woody litter	8.4	0.6	1.6	5.4	2.3			
Standard deviation	*4.0*	*0.3*	*0.8*	*2.6*	*1.1*			
Post-cyclone woody litter	27.6	2.0	5.2	17.7	7.4			
Standard deviation	*8.9*	*0.6*	*1.7*	*5.7*	*2.4*			
Pre-cyclone male flower litter	2.0	0.1	0.1	0.9	0.4			
Standard deviation	*0.4*	*0.0*	*0.0*	*0.2*	*0.1*			
Post-cyclone male flower litter	1.2	0.1	0.1	0.5	0.2			
Standard deviation	*0.5*	*0.0*	*0.0*	*0.2*	*0.1*			
Pre-cyclone undergrowth litter	24.4	1.3	2.2	19.2	6.1			
Standard deviation	*9.5*	*0.5*	*0.8*	*7.4*	*2.4*			
Post-cyclone undergrowth litter	39.6	2.1	3.5	31.1	10.0			
Standard deviation	*10.6*	*0.6*	*0.9*	*8.3*	*2.7*			
Pre-cyclone total	**71.2**	**2.9**	**11.6**	**85.1**	**26.5**			
Post-cyclone total	**154.3**	**9.1**	**20.5**	**125.9**	**40.9**			

have been plotted against forest age in Figure 12.6 and show a general increase with age. The production of the Puerto Rican forests was high compared to those of the Fijian and Nigerian forests, which may be related to differences in the rainfall regimes (Figure 12.6). If the impact of cyclones on litterfall is taken into account for the Fijian forests, litter production becomes higher than the values presented for any of the forests in Nigeria or Puerto Rico (Table 12.13). However, because Puerto Rico is also situated in a zone that is occassionally traversed by hurricanes (return period 21 years according to Salivia, 1972), the average annual production of litter over the period of a rotation (including that induced by cyclones) may be somewhat higher than the values presented by Cuevas (1991) and Lugo (1992). Lodge *et al.* (1991) measured pre-hurricane and hurricane litterfall after hurricane Hugo (1989) passed over rain forests in Puerto Rico and obtained results similar to those found in the present study.

An overview of nutrient returns in litterfall for several *Pinus caribaea* plantation forests of varying age in Fiji, Nigeria and Puerto Rico is presented in Table 12.13. Because concentrations of nutrients in litterfall did not vary too much between forests, the return of nutrients to the forest floor via litterfall was strongly related to the annual litterfall amounts. Similar nutrient returns were therefore found for the Nigerian and Fijian forests, whereas a higher return was observed for the 19.5 year old forest in Puerto Rico. However, if nutrients in litterfall during the passage of cyclones are taken into consideration, the returns for the Fijian forests are higher than those of any of the other forests.

The accumulation of litter with increasing forest age in the Fijian study forests has been plotted in Figure 12.9 (both pre- and post-cyclone data), together with those measured in *Pinus caribaea* forests in other tropical countries. The actual amounts

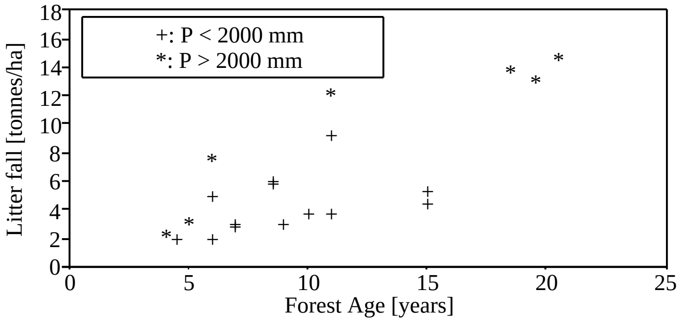

Figure 12.7: *Litterfall in Pinus caribaea forests in Fiji, Nigeria and Puerto Rico, differentiated according to the annual rainfall total (P).*

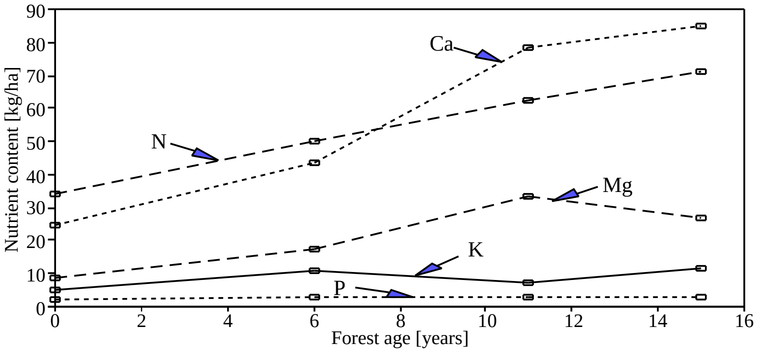

Figure 12.8: *Amounts of macronutrients in the pre-cyclone litter layer* versus *forest age in the study forests.*

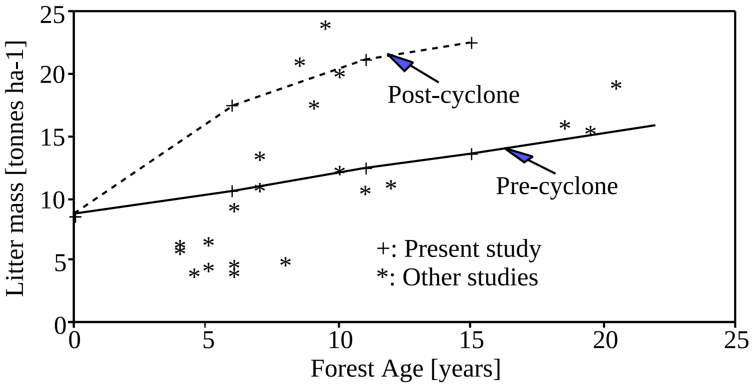

Figure 12.9: *Amounts of litter on the forest floor* versus *forest age for Pinus caribaea plantation forests in various tropical countries. The solid regression line describes the accumulation of litter with forest age in the study sites.*

Table 12.13: *Annual amounts of litterfall (t ha^{-1}) and associated nutrient returns in litterfall (kg ha^{-1}) for Pinus caribaea plantations of varying age in Fiji, Nigeria and Puerto Rico.*

Location	**Alt.**	**P**	**Dry**	**Age**	**Litter fall**		**Nutrient returns**					**Reference**
	[m]	[mm]	**months**		Total	Needle	N	P	K	Ca	Mg	
FIJI												
Cyclone Sina excluded												
Tulasewa	116	1800	6	6	5.0	4.8	19.0	0.8	4.6	43.1	9.7	Present study
Korokula	50			11	9.3	6.7	34.2	1.9	8.9	56.9	24.7	
Koromani	90			15	5.4	4.6	20.6	0.9	5.5	33.1	10.4	
Cyclone Sina included												
Tulasewa	116	1800	6	6	26.5	10.9	92	10	51	102	31	Present study
Korokula	50			11	26.1	15.4	137	9	42	119	59	
Koromani	90			15	23.8	10.8	108	7	37	99	32	
NIGERIA												
Kaduna	610	1250	5	7	3.0							Kadeba(1991)
				9	3.1							
				11	3.7							
				15	4.5							
Afaka	610	1250	5	7	3.1		13.1	0.6	7.3	16.7	5.8	Kadeba & Aduayi {1985)
				10	3.7		16.8	0.7	7.3	19.6	6.8	
Ibadan	230	1330	5	6	2.0							Egunjobi (1975)
Ibadan	230	1330	5	4-5	1.9	1.9	7.3	0.4	6.9	11.4	2.7	Egunjobi & Fasehun (1972)
				7-10	6.0		26.9	0.6	13.6	35.9	10.7	
Ibadan	230	1330	5	7-10	5.8		25.5	0.6	14.5	34.0	10.9	Egunjobi & Onweluzo (1979)
PUERTO RICO												
Luquillo	350	3360	0	11	12.1	9.1						Cuevas et al. (1991)
Luquillo	220	3900	0	4	2.1	2.1						Lugo (1992)
				5	3.1	3.0	14.0	0.7	3.4			
				6	7.4	6.8						
				18.5	13.6	11.9						
				19.5	12.9	11.9	86.0	2.5	9.6			
				20.5	14.5	12.6						

are given in Table 12.15. The data show a general accumulation of litter with forest age, although the scatter is considerable. A regression line was fitted through the grassland and pre-cyclone forest litter standing crop data collected in Fiji to describe the increase in litter layer mass (M_l, kg ha^{-1}) with forest age (A_f, in years):

$$M_l = 8709(\pm 167) + 327(\pm 15) \cdot A_f$$
$$\text{n}= 4,\ r^2 = 1.00 \qquad (12.2)$$

A comparison of litter accumulation in the Nigerian stands with those in Puerto Rico shows that the scatter must be due to differences in decomposition rates rather than litter production rates, because litter production was highest in the Puerto Rican forests (Table 12.13). The high values found for the Brazilian forests may be due to inclusion of decomposing slash from the previous rain forest (Table 12.15).

The accumulation of macronutrients in the litter layer of the Fijian plantations during a rotation period is shown in Figure 12.8. Nutrient contents increased over a rotation period but the accumulation rate was not similar for all nutrients.

The largest relative accumulations were observed for Ca and Mg, with amounts stored in the litter layer at the end of the rotation being 3.5 (Ca) to 3.0 (Mg) times those in the litter layer in the Nabou grassland site. Contents of N and K increased by factors of 2.1 and 2.4, respectively, whereas the accumulation of P was relatively slow as the content increased by a factor of 1.4 only. The Ca and Mg contents of the litter layer in Korokula forest were relatively high, whereas the K content was relatively low. This was attributed to differences in the site quality. In contrast to the other macronutrients, N and P contents showed a linear increase with forest age and the accumulation of these nutrients therefore seemed rather independent of site quality (Figure 12.8). Linear regression analysis was used to obtain expressions ($Y = a \cdot X + b$) describing the change in nutrient content of the litter layer (Y) with forest age (X). The resulting regression constants and coefficients of determination (r^2) are given in Table 12.14. The latter were particularly low for Zn, which showed little variation with age, and for K, which was exceptionally low at Korokula forest. The mean annual increase in the nutrient content of the litter layer over a rotation is given by the regression constant a, whereas b approximates the nutrient content of the litter layer in the preceding grassland.

Table 12.14: *Regression constants and their standard errors (between brackets) and coefficients of determination for expressions describing the changes in nutrient content (kg ha^{-1}) of the litter layer with forest age (years) in SW Viti Levu. Lines were fitted through four data points representing age 0, 6, 11 and 15 years.*

Nutrient	**a**	**b**	**r2**	**Nutrient**	**a**	**b**	**r2**
N	2.47(0.07)	34.62 (0.76)	1.00	**Mg**	1.42 (0.57)	10.20 (6.42)	0.75
P	0.05 (0.01)	2.17 (0.11)	0.94	**Mn**	0.21 (0.09)	1.65 (0.98)	0.75
K	0.34 (0.25)	5.97 (2.82)	0.48	**B**	0.0048 (0.0026)	0.0284 (0.0296)	0.62
Ca	4.35 (0.64)	23.22 (7.22)	0.96	**Zn**	0.0004 (0.0022)	0.1180 (0.0252)	0.01

[thb]

Table 12.15 illustrates the large variation exist between the amounts of nutrients that may be immobilized in the litter layers of *Pinus caribaea* forests of similar age. For instance, the N content of the litter layer in 9–11 year old forests ranged from 62 to 160 kg ha^{-1} with an average of 91 kg ha^{-1}. Similar differences were observed for the other nutrients. Some of these variations may be explained by differences in density and composition of the undergrowth.

Table 12.15: *Amounts of litter (t ha^{-1}) and nutrient content of litter (kg ha^{-1}) for Pinus caribaea plantations in the tropics.*

Location	Alt.	P	Dry	Age	**Litter on the forest floor**							Reference
	[m]	[mm]	months		Total	Needle	N	P	K	Ca	Mg	
FIJI												
Tulasewa	116	1800	6	6	10.6	3.0	50	2.6	11.0	44	17.6	Present study
Korokula	50	1800	6	11	12.5	9.0	62	2.8	7.4	79	33.2	Present study
Koromani	90	1800	6	15	13.5	8.4	71	2.9	11.6	85	26.5	Present study
BRAZIL												
Jari Florestal	50	2300	5	6	64.7		227	12.9	12.9	175	84.1	Chijioke (1980)*
Jari Florestal	50	2300	5	9.5	23.8		160	4.8	11.9	76	21.5	Russell (1983)
NIGERIA												
Afaka	610	1250	5	7	10.6		53.1	2.1	14.9	67	17	Kadeba & Aduayi {1985)
				10	12.1		66.7	2.4	15.8	83	20.6	
Ibadan	230	1330	5	6	3.7		18.1	0.4	8.9	7	3.6	Egunjobi & Bada (1979)
				8	4.6							
				9	17.3							
				10	19.7		88.7	2	47.3	39.4	13.8	
Ibadan	230	1330	5	4-5	3.7		13.3	0.7	10	24.1	5.2	Egunjobi & Fasehun (1972)
Ibadan	230	1330	5	7-10	20.7							Egunjobi & Onweluzo (1979)
AUSTRALIA												
Beerburrum, A	20		5	5	4.2							Richards & Bevege (1967)
TRINIDAD												
Matura		2800	0	4	6.1		39	2.0	7.0	51	10.0	Cornforth (1970)
Valencia	70	3300	0	6	4.4		30	1.0	4.0	39	7.0	
Melajo	200	3000	0	7	13.1		90	4.0	5.0	123	29.0	
Cumuto	10	2500	0	4-12	11.0		77	8.0	12.0	94	16.0	
PUERTO RICO												
Luquillo	350	3360	0	11	10.5	6.1						Cuevas et al. (1991)
Luquillo	220	3900	0	4	5.6	5.2						Lugo (1992)
				5	6.2	5.7	37	1.8	6.5			
				6	9.1	7.8						
				18.5	15.7	12.6						
				19.5	15.2	12.3	102	3.8	9.8			
				20.5	18.9	13.8						

*: includes undergrowth

Chapter 13

Nutrient Fluxes in Water

13.1 Introduction

Water is the medium in which considerable amounts of non-gaseous elements are transferred between the various compartments of an ecosystem (*e.g.* atmosphere, vegetation, soil). The amounts of rainfall, throughfall, litter percolate and drainage were quantified for each of the forest plots in Chapter 6, whereas the cycling of nutrients via litterfall was discussed in the previous chapter. To complete the picture, changes in the chemical composition of rain water as it passes through the forest ecosystem and associated nutrient fluxes between the various system compartments will be discussed in this chapter.

13.2 Field and Laboratory Procedures

13.2.1 Sampling of Soil Moisture

The sampling procedures for rain water, throughfall, stemflow and litter percolate have already been discussed in Section 6.2. Vacuum tube lysimeters (Wood, 1973) were used to sample soil moisture for the determination of its chemical composition. The lysimeters were pre-treated by leaching with a 0.1 N HCl solution and rinsing with distilled water (EC= 2 μS cm^{-1}) until the electrical conductivity (EC) of the extracted solution was similar to that of the distilled water. The samplers were installed with their ceramic cups just below the A-horizon at depths of 20–30 cm, or well within the B/C- horizon at depths of 60–90 cm. The dates of installation and removal of the lysimeters, the number of lysimeters in each plot, and the depths of the cups are given in Table 13.1. A vacuum of about 500 mbar was obtained with a hand vacuum pump. The determination of the quality of soil moisture is difficult as there are sources of error (Haines *et al.*, 1982) associated with the method used to extract the moisture, as well as with spatial variation. The chemical composition of moisture collected with suction lysimeters is known to vary with the suction that is applied, with moisture being extracted from increasingly smaller pores with increasing suction (Nortcliff and Thornes, 1989). In addition, the volume of soil from which the moisture is extracted is unknown. If the applied suction exceeds that prevailing in the soil, H_2CO_3 may leave the soil solution in gaseous form, thereby changing its pH and HCO_3^- concentration.

Table 13.1: *Depths, installation dates and removal dates of vacuum tube lysimeters in the Tulasewa, Korokula and Koromani forest plots.*

Plot	Code	Number	Depth	Start	End	Remarks
Tulasewa	PU 20-2	2,4,6,8	30- 35 cm	Dec/Jan 1989	Sep 1991	A/B horizon, clay-loam
Forest		1,3,5,7	90-110 cm	Dec/Jan 1989	Sep 1991	C horizon, RR, sandy loam
Korokula	PU 09-5	2,4,6	19- 25 cm	Jan 1990	Sep 1991	A-horizon, fine sand
Forest		1,3,5	37- 95 cm	Jan 1990	Sep 1991	At bedrock, gravelly sandy loam
Koromani	PU 09-4	2,4	25- 30 cm	Dec 1989	Sep 1991	B horizon, sandy loam
Forest		1,3	100 cm	Dec 1989	Sep 1991	C horizon, RR, sandy loam
		6,8	25- 30 cm	Jul 1990	Sep 1991	B horizon, sandy loam
		5,7	80- 85 cm	Jul 1990	Sep 1991	C horizon, clay loam

Furthermore, the ceramic material of the cup may selectively absorb some of the ions from the solution passing through its pores (particularly P, NO_3, NH_4), and release other ions (notably Na, Mg, Si, SO_4; Hansen and Harris, 1975; Zimmermann *et al.*, 1978). To minimize such influences on the composition of soil moisture samples, water extracted on the first two occasions after installation was not sampled. The first sample was therefore usually not collected within two weeks after the installation of the lysimeter. The lysimeters were emptied at least once a week during the wet season when the soil was sufficiently moist, but less regular during the dry season. The moisture was collected in 250 ml plastic measuring cylinders. Samples collected at corresponding depths were bulked for each plot and stored in the dark until sufficient water had been collected for analysis.

13.2.2 Sampling and Analytical Procedures

The EC of rainfall, throughfall, litter percolate and soil moisture were measured in the field on each sampling occasion with an EC-meter developed at the electronics department of FES-VUA. The EC-values (μS cm^{-1}) were automatically normalized to a temperature of 25 °C. The accuracy was 2 μS cm^{-1} for the most frequently used range of 0–100 μS cm^{-1} and 4 μS cm^{-1} for the range 0–200 μS cm^{-1}. Separate readings were made for each gauge unless the collected amounts were not sufficient. In such cases measurements were made after bulking of individual samples.

Rain water samples for chemical analysis were taken at monthly intervals during dry periods and more frequently during wet periods from water collected by the special raingauge, as described in Section 6.2. The samples were collected shortly after large storms ($P > 30$ mm) to include both wet and dry deposition of the preceding period. The weekly or bi-weekly bulk samples of throughfall, litter percolate and soil moisture were stored in the dark until sampling occurred. Throughfall and litter percolate samples were always collected on the same day as rain water samples. Soil moisture samples were taken less frequently, normally after enough moisture had been extracted (about 1.5 l).

In addition, two seawater samples were collected in December 1990 and July 1991 at Natadola Harbour to enable the determination of the contribution of maritime components to the chemical composition of rainfall. The EC of seawater was measured after dilution with pure rain water (EC= 2 μS cm^{-1}) by a factor 20 to remain within the range of 0–5000 μS cm^{-1}.

To obtain estimates of the nutrient output in streamflow from the forested Oleolega catchment, 21 samples were collected under baseflow conditions. Due to time and manpower constraints, the remoteness of the site which could be reached by car during periods with high rainfall only with great difficulty, and the high spatial variation of rainfall in the Nabou area, only 27 stormflow samples could be collected despite numerous attempts. To overcome this problem to some extent, the EC (a measure of the total ion concentration in the solution) and temperature of the streamflow were measured at 20 minute intervals with an EC datalogger system developed at the FES-VUA from April 19, 1990, onwards. The EC measurements by the datalogger system had to be corrected for temperature variations and were normalized to a temperature of 25 °C. Linear regression equations were used to calibrate the EC datalogger system against the manually operated EC meters (Schellekens, 1992; Assenberg, 1993). Although no diurnal variation was observed in the EC readings of streamflow as read with the manually operated EC meters, the datalogger system suggested such a variation even after temperature correction. Furthermore, unexplained variations occurred occasionally due to malfunctioning of the datalogger system, which also showed a lack of sensitivity when the instrument was not properly adjusted (Schellekens, 1992; Assenberg, 1993).

Pre-cyclone baseflow samples were collected at the usual sampling site in the Oleolega catchment (Figure 3.4), at a location further downstream near the junction of Oleolega Creek and the Kubuna River (Planning Unit 10-5), and in the adjacent Naruku catchment (Planning Unit 10-3) (see also Figure 2.2) to give an impression of the spatial variability of baseflow composition for forested catchments of varying size in the area. Samples representing baseflow from a nearby grassland catchment were collected from the Ividamu creek (Planning Unit 10-1, 10-6; see Figure 2.2) upstream from the junction with the Kubuna River. This catchment drains the area SW of the Naruku Catchment and the geology of the area was thought to be similar to that of the Naruku catchment, where the parent rock consisted of Kalaka dacite. Samples were collected on the same day on five occasions between August 1990 and December 1990. However, only 3 samples could be collected from the Naruku catchment because the creek fell dry at the end of the dry season. Another 10 samples were collected at each site during the post-cyclone period.

Water samples for cation analysis, Si and PO_4 were collected in 100 ml polyethylene bottles after filtering through a 0.45 μm Millipore filter. Each bottle had been rinsed with a 10% HNO_3 solution to remove any adsorbed ions before rinsing six times with distilled water (EC= 2 μS cm^{-2}). For conservation purposes 0.7 ml of 65% HNO_3 suprapur was added to the bottle prior to the sampling, resulting in a final sample pH of about 1. Streamflow samples for cation analysis were collected with a syringe from the center of the creek some 15 m upstream from the culvert to avoid any contamination of the samples by Ca and HCO_3 from the cement of the culvert.

Water samples for anion analysis, total N, total P and laboratory measurements of EC and pH were collected in 200 ml polyethylene bottles. These bottles had been rinsed 6 times with distilled water and another six times with the sampling solution prior to sampling. To avoid any contamination with NO_3 the 200 ml sample was always collected before the acidified sample. Streamflow samples for anion analysis were collected in the center of the Oleolega creek after the bottles had been rinsed 6 times with streamwater collected at a spot downstream from where the sample would be collected. The bottles were closed below the waterlevel to avoid air bubbles in the sample and the acidified sample was collected at the same spot immediately afterwards. All samples were stored in a refrigerator at about 4 °C before shipment to the Netherlands by airfreight for analysis at FES-VUA.

The EC, pH and the presence of NO_3/NO_2 were determined in the field during sampling. The pH was measured with a combined electrode (INGOLD, type U402-S7/120) connected to a pH-meter (Metrohm AG., Model E-604). The electrode was calibrated before each measurement using two buffer solutions (Baker Chemical Co.) with pHs of 4.00 and 7.00 at 25 °C, respectively. The error in the pH measurements was typically less than 0.1 pH unit. An estimate of the nitrate concentration of the samples was obtained using non-bleeding nitrate test strips (Merckoquant 10020, Merck).

Separate water samples were collected for the determination of alkalinity (HCO_3) and hardness (Ca+Mg). These were determined in a field laboratory in Nadi, usually within 24 hours after the sampling. Alkalinity was measured by titration (HACH Digital Titrator) of the solution with 0.4 N H_2SO_4 after adding an indicator consisting of a mixture of Br-Cresolgreen (150 mg), methylred (100 mg) and 96% ethanol (200 ml). Hardness was determined by titration of the solution with Na-EDTA after adding an indicator (Merck, No. 11122).

13.2.3 Laboratory Procedures

The EC and pH were remeasured in the laboratory at FES-VUA with a Phillips digital conductivity meter (Model PW-9526) and a digital pH-meter (Orion Research, Model 701A) connected to a combined electrode (Orion Research), respectively. The pH-meter was calibrated against buffer solutions (Baker Chemical Co.) with pHs of 4.00 and 7.00 at 25°C.

Concentrations of Na and K were determined by flame photometry using an Eppendorf flame photometer. Concentrations of Al, Ca, total Fe, Mg, Mn and Si were determined on a Perkin-Elmer (Model 6500) Inductively Coupled Plasma (ICP) emission spectrophotometer. Concentrations of Cl, SO_4, NO_3, PO_4 and NH_4 were determined by spectrophotometry on Technicon and Skalar Auto-analyzers according to the following automated methods. Chloride was determined with the ferricyanide method of Zall *et al.* (1956), SO_4 was determined with the methylthymol-blue method of Greenberg *et al.* (1980), NO_3 by cadmium reduction (Hendrikson and Selmer-Olsen, 1970), PO_4 by ascorbic acid reduction (Black *et al.* 1965) and NH_4 with the modified Berthelot reaction using salicylate and dichloroisocyanurate (Krom, 1980). Total P was determined on the ICP after destruction using the molybdiphosphoric acid method of Boltz and Mellon (1948). Total N was determined as NH_4 on the ICP after destruction (Kjeldahl digest). HCO_3 was not remeasured.

The analytical accuracy was assumed to be within 2% of the concentrations in the highest standard solutions and the maximum errors for each constituent are given in Table 13.2.

13.3 Chemical Composition of Rainfall and Atmospheric Inputs

The atmospheric input of chemical constituents to a forested ecosystem is governed by two processes, wet and dry deposition (Whitehead and Feth, 1964). The deposited solids during intermediate dry periods may dissolve rapidly during periods with rain-

Table 13.2: *Maximum absolute analytical errors in concentrations (mg l^{-1}) of constituents in water samples as determined st FES-VUA (Mrs. T. Bäer, pers. comm.).*

Species	Error	Species	Error	Species	Error	Species	Error
Na	0.40	NH_4^+	0.03	Cl^-	0.40	Fe-Total	0.04
K	0.10	Al^{3+}	0.04	SO_4^{2-}	0.60	N-Total	0.02
Ca	0.24	Mn^{2+}	0.04	NO_3^-	0.20	P-Total	0.02
Mg	0.20	Si^{4+}	0.40	PO_4^{3-}	0.02		

fall. During the present study bulk samples of rainfall were collected shortly after large storms. In this way composite samples of dry deposition, as intercepted by the rainfall gauges during preceding dry periods, and wet deposition during the rainfall events were obtained. There are several problems associated with the measurement and calculation of atmospheric inputs to an ecosystem (Waring and Schlesinger, 1985; Bruijnzeel, 1991), some of which are listed below. Ion concentrations in rain water are generally low which can lead to large analytical errors if the sensitivity of the analysis is not sufficient. Because the trapping surface area for dry deposition of a raingauge is smaller than that of forests, and because forests are better exposed to winds, the dry deposition component may be underestimated by a rain gauge. To complicate the matter further, some of the dry deposition may be produced by the ecosystem under consideration (*e.g.* pollen; gaseous emissions) and therefore does not constitute a real input to the system (Stoorvogel, 1993).

The chemical composition of rain water collected by a rain gauge depends on the source of water (*e.g.* maritime or terrestrial), on constituents (*e.g.* aerosols, gaseous emissions by industry or volcanoes) picked up during transport through the atmosphere and on the composition of the dry deposition (Appelo and Postma, 1993). Particles of salt may be considered the main source of ions for both wet and dry deposition. In the atmosphere above the oceans such salt particles form during the breaking of waves when fine droplets of seawater are ejected into the atmosphere. After evaporation of the water, solid salt particles are formed which can be transported upwards by winds and may act as condensation nuclei for the generation of raindrops in clouds (Drever, 1982). Fractionation during the forming of these salt particles does not play an important role for the major ions (Na, K, Ca, Mg, Cl, SO_4) (Duce and Hoffman, 1976). Therefore these ions are present in precipitation in the same proportions as they were in seawater and rainfall on small oceanic islands may therefore be considered as very dilute seawater.

On larger islands or continents the composition of rain water may be influenced by dust, smoke from burning vegetation or natural and industrial emissions (Appelo and Postma, 1993). The source of ions in rain water may be evaluated by subtraction of the oceanic contribution from the total ion content for each constituent. So-called excess concentrations are then assumed to originate from continental sources (Eriksson, 1960). Chloride ions are only marginally added to rain water by terrestrial sources (at least in non-volcanic and non-industrial areas) and the Cl concentration may therefore be taken to reflect the oceanic contribution. If fractionation during the forming of salts can be neglected, expected oceanic contributions of other ions ($[X_{expected}]$) may be calculated using their proportions with respect to the Cl concentration in seawater

($[Cl_{sea}]$) as shown in Equation 13.1 (Eriksson, 1960).

$$[X_{expected}] = \frac{[X_{sea}]}{[Cl_{sea}]} \cdot [Cl_{rain}] \tag{13.1}$$

The average EC, pH and chemical composition of locally sampled seawater are shown in Table 13.3. The contribution of cations to the total dissolved solids (TDS) in seawater decreased in the order Na > Mg > Ca > K > NH_4 > Si, whereas that of anions decreased in the order Cl > SO_4 > HCO_3 > PO_4 > NO_3. Levels of NO_3, Al, Fe and Mn were below the detection limits.

Weighted averages of EC and pH, as measured in the field during sampling (shown in Table 13.3) with those measured in the laboratory of the FES-VUA (not shown), differed by less than 3 μS cm^{-1} and less than 0.1 pH unit respectively, which is within the range of the instrumental errors, suggesting that no major changes had occurred between sampling and analysis.

Throughout this chapter the 'pre-cyclone period' will represent the period between January 1 and November 23, 1990, the 'cyclone period' the period between November 24 and December 3, 1990, and the 'post-cyclone period' that between December 4, 1990 and September 30, 1991. Weighted average ion concentrations in pre- and post-cyclone rainfall, as well as those in cyclone rainfall (single samples) are presented in Table 13.3. If concentrations fell below the detection limit, the latter was used to calculate the weighted averages, leading to an unavoidable overestimation of the concentration. The concentrations of K, Ca, Mg, SO_4, NO_3, Si, Al, Mn, total Fe and total P in rainfall were often below the detection limits, whereas those of the other ions were just above the detection limits and large analytical errors are therefore to be expected (*cf.* Table 13.2). However, measured concentrations of most ions were consistent throughout the data set and the sensitivity of the analysis was therefore considered sufficient. This suggested that the analytical errors were in fact lower than given in Table 13.2. Some uncertainty existed with respect to the field analysis of HCO_3 in rain water collected at Tulasewa and Oleolega forests because concentrations were usually close to zero, but extremes of 18.3 mg l^{-1} and 24.4 mg l^{-1} were also observed without corresponding increases in EC. Concentrations of HCO_3 at the Korokula and Koromani forest plots remained below 6.7 and 3.7 mg l^{-1}, respectively. This suggested that some contamination may have occurred at the Tulasewa and Oleolega sites and the weighted averages of the HCO_3 concentration given in Table 13.3 for the pre-cyclone period may therefore be seriously overestimated[1].

The concentrations of all constituents in pre- and post-cyclone rain water were extremely low, with weighted averages of EC ranging from 6–7 μS cm^{-1} for the inland rainfall stations at Oleolega and Tulasewa, to 8–9 μS cm^{-1} for the more coastal stations at the Korokula and Koromani sites (See Figure 2.2). Therefore the EC showed a (very weak) negative trend with distance from the ocean. This may be ascribed to lower concentrations of Na and Cl in rain water collected at inland stations, possibly also as a result of dilution due to the increase of rainfall amounts with distance to the coast (*cf.* Weijers and Vugts, 1990; Stuijfzand, 1993).

The chemical composition of rain water collected at any location may vary considerably with time and depends on the amount of rainfall (dilution effect, washing out of aerosols), the length of the preceding dry period (accumulation of dry deposition) as

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[1] When contaminated samples were excluded average pre- and post-cyclone concentrations were 1.08 and 0.87 mg l^{-1} at Tulasewa forest, and 1.27 and 1.05 mg l^{-1} at the Oleolega catchment, respectively.

Table 13.3: *Weighted pre- and post-cyclone averages of EC ($\mu S\ cm^{-1}$), pH, and ion concentrations ($mg\ l^{-1}$) in rain water with analytical detection limits ($mg\ l^{-1}$), corresponding concentrations in seawater and derived oceanic contributions for each constituent added for comparison. Analyses of rain water collected after the passage of cyclone Sina represent single samples.*

Location	**EC**	**pH**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Detection limit			*0.05*	*0.05*	*0.05*	*0.05*	*0.05*	*0.05*	*0.00*	*0.30*	*0.05*	*0.02*	*0.05*	*0.05*	*0.02*	*0.02*	*0.02*	*0.02*
Seawater																		
Natadola	60850	8.34	10820	408	1356	392	0.26	20210	140	2754	0.05	0.39	0.10	0.05	0.02	0.02	0.11	0.03
Bulk precipitation, excluding cyclone events																		
Tulasewa	6	5.62	0.61	0.28	0.06	0.09	0.27	1.20	3.27	0.56	0.15	0.02	0.05	0.05	0.02	0.02	0.16	0.02
Korokula	8	5.50	0.80	0.13	0.06	0.09	0.34	1.52	1.02	0.73	0.24	0.02	0.05	0.05	0.02	0.02	0.56	0.02
Koromani	9	5.49	0.87	0.12	0.06	0.08	0.22	1.61	0.97	0.80	0.11	0.02	0.07	0.03	0.03	0.02	0.32	0.02
Oleolega	7	5.67	0.61	0.15	0.07	0.10	0.28	1.23	5.83	0.87	0.18	0.03	0.09	0.06	0.05	0.03	0.15	0.03
Pre-cyclone bulk precipitation																		
Tulasewa	8	5.57	0.66	0.32	0.06	0.12	0.27	1.33	5.71	0.57	0.17	0.02	0.05	0.05	0.02	0.02	0.13	0.02
Korokula	8	5.42	0.85	0.11	0.07	0.09	0.25	1.55	1.18	0.68	0.10	0.02	0.05	0.05	0.02	0.02	0.34	0.02
Koromani	9	5.50	0.99	0.10	0.07	0.09	0.15	1.62	1.00	0.63	0.09	0.02	0.08	0.03	0.03	0.02	0.22	0.02
Oleolega	7	5.85	0.63	0.12	0.07	0.11	0.23	1.18	9.84	0.70	0.14	0.09	0.10	0.07	0.07	0.05	0.12	0.03
Cyclone precipitation																		
Tulasewa										Not available								
Korokula	100	5.19	15.95	0.65	2.02	0.67	0.12	29.16	0.61	4.57	0.06	0.01	0.05	0.05	0.02	0.02	0.13	0.02
Koromani	120	5.43	19.45	1.17	2.44	0.81	0.13	35.74	0.00	5.83	0.09	0.01	0.05	0.02	0.02	0.02	0.12	0.02
Oleolega	76	4.95	12.10	0.65	1.51	0.54	0.19	21.83	0.00	3.07	0.20	0.01	0.10	0.02	0.02	0.02	0.21	0.02
Post-cyclone bulk precipitation																		
Tulasewa	5	5.67	0.56	0.24	0.06	0.06	0.26	1.08	0.88	0.54	0.13	0.02	0.05	0.06	0.03	0.02	0.17	0.02
Korokula	8	5.64	0.70	0.15	0.06	0.09	0.48	1.46	0.75	0.81	0.46	0.02	0.05	0.05	0.02	0.02	0.67	0.02
Koromani	8	5.47	0.71	0.14	0.05	0.07	0.32	1.59	0.93	1.04	0.14	0.02	0.05	0.03	0.02	0.02	0.37	0.02
Oleolega	8	5.45	0.58	0.18	0.06	0.08	0.34	1.24	1.05	1.11	0.16	0.03	0.09	0.06	0.02	0.02	0.16	0.03
Marine component of bulk precipitation excluding cyclones [%]																		
Tulasewa			106	9	136	25	0	100	0	29	0	0	0	0	0	0	0	0
Korokula			102	24	162	33	0	100	1	28	0	0	0	0	0	0	0	0
Koromani			98	28	172	39	0	100	1	28	0	0	0	0	0	0	0	0
Oleolega			107	17	119	24	0	100	0	19	0	0	0	0	0	0	0	0
Marine component of cyclone precipitation [%]																		
Tulasewa										Not available								
Korokula			98	91	97	84	0	100	33	87	0	6	0	0	0	0	0	0
Koromani			98	62	98	86	0	100	>33	83	0	14	0	0	0	0	0	0
Oleolega			97	68	97	78	0	100	>33	97	0	3	0	0	0	0	0	0

Fe-T: Total Fe; N-T: Total N; P-T: Total P

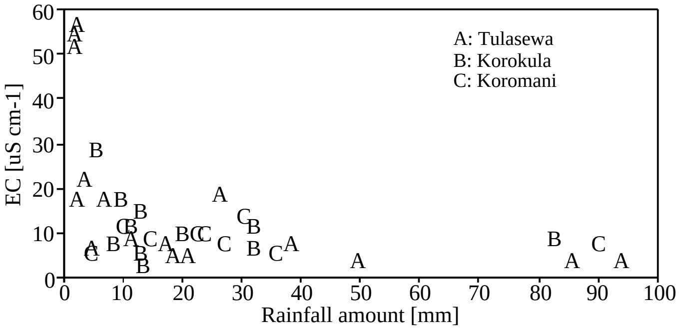

Figure 13.1: *EC-values in rain water from single storm events near the Tulasewa, Korokula and Koromani forest plots against corresponding storm sizes.*

well as on wind speed (cyclones). The EC of rain water collected during periods without cyclones decreased with the storm size as shown in Figure 13.1. EC-values greater than 10 μS cm^{-1} were not observed when rainfall exceeded 35–40 mm. EC-values of rainfall, collected in clean containers (no dry deposition) during large storms in Nadi ranged between 2 to 3 μS cm^{-1}. Such low EC-values in rainfall were also observed by Malmer (1993) in a catchment study in Sabah, Malaysia.

At the height of cyclone Sina large amounts of sea spray were carried inland. This resulted in major increases in the concentrations of Na, K, Mg, Ca, Cl and SO_4 in rain water collected after the cyclone event, as shown in Table 13.3. The highest concentrations were found at Korokula forest which was located at a distance of less than 2 km from the coast. Here the EC of rain water increased from a weighted average of 8 μS cm^{-1} for periods without cyclones to 120 μS cm^{-1} after the event. The deposition of sea spray during the event decreased with the distance from the coast and EC-values of 100 μS cm^{-1} and 76 μS cm^{-1} were observed for rain water collected at the Koromani and Oleolega sites, respectively. Because the funnel of the gauge at the Tulasewa forest site was blown away during the cyclone no samples could be collected. However, EC measurements of throughfall after the cyclone (Section 13.4) suggested that the EC of rain water at Tulasewa must have been considerably lower than those measured at Korokula or Koromani. No such increases in concentrations were observed for rainfall associated with the passage of cyclone Rae in March, 1990, during which wind speeds in SW Viti Levu were much lower than those observed during cyclone Sina (Section 2.4.4).

The oceanic contributions of ions in rain water, expressed as a percentage of the total, are shown Table 13.3 as well. Calculation of excess concentrations for pre- and post-cyclone rain water showed that Na and Mg originated from maritime sources exclusively. Measured Mg concentrations were lower than expected, especially at the coastal stations for which values up to 172% were calculated. However, concentrations of Mg were close to the detection limit, and the adjustment in concentration necessary to obtain a 100% maritime origin was within the range of the maximum analytical error given in Table 13.2. As such it can be safely assumed that all Mg in rainfall was derived from oceanic sources. Ca, SO_4 and K originated partly from maritime and partly from terrestrial sources, whereas the other constituents originated from terrestrial sources exclusively. The contribution of cations to the TDS decreased in the following order Na > NH_4 > K > Mg > Ca > Si. Therefore the addition of NH_4 and K from terrestrial sources in rain water changed the cationic sequence as compared to that in seawater. Dust particles form the main terrestrial source of Si ions and a good correlation with concentrations of K or Ca should be observed if these had been derived from the dissolution of such particles. However, Assenberg (1993) observed no correlation between Si and K or Ca in rain water collected in the Oleolega catchment and suggested that biological sources may have provided the excess concentrations of these constituents. The importance of NH_4 in the cationic sequence also points to a biological source.

As a result of the large contributions of sea spray in cyclone rain water the maritime contributions of Ca, K, SO_4, HCO_3 and PO_4 increased considerably compared to those in pre- and post-cyclone rainfall. similarly, the relative importance of the cations decreased in the order Na > Mg > K > Ca > NH_4 > Si resembling more that observed in seawater.

Atmospheric inputs of nutrients during the study period were calculated by multiplying the ionic concentrations in rain water with the corresponding rainfall totals. Separate estimates were obtained for inputs during the pre- and post-cyclone periods as well as for inputs by cyclone Sina. The results are shown in Table 13.4. As indicated earlier, if the concentration of a constituent dropped below the detection limit, the latter was used in the calculations and actual inputs could therefore be (much) lower than the values presented in Table 13.4. Annual inputs for most constituents, except Na, Cl, SO_4 and HCO_3 were very low compared to many other tropical locations as reviewed by Bruijnzeel (1989a, 1991). In fact, inputs were as low as those observed by Parker (1985) above natural rain forest in Costa Rica. Ionic concentrations in pre- and post-cyclone rain water were fairly similar and differences in corresponding atmospheric inputs were mainly due to differences in rainfall totals. The large inputs of HCO_3 for the pre-cyclone period in Tulasewa and Oleolega were attributed to contamination of some of the samples and the post-cyclone values were therefore thought to be more realistic. Atmospheric nutrient inputs varied relatively little between sites and estimates for the average inputs at Nabou station for years with and without cyclones were made by combining the average annual rainfall for Nabou (Section 6.3) and respective mean weighted average concentrations of the bulk precipitation for all sites. Post-cyclone data only were used for the calculation of annual atmospheric inputs of HCO_3.

As shown in Table 13.4 inputs of Na, Cl and Mg by cyclone Sina exceeded the estimated annual inputs for years without cyclones by two to three times, whereas cyclone inputs of K, Ca and SO_4 were equal to or slightly lower than the corresponding annual inputs. Inputs of constituents supplied by terrestrial sources during cyclone Sina were low compared to their annual inputs, although the latter could have been seriously overestimated. The present data show that cyclones may contribute significant amounts of nutrients (*e.g.* K, Mg) to the ecosystem. Therefore, estimates of the annual atmospheric inputs of nutrients for years with major cyclone events were also calculated (Table 13.4).

Table 13.4: *Rainfall totals (mm) and associated atmospheric inputs of nutrients (solutes, in kg ha^{-1}) for pre- and post-cyclone periods, as well as during cyclone Sina at the four research forests. derived estimates for mean annual atmospheric inputs with standard deviations (SD) at Nabou station for years with and without cyclones added for comparison.*

Location	**Rain**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Pre-cyclone atmospheric input																	
Tulasewa	1710	11.3	<5.5	<1.0	<2.1	<4.5	22.8	97.9	<9.8	<2.9	<0.4	<0.9	<0.8	<0.3	<0.3	2.2	<0.4
Korokula	1497	12.8	<1.7	<1.0	<1.3	3.7	23.2	17.6	<10.1	<1.5	<0.3	<0.7	<0.8	<0.3	<0.3	5.1	<0.3
Koromani	1661	16.5	<1.6	<1.1	<1.4	2.5	27.0	16.6	<10.4	<1.5	<0.3	<1.3	<0.5	<0.4	<0.3	3.7	<0.4
Oleolega	1545	9.7	<1.8	<1.1	<1.7	<3.6	18.2	152.0	<10.7	<2.1	<1.4	<1.5	<1.0	<1.2	<0.7	1.9	<0.4
Cyclone input																	
Tulasewa	238	Not available															
Korokula	179	28.6	1.2	3.6	1.2	0.2	52.2	1.1	8.2	0.1	<0.0	<0.1	0.1	<0.0	<0.0	0.2	<0.0
Koromani	195	37.9	2.3	4.7	1.6	0.2	69.7	0.0	11.4	0.2	<0.0	<0.1	<0.0	<0.0	<0.0	0.2	<0.0
Oleolega	239	28.9	1.6	3.6	1.3	0.5	52.1	0.0	7.3	0.5	0.0	<0.2	<0.0	<0.0	<0.0	0.5	<0.0
Post-cyclone atmospheric input																	
Tulasewa	1706	9.5	<4.2	<1.0	<1.0	4.4	18.4	15.0	<9.3	<2.2	<0.4	<0.9	<1.0	<0.4	<0.3	2.9	<0.4
Korokula	1128	7.9	<1.7	<0.6	1.0	5.5	16.5	8.4	<9.2	5.2	<0.3	<0.6	<0.6	<0.3	<0.2	7.5	<0.2
Koromani	1150	8.1	<1.6	<0.6	<0.8	3.7	18.2	10.7	<11.9	1.6	<0.3	<0.6	<0.3	<0.3	<0.2	4.2	<0.2
Oleolega	1241	7.3	<2.2	<0.7	<1.0	4.2	15.4	13.0	<13.8	<2.0	<0.4	<1.1	<0.8	<0.2	<0.2	<2.0	<0.4
Annual atmospheric input for years without cyclones																	
Average	1695	12.3	<2.9	<1.1	<1.5	<4.7	23.5	15.3	<12.5	<2.9	<0.4	<1.1	<0.8	<0.5	<0.4	<5.1	<0.4
SD	*408*	*2.9*	*0.7*	*0.3*	*0.4*	*1.1*	*5.7*	*3.7*	*3.0*	*0.7*	*0.1*	*0.3*	*0.2*	*0.1*	*0.1*	*1.2*	*0.1*
Annual atmospheric input for years with cyclones																	
Average	1695	42.5	<4.2	<4.9	<2.7	<4.4	78.6	13.7	<19.9	<2.9	<0.4	<1.1	<0.8	<0.5	<0.4	<4.7	<0.4
SD	*408*	*10.2*	*1.0*	*1.2*	*0.6*	*1.1*	*18.9*	*3.3*	*4.8*	*0.7*	*0.1*	*0.3*	*0.2*	*0.1*	*0.1*	*1.1*	*0.1*

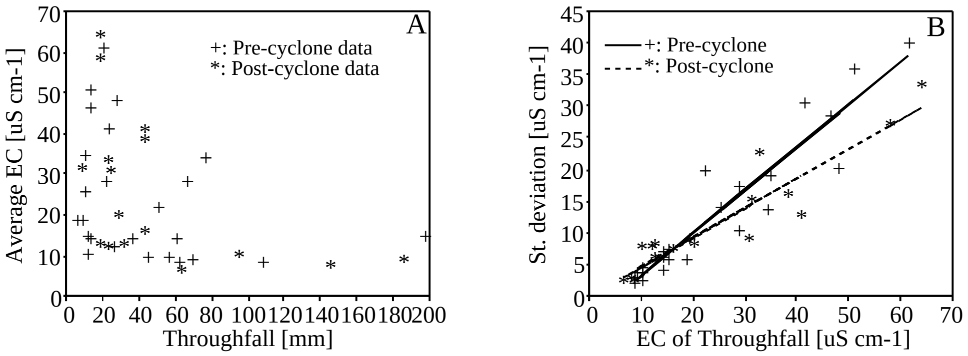

Figure 13.2: *Throughfall amounts against corresponding EC values (A) and the EC of throughfall against corresponding standard deviations (B) for pre- and post-cyclone data collected in the Korokula forest plot.*

13.4 Chemical Composition of Throughfall

Ion concentrations in rain drops hitting the forest canopy generally increase due to the dissolution of dry deposition previously intercepted by the canopy. Subsequent evaporation from the wet canopy (Section 6.4) causes an additional increase proportional to the amount of water evaporated. Furthermore, leaching of nutrients from the foliage and branches occurs and this leads to increases in the concentrations of relatively mobile ions (particularly K), and to a lesser extent of ions immobilised in structural tissue (*e.g.* Ca) (Parker, 1983). Ion concentrations in rain drops falling through the canopy without striking it (free throughfall) do not change and the concentrations in the bulk throughfall measured at the forest floor therefore depend on the collected proportions of crowndrip and free throughfall. This tends to increase the small-scale spatial variation of the chemical composition of throughfall as compared to that of rainfall (Kimmins, 1987).

As observed for rainfall amounts of TDS in throughfall (represented by the EC) decreased with the storm size due to dilution as shown in Figure 13.2A for in the Korokula forest plot. Similar patterns were observed at the other sites. An impression of the magnitude of the spatial variation in ion concentrations in throughfall was obtained from an analysis of EC measurements of the throughfall collected by each of the 20 gauges. Figure 13.2B shows the standard deviations of the EC against average EC for both pre- and post-cylone throughfall data in Korokula forest. The standard deviations, taken to represent the spatial variation, showed a linear correlation with EC, suggesting that the spatial variation in throughfall composition decreased with storm size (dilution effect). The slope of the regression line through the post-cyclone data, however, was lower than that of the line through the pre-cyclone data suggesting that the spatial variation had decreased as a result of cyclone damage (Figure 13.2B).

Weighted average values of EC, pH and ion concentrations of the throughfall collected in the Tulasewa, Korokula and Koromani forest plots, and that of stemflow collected in the Tulasewa forest plot are presented in Table 13.5. Values for the cyclone event are based on single samples. Pre-cyclone throughfall samples in the Koromani forest plot were collected during the dry season only and may therefore be

Table 13.5: *Pre-, post-cyclone and cyclone EC values ($\mu S\ cm^{-1}$), pH values and ion concentrations ($mg\ l^{-1}$) of throughfall and stemflow collected in the Tulasewa, Korokula and Koromani forest plots.*

Location	EC	pH	Na	K	Mg	Ca	NH4	Cl	HCO3	SO4	NO3	PO4	Si	Al	Fe-T	Mn	N-T	P-T
Pre-cyclone throughfall																		
Tulasewa	14	5.68	1.03	1.10	0.18	0.18	0.27	2.34	2.45	0.90	0.17	0.06	0.26	0.02	0.02	0.02	0.22	0.03
Korokula	22	5.68	2.12	1.08	0.39	0.27	0.24	4.02	3.43	1.18	0.15	0.02	0.19	0.06	0.02	0.02	0.39	0.03
Koromani	19	5.48	1.62	1.34	0.26	0.25	0.17	2.89	4.86	1.05	0.06	0.07	0.23	0.03	0.02	0.02	0.29	0.03
Cyclone throughfall																		
Tulasewa	48	5.45	6.80	1.00	0.88	0.40	0.06	12.9	0.61	2.03	0.12	0.01	0.17	0.02	0.02	0.03	0.02	0.02
Korokula	384	5.33	56.7	3.71	8.55	3.20	0.12	124.6	2.42	17.7	0.31	0.01	0.10	0.03	0.02	0.08	0.02	0.02
Koromani*	76	5.54	11.1	1.30	1.39	0.85	0.08	19.8	0.61	3.68	0.06	0.01	0.10	0.02	0.02	0.02	0.04	0.02
Post-cyclone throughfall																		
Tulasewa	10	5.76	0.77	0.91	0.13	0.13	0.16	1.51	1.61	0.60	0.14	0.05	0.15	0.05	0.02	0.02	0.10	0.03
Korokula	16	5.54	1.75	0.64	0.22	0.22	0.12	3.30	0.94	0.98	0.11	0.02	0.11	0.07	0.02	0.02	0.11	0.02
Koromani	15	5.65	1.42	0.76	0.19	0.21	0.08	2.67	2.59	1.24	0.09	0.03	0.10	0.02	0.02	0.02	0.14	0.02
Stemflow, excluding cyclone events																		
Tulasewa	36	4.38	2.81	1.79	0.43	0.32	0.36	5.18	0.30	3.14	0.12	0.06	0.11	0.08	0.04	0.03	0.24	0.08
Cyclone stemflow																		
Tulasewa	360	4.00	45.7	5.90	6.70	3.80	0.54	102.7	0.00	16.1	0.18	0.19	0.19	0.03	0.11	0.23	0.18	0.10

Fe-T: Total Fe; N-T: Total N; P-T: Total P
*: Underestimated due to errors in bulking

less representative. Although the concentrations in throughfall were higher than those in rainfall, most constituents remained close to the detection limit, implying that the errors in the presented values may still be considerable.

The increase in mean EC of throughfall compared to the corresponding rainfall could be attributed mainly to increases in the concentrations of Na, K, Cl and SO_4. The EC decreased again with distance from the ocean, corresponding with decreases in the concentrations of constituents of maritime origin. This trend was more pronounced in throughfall than that in rainfall presumably because of the more efficient trapping of sea spray by the forest canopy as compared to the rain gauge. The pH of throughfall was similar to that of the corresponding rainfall.

The higher ion concentrations in throughfall could be explained only partly by evaporation losses from the wet canopy. Leaching of ions from the canopy, in combination with the higher trapping efficiency already referred to constitute a plausible explanation for the excess concentrations. This was supported by the fact that not all constituents showed similar increases in concentrations after correction for evaporative losses (Table 13.6). The only constituent showing very little variation in these ratios between sites during both pre- and post-cyclone periods was SO_4. Ratios of 1.0 were found for the post-cyclone period, suggesting that leaching from the canopy could be considered negligible. Hence SO_4 may be considered to be a conservative constituent and the observed increases in concentrations of SO_4 in pre-cyclone throughfall compared to those in corresponding rainfall may be attributed to the higher trapping efficiency of the forest canopy compared to the rain gauge (Miller *et al.*, 1976; Parker, 1983). The ratios of SO_4 concentrations in throughfall and rainfall suggested that the actual atmospheric nutrient inputs to the forest during the pre-cyclone period were

Table 13.6: *Ratios of ion concentrations in throughfall (after correction for losses due to evaporation) to those in rainfall in the Tulasewa, Korokula and Koromani forest plots for the pre- and post-cyclone periods and for the cyclone event.*

Location	EC	Na	K	Mg	Ca	NH4	Cl	HCO3	SO4	NO3	PO4	Si	Al	Fe-T	Mn	N-T	P-T
Pre-cyclone period																	
Tulasewa	1.5	1.3	2.8	2.4	1.2	0.8	1.5	0.4	1.3	0.8	2.4	4.3	0.4	0.8	0.8	1.5	1.1
Korokula	2.3	2.1	7.9	4.9	2.5	0.8	2.2	2.4	1.5	1.2	1.0	3.2	0.9	0.8	0.8	1.0	1.2
Koromani	1.8	1.4	11.2	3.1	2.4	0.9	1.5	4.0	1.4	0.6	2.9	2.5	0.8	0.7	0.8	1.1	1.3
Cyclone Sina																	
Tulasewa									Not available								
Korokula	3.2	2.9	4.7	3.5	4.0	0.8	3.5	3.3	3.2	3.9	0.8	1.7	0.5	0.8	3.3	0.1	0.8
Koromani									Not available								
Post-cyclone period																	
Tulasewa	1.8	1.2	3.2	1.9	2.0	0.5	1.2	1.6	1.0	1.0	1.9	2.6	0.7	0.6	0.9	0.5	0.9
Korokula	1.7	2.1	3.6	3.3	2.2	0.2	1.9	1.1	1.0	0.2	0.9	1.9	1.2	0.8	0.9	0.1	0.9
Koromani	1.5	1.7	4.6	2.9	2.5	0.2	1.4	2.4	1.0	0.6	0.9	1.7	0.7	0.6	0.9	0.3	0.9

31–45% higher than those based on rain gauge sampling and given in Table 13.4. The high ratio associated with the cyclone event at Korokula indicated that the interception of sea spray by the forest was three times larger than that caught by the rain gauge. Therefore the atmospheric inputs during cyclone Sina, as given in Table 13.4, were seriously underestimated.

Again assuming that SO_4 behaved conservatively, leaching of ions from the canopy occurred if their ratios exceeded that for SO_4 (Table 13.6). In this way leaching of K, Mg and Si was observed at all sites, although not everywhere at the same rate, during both the pre- and post-cyclone periods. Leaching of K also seemed to increase with forest age, whereas the opposite was observed for Si. Leaching of Mg was pronounced most in the Korokula forest plot. However, the high ratio found for K in Koromani forest may reflect differences in the periods of sampling for throughfall (dry season) and rainfall (dry and wet season). Otherwise, both pre- and post-cyclone leaching rates were fairly similar in the Korokula and Koromani forest plots. The data for the Tulasewa forest plot indicated that Ca had not been leached from the canopy during the pre-cyclone period, whereas the leaching rate was similar to those observed at the other sites during the post-cyclone period. Leaching of Na and Cl was highest in Korokula forest and occurred at much lower rates in Tulasewa and Koromani forests. PO_4 was leached from the canopy in Tulasewa and Koromani forests, but for some unknown reason (biological activity?) not in Korokula forest.

Concentrations of NO_3, PO_4, Al, total Fe, Mn and total P in both rainfall and throughfall were frequently below the detection limits and their ratios may therefore not accurately reflect the actual enrichments in throughfall. Concentrations of NH_4, and occasionally NO_3, in throughfall were lower than those in rainfall after correction for evaporative losses. However, it is unlikely that NH_4 or NO_3 were taken up by the canopy. Therefore, the measured concentrations were either too high in rainfall, or concentrations were reduced in throughfall as a result of biological activity (*e.g.* uptake by algae) in the throughfall gauges (Bruijnzeel, 1983a; Ridder *et al.*, 1985). The use of the corresponding ratio for total N may therefore be more accurate for the determination of leaching. Pre- and post-cyclone patterns for the latter were quite different (Table 13.6) and suggested little leaching before the cyclone and indeed net absorption of N after the event.

A reduction in the leaf area surface (Section 11.3.6) as a result of cyclone damage is likely to reduce the amount of dry deposition intercepted by the canopy and will increase the amount of free throughfall. This would result in lower evaporation from the forest canopy during rainfall (Section 6.4) and also reduce the amount of nutrients washed from the canopy. Therefore concentrations in throughfall collected after cyclone Sina were expected to be lower than those observed before the temporary defoliation. Such lower concentrations were indeed observed for constituents of maritime origin associated with dry deposition (*e,.g.* Na, Cl) as well as for constituents subject to leaching (*e.g.* K, Si, total N).

Stemflow remains in contact with the canopy and stem for a longer period of time than crowndrip and ion concentrations should consequently be higher in the former (Parker, 1983). Stemflow was measured in Tulasewa forest only and records began shortly before the passage of cyclone Sina. As such the pre- and post-cyclone data were pooled. Ion concentrations in stemflow were indeed substantially higher than in throughfall with the exception of HCO_3 (which decreased as a result of the low pH), NO_3, Si and total N (Table 13.5). The lower concentration of Si in stemflow indicates that this ion may be leached from the foliage rather than from woody components. Concentrations in stemflow collected after cyclone Sina again reflected the effect of interception of sea spray by the vegetation (Table 13.5).

The total amounts of nutrients reaching the forest floor in throughfall and stemflow, and the contributions from canopy wash to the totals are given in Table 13.7. Large differences were observed between the sites, both for the pre-and post-cyclone periods. The largest increases with respect to atmospheric inputs were observed for K, as is generally reported from the literature for both temperate and tropical forests (Parker, 1983; Forti and Neal, 1992; Burghouts, 1993).

This canopy wash represents the transfer of nutrients from the canopy and stems to the forest floor and was calculated by substracting the atmospheric inputs from the totals reaching the forest floor in throughfall and stemflow (Parker, 1983). Estimates of nutrient inputs via stemflow in the Korokula and Koromani forest plots were obtained by multiplying the totals in throughfall for these forests with the ratio of the nutrient totals in stemflow to those in throughfall obtained for the Tulasewa forest site. The canopy wash data clearly showed which constituents were leached from the canopy and which were not (Table 13.7).

Although stemflow amounted to less than 2% of corresponding throughfall, relatively high concentrations of Na, K, Mg, Ca NH_4, Cl, SO_4 and total P in stemflow resulted in relative contributions of nutrients in stemflow being higher than that. Values ranged from 2% to 6% of the totals in throughfall. Stemflow reaches the forest floor in an area close to the stem and these nutrients may therefore be immediately available for uptake by tree roots (*cf.* Herwitz, 1986). Stemflow may therefore be an important source of nutrients for the tree.

13.5 Chemical Composition of Litter Percolates

Litter decomposition rates and the patterns of release of nutrients from decomposing litter were discussed earlier in Section 12.4. Two processes govern the transfer of nutrients from the litter layer to the underlying soil. The first process is physical,

Table 13.7: *Estimated total amounts of nutrients (kg ha^{-1}) in throughfall and stemflow, as well as amounts washed from the canopy (kg ha^{-1}) for various periods. Corresponding totals of throughfall and stemflow (both labelled as TF) are given for comparison.*

Location	**TF**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Totals in pre-cyclone throughfall																	
Tulasewa	1366	14.0	15.0	<2.4	<2.4	<3.7	31.9	33.5	<12.3	<2.3	<0.8	3.5	<0.3	<0.3	<0.3	3.1	<0.5
Korokula	1138	24.2	12.3	4.5	<3.0	2.8	45.8	39.1	<13.5	<1.7	<0.3	2.2	<0.6	<0.2	<0.2	9.4	<0.8
Koromani	1341*	21.7	17.9	<3.4	<3.3	2.2	38.7	65.1	<14.1	<0.8	0.9	3.0	<0.4	<0.3	<0.3	3.8	<0.4
Totals in cyclone throughfall																	
Tulasewa	208	14.1	2.1	1.8	0.8	0.1	26.9	1.3	4.2	0.2	<0.0	0.4	<0.0	<0.0	0.1	<0.0	<0.0
Korokula	164	93.0	6.1	14.0	5.2	0.2	204.3	4.0	29.0	0.5	<0.0	<0.2	0.0	<0.0	0.1	<0.0	<0.0
Koromani	166*								Not available								
Totals in post-cyclone throughfall																	
Tulasewa	1439	11.1	13.1	<1.8	<1.9	2.3	21.7	23.2	<8.7	<2.1	<0.8	<2.2	<0.7	<0.3	<0.3	<1.5	<0.4
Korokula	975	17.1	6.3	<2.1	2.1	1.1	32.2	9.1	9.6	<1.1	<0.2	<1.1	<0.7	<0.2	<0.2	<1.1	<0.2
Koromani	956	13.6	7.2	<1.8	<2.0	0.7	25.5	24.7	11.8	<0.9	<0.2	<1.0	<0.2	<0.2	<0.2	1.3	<0.2
Pre-cyclone stemflow																	
Tulasewa	23*	0.6	0.4	<0.1	0.1	0.1	1.2	0.1	0.7	<0.0	<0.0	<0.0	<0.0	<0.0	<0.0	0.1	<0.0
Cyclone stemflow																	
Tulasewa	3.3*	1.5	0.2	0.2	0.1	0.0	3.4	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Post-cyclone Stemflow																	
Tulasewa	24.3*	0.7	0.4	<0.1	0.1	0.1	1.3	0.1	0.8	<0.0	<0.0	<0.0	<0.0	<0.0	<0.0	0.1	<0.0
Pre-cyclone canopy wash																	
Tulasewa		3.4	9.9	1.5	0.4	-0.8	10.3	-64.1	3.3	-0.5	0.5	2.7	-0.5	-0.1	-0.1	0.9	0.0
Korokula		12.5	11.0	3.6	1.8	-0.8	24.3	21.5	4.1	0.2	-0.0	1.5	-0.1	-0.1	-0.1	-0.6	0.1
Koromani		6.2	16.8	2.5	2.0	-0.2	13.2	48.6	4.5	-0.6	0.6	1.8	-0.1	-0.1	-0.1	0.2	0.1
Cyclone canopy wash																	
Tulasewa									Not available								
Korokula		74.3	5.5	12.1	4.8	0.0	177.9	2.9	24.4	0.4	0.0	0.1	-0.0	-0.0	0.1	-0.2	-0.0
Koromani									Not available								
Post-cyclone canopy wash																	
Tulasewa		2.3	9.3	1.0	1.0	-2.0	4.6	8.3	0.2	-0.1	0.4	1.4	-0.3	-0.2	-0.0	-1.4	-0.0
Korokula		10.2	4.7	1.6	1.2	-4.3	17.6	0.7	1.3	-4.1	-0.0	0.5	0.1	-0.0	-0.0	-6.4	-0.0
Koromani		6.3	5.9	1.2	1.2	-2.9	8.8	14.1	1.0	-0.7	-0.0	0.4	-0.1	-0.1	-0.0	-2.8	-0.0

*: Estimated using Gash's analytical model

Table 13.8: *Amounts of litter percolate and ion concentrations (mg l^{-1}) in litter percolate for the pre- and post-cyclone periods (weighted averages) and for the cyclone period in the Tulasewa, Korokula and Koromani forest plots.*

Location	EC	pH	Na	K	Mg	Ca	NH4	Cl	HCO3	SO4	NO3	PO4	Si	Al	Fe-T	Mn	N-T	P-T
Litter percolate, pre-cyclone																		
Tulasewa	37	5.78	1.83	3.71	1.15	1.50	0.37	5.38	6.66	2.50	0.14	0.09	2.00	0.09	0.02	0.02	0.43	0.04
Korokula	47	5.70	3.13	2.63	2.23	1.70	0.38	8.24	6.40	3.79	0.52	0.14	1.46	0.06	0.05	0.02	0.60	0.07
Koromani	35	5.54	2.63	1.98	1.27	1.44	0.33	3.89	6.66	2.71	0.19	0.10	0.54	0.10	0.04	0.02	0.62	0.03
Litter percolate, cyclone																		
Tulasewa	135	5.87	15.5	5.02	3.25	3.60	0.40	38.0	8.54	6.59	0.05	0.04	1.40	0.04	0.02	0.09	0.23	0.03
Korokula	1570	5.19	229.0	14.1	42.3	23.1	0.38	526.1	5.49	73.4	0.05	0.02	0.62	0.02	0.03	0.61	0.29	0.03
Koromani	570	5.61	77.9	6.68	13.1	10.2	0.21	175.8	3.66	24.0	0.06	0.06	0.25	0.09	0.32	0.44	0.22	0.02
Litter percolate, post-cyclone																		
Tulasewa	38	6.07	1.51	6.94	0.70	1.25	0.43	4.24	5.55	2.30	0.38	0.94	2.09	0.06	0.02	0.02	0.48	0.33
Korokula	74	5.99	8.04	4.85	2.52	2.15	0.31	13.66	10.0	5.23	0.47	0.44	1.55	0.05	0.06	0.02	0.76	0.20
Koromani	56	6.10	4.49	4.66	1.78	2.16	0.23	8.73	8.50	3.77	1.12	0.31	0.69	0.13	0.05	0.04	0.61	0.14

Fe-T: Total Fe; N-T: Total N; P-T: Total P

involving the transport of small solid particles of decomposed litter into the topsoil by percolating water or by soil animals. Further decomposition of these particles in the soil results in the slow release of the incorporated nutrients. The second process is chemical and involves the leaching of constituents from decomposing litter, from dead soil animals and from soil animal excrements present in the litter layer (Duchaufour, 1982; Swift and Anderson, 1989). As these nutrients are already in ionic form they may be more readily taken up by the vegetation than those transported into the soil in organic matter.

As a result of dry deposition on the forest floor, evaporation of water from the forest floor (Section 6.4.2) and, most importantly, leaching of constituents from the decomposing litter, throughfall and stemflow reaching the forest floor become enriched while percolating through the litter layer (Turvey, 1974; Bruijnzeel, 1983a; Burghouts, 1993). The concentrations of ions in litter percolate collected in the Tulasewa, Korokula and Koromani forest plots during various periods of time are shown in Table 13.8. The pre-cyclone data for Koromani forest were collected during the dry season of 1990, whereas those for the other sites included the wet season as well. Because litter percolate trays were not positioned against tree stems, the samples did not include contributions from stemflow. Furthermore, some uncertainty in the concentrations was introduced by overflow of the collectors during large storms. The spatial variation in the chemical composition of litter percolate was high, depending on the thickness and composition of the litter layer, as well as on the spatial variation of the throughfall (amounts and composition, *cf.* Burghouts, 1993).

The pH of pre-cyclone litter percolate was similar to that of the corresponding throughfall at all sites, but EC and concentrations of most constituents increased. The largest increases were observed for Ca, Si, Mg, K, Cl and SO_4 (Tables 13.8 and 13.5). The relatively high concentration of K in the litter percolate in the Tulasewa forest plot as compared to the other sites may be the result of leaching from the K-rich undergrowth vegetation (Table 10.4), which died at the end of the wet season. The litter decomposition experiment (Section 12.4) indicated that P was leached rapidly after incubation of the litter bags. However, no evidence of leaching of P was found from the pre-cyclone litter percolate data. The needles used in the litter bag experiments were relatively fresh compared to those reaching the forest floor in litterfall and perhaps considerable amounts of P (and K) were already leached from dying needles and detached needles suspended in the canopy. This hypothesis is supported by the fact that leaching of P from the litter layer increased greatly after the sudden addition of fresh litter to the forest floor by cyclone Sina (Table 13.8). A similar lack of increased P concentrations in litter percolates during steady state conditions was observed for pine forest in Central Java (Bruijnzeel, 1983a) and lowland rain forest in Sabah, Malaysia, (Burghouts, 1993) using similar methodology to that of the present study.

As indicated earlier, deposition of sea spray occurred at the height of the cyclone and because most of the rainfall was recorded in the preceding 48 hours, the contribution of ions from sea spray to the litter percolate samples was overestimated at all sites due to overflow of the containers. The presented values therefore represent the concentrations during the final stage of the cyclone rather than bulk averages over the whole event. However, because leaching from the litter layer before the deposition of fresh litter by the cyclone will not have been larger than usual and because most of the sea spray will have been intercepted initially by the forest canopy rather than by the litter layer, the actual concentrations of bulk litter percolate after cyclone Sina may be expected to be only slightly higher than observed in the corresponding bulk throughfall samples.

The large deposition of fresh litter by cyclone Sina resulted in an increase in the pH of litter percolate compared to that of throughfall in the post-cyclone period (Tables 13.8 and 13.5). This suggested that protons were extracted from the percolating water in order to release other constituents from the fresh litter. The flushing of sea spray deposited on the litter and increased leaching from the fresh litter during the first month after the cyclone caused large increases in the EC of the litter percolate in the Korokula and Koromani forest plots (Table 13.8). Such large amounts of sea spray were not deposited in the Tulasewa forest plot and the EC of the litter percolate collected shortly after cyclone Sina was therefore not influenced as much (Table 13.8). However, a closer look at the nutrient concentrations in the litter percolate at this site revealed large increases in K, PO_4, total P and NO_3, all constituents which contribute little to the EC, but which must have been intimately connected with the deposition of large amounts of fresh litter by the cyclone. Similar increases in K, PO_4, total P and NO_3 were observed at the other sites but these were accompanied by corresponding increases in Na, Cl, Mg, Ca and SO_4 (sea spray) which explained the increase in the EC values observed at these sites. A possible reason for the lack of leaching of Ca and Mg from the litter layer in the Tulasewa forest plot could be that, unlike in the older forests, the decomposer community had not yet adapted to having to decompose large amounts of pine litter. As indicated earlier, the pre-cyclone litter layer at Tulasewa consisted predominantly of mission grass litter.

Estimates of the inputs of nutrients to the mineral soil are presented in Table 13.9. The volumes of litter percolate for the various periods were obtained using the model described in Section 6.4.2. By subtracting the inputs to the soil in litter percolate from the corresponding inputs to the litter layer in throughfall and stemflow, estimates were obtained for the amounts of nutrients mineralised in and leached from the litter layer.

Table 13.9: *Amounts of litter percolate (LP, in mm), associated nutrient contents (kg ha^{-1}) reaching the mineral soil and estimated amounts (kg ha^{-1}) leached at the Tulasewa, Korokula and Koromani forest plots during various periods.*

Location	**LP**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Totals in pre-cyclone litter percolate																	
Tulasewa	1223	22.3	45.3	14.0	18.3	<4.6	65.8	81.5	30.6	<1.7	1.1	24.4	<1.0	<0.2	<0.2	5.2	<0.5
Korokula	1014	31.8	26.7	22.6	17.2	3.9	83.5	64.9	38.4	<5.3	<1.4	14.8	<0.6	<0.5	<0.2	6.1	<0.7
Koromani	1179	31.0	23.3	14.9	16.9	3.9	45.9	78.6	31.9	<2.3	<1.2	6.4	<1.2	<0.5	<0.2	7.3	<0.4
Totals in cyclone litter percolate																	
Tulasewa	215	33.2	10.8	7.0	7.7	0.9	81.6	18.4	14.2	<0.1	0.1	3.0	0.1	<0.0	0.2	0.5	0.1
Korokula	150	344	21.1	63.4	34.6	0.6	789	8.2	110.1	0.1	0.0	0.9	<0.0	0.0	0.9	0.4	0.0
Koromani	156	122	10.4	20.4	15.9	0.3	274	5.7	37.5	0.1	0.1	0.4	0.1	0.5	0.7	0.3	0.0
Totals in post-cyclone litter percolate																	
Tulasewa	1290	19.5	89.5	9.0	16.1	5.6	54.7	71.6	<29.6	<4.9	12.1	27.0	<0.8	<0.2	<0.2	6.2	4.2
Korokula	853.2	68.6	41.3	21.5	18.4	2.6	117	85.5	44.6	<4.0	3.7	13.2	<0.4	0.5	<0.2	6.5	1.7
Koromani	817.3	36.7	38.1	14.6	17.7	1.8	71.4	69.5	30.8	<9.1	<2.6	5.6	<1.1	<0.4	<0.3	5.0	1.2
Pre-cyclone litter mineralisation																	
Tulasewa		7.7	29.9	11.5	15.8	0.8	32.7	47.9	17.5	-0.7	0.3	20.9	0.8	-0.0	-0.0	2.1	0.1
Korokula		6.5	14.0	17.9	14.1	1.0	36.1	25.7	24.1	3.6	1.1	12.6	-0.0	0.3	-0.0	1.6	0.3
Koromani		8.3	4.9	11.3	13.5	1.6	5.7	13.3	17.0	1.4	0.3	3.3	0.8	0.2	-0.0	3.4	-0.1
Cyclone litter mineralisation																	
Tulasewa		17.6	8.5	4.9	6.8	0.7	51.4	17.1	9.4	-0.1	0.1	2.6	0.0	-0.0	0.1	0.4	0.0
Korokula		241	14.4	47.7	28.5	0.3	559	4.3	77.5	-0.4	0.0	0.8	-0.0	0.0	0.8	0.4	0.0
Koromani									Not available								
Post-cyclone litter mineralisation																	
Tulasewa		7.8	76.0	7.1	14.1	3.2	31.7	48.3	20.2	2.8	11.3	24.7	0.1	-0.0	-0.1	4.6	3.9
Korokula		50.5	34.9	19.3	16.1	1.4	82.5	76.3	34.2	2.9	3.5	12.1	-0.3	0.3	-0.0	5.4	1.5
Koromani		22.3	30.6	12.7	15.6	1.1	44.4	44.7	17.9	8.2	2.3	4.7	0.9	0.3	0.1	3.6	1.0

13.6 Chemical Composition of Soil Moisture

Various chemical and physical processes in the soil act to change the chemical composition of infiltrating water. Removal of soil moisture by evapotranspiration results in increased concentrations of all constituents, proportional to the amount of moisture removed. Further changes are caused by biological activity (*e.g.* selective uptake and exudation of nutrients by the vegetation), buffering reactions with the soil exchange complex, precipitation of minerals from the soil solution, contributions by decaying organic matter and weathering or dissolution of minerals (Duchaufour, 1982). The largest changes usually occur in the root zone, although some processes are particularly active in the subsoil (notably weathering). Samples of the soil solution obtained with suction lysimeters may not accurately reflect the chemical composition of the ambient soil moisture due to interaction with the ceramic material of the cup and the concentrations of certain constituents presented below may therefore deviate from the actual concentrations in the soil moisture (see also Section 13.2).

The spatial variation in soil moisture composition was accounted for by installing 3–4 sets of lysimeters at the same depth within a plot. Variations in EC of the moisture collected from the samplers provided a first indication of the spatial variation within the plot at each depth. Values during the pre-cyclone period varied between 22–48 μS cm^{-1} in both top- and subsoil in the Tulasewa forest plot, between 41–117 μS cm^{-1} and 94–180 μS cm^{-1} in top- and subsoil in the Korokula forest plot, respectively, and between 48–58 μS cm^{-1} and 44–73 μS cm^{-1} in top- and subsoil in the Koromani forest plot, respectively. Temporal variations were small.

Post-cyclone EC values in the Korokula forest plot were much higher than the pre-cyclone values, and decreased from a maximum of 700–800 μS cm^{-1} shortly after cyclone Sina in January to 110–170 μS cm^{-1} in March, 1991, as the salts deposited during the passage of the cyclone were rapidly leached. The change was less pronounced in Koromani forest where the EC decreased from 54–156 μS cm^{-1} to 59–110 μS cm^{-1} over the same period. Only a very slight increase in EC was observed at Tulasewa forest following the passage of cyclone Sina.

The EC, pH and ion concentrations in pre- and post-cyclone soil solutions (volume weighted averages) for the various forest sites are presented in Table 13.10. The dominant ions in the soil solution were Cl and Na, followed by Si, HCO_3, SO_4 and Mg. Concentrations of all ions, with the exception of K, were highest in the Korokula forest plot, where the soil contained the largest amount of weatherable minerals (Section 4.4). Gradients in ion concentrations in the soil solution with soil depth were small in the Tulasewa and Koromani forest plots. However, the large contrast in chemical properties of the top- and subsoil in the Korokula forest plot (Section 4.4) was reflected in the composition of soil moisture which showed considerable increases in concentrations of Na, Mg, Cl, HCO_3 and SO_4 with depth (Table 13.10).

Post-cyclone ion concentrations at the Korokula and Koromani forest plots, which were both situated relatively close to the ocean, reflected the large inputs of sea salt by cyclone Sina, with large increases in concentrations of Na, Cl, Mg and Ca. Concentrations of K increased at all sites which may be explained by leaching of K from the large quantities of fresh litter deposited by the cyclone. No such increase was observed for PO_4 or total P, the concentrations of which remained below or just above the detection limit, although the needle decomposition data indicated that P would be released shortly after the deposition of the needles on the forest floor (Section 12.4). This finding also stands in contrast to the observed rises in concentrations of PO_4 in litter percolate after the cyclone (Table 13.8). Whilst P is known to become rapidly

Table 13.10: *Average pre- and post-cyclone values of EC ($\mu S\ cm^{-1}$), pH and ion concentrations ($mg\ l^{-1}$) in top- and subsoil moisture in the Tulasewa, Korokula and Koromani forest plots.*

Location	**EC**	**pH**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Topsoil moisture, pre-cyclone																		
Tulasewa	32	5.73	3.31	0.19	1.00	0.37	0.18	6.22	4.92	1.60	0.28	0.02	3.54	0.05	0.02	0.02	0.05	0.02
Korokula	82	5.93	8.08	0.09	2.91	1.49	0.20	14.30	5.28	3.92	6.55	0.03	7.38	0.05	0.02	0.02	0.48	0.02
Koromani	52	5.30	6.12	0.12	1.03	0.67	0.20	7.64	2.71	2.90	6.73	0.03	2.18	0.08	0.05	0.05	0.23	0.02
Subsoil moisture, pre-cyclone																		
Tulasewa	30	5.75	3.08	0.22	0.88	0.13	0.12	4.51	6.62	0.80	0.17	0.02	3.68	0.05	0.04	0.02	0.06	0.03
Korokula	141	6.27	18.21	0.12	4.57	1.28	0.21	25.40	24.86	6.32	7.50	0.04	6.54	0.05	0.03	0.02	0.37	0.04
Koromani	52	4.88	7.35	0.17	0.66	0.29	0.20	10.64	1.64	1.58	4.08	0.02	1.89	0.07	0.05	0.05	0.22	0.02
Topsoil moisture, post-cyclone																		
Tulasewa	33	5.95	3.44	0.28	0.95	0.32	0.19	6.71	2.91	1.38	0.14	0.02	2.82	0.05	0.02	0.02	0.11	0.02
Korokula	321	6.17	23.17	0.34	17.4	9.81	0.24	93.36	6.91	7.10	5.16	0.02	7.89	0.06	0.02	0.03	0.31	0.02
Koromani	106	4.85	12.89	0.55	2.73	2.28	0.35	30.69	1.47	1.33	2.13	0.04	3.83	0.06	0.04	0.02	0.34	0.03
Subsoil moisture, post-cyclone																		
Tulasewa	33	6.01	4.14	0.19	1.14	0.12	0.11	7.37	4.56	0.93	0.08	0.02	3.35	0.08	0.02	0.02	0.05	0.02
Korokula	328	6.45	35.64	0.25	15.7	2.75	0.11	94.82	8.22	5.02	1.92	0.02	6.83	0.05	0.02	0.02	0.12	0.02
Koromani	79	5.83	12.44	0.23	0.97	0.71	0.18	20.84	1.05	0.98	2.92	0.02	2.71	0.06	0.02	0.02	0.10	0.03

Fe-T: Total Fe; N-T: Total N; P-T: Total P

immobilized in many tropical soils due to complexing with various organic, Al, and Fe compounds (Sanchez, 1976), the observed lack of response of PO_4 concentrations in soil moisture may well be an artefact of the method of sampling with ceramic cups which tends to underestimate the concentrations of P (Zimmermann *et al.*, 1978). Post-cyclone concentrations of NO_3 and total N were lower than pre-cyclone ones, which may be explained by the uptake of N by the forest for the regeneration of needles, because N is only slowly released from decomposing needles (Section 12.4). The effect of the cyclone on the concentrations of NH_4 was inconclusive, with little change in the concentrations in top- and subsoil moisture in the Tulasewa forest plot, and relatively large changes in the top- and subsoil at the Koromani plot. Increases of the NH_4 concentration were observed in the topsoils in the Korokula and Kormani forests, whereas concentrations decreased in the subsoils.

Steudler *et al.*, (1991) observed increases in concentrations of NH_4, as well as in those of NO_3, in the surface soils four months after hurricane Hugo badly damaged natural rain forests in Puerto Rico. The hurricane also increased the net N-mineralization in the surface soil. No data was presented for the subsoils.

13.7 Nutrient Exports in Water Leaving the Forest Plots

13.7.1 Nutrient Exports from the Forest Plots

Nutrient exports from the forest plots in drainage water were calculated by combining amounts of water leaving the site as drainage (D, Section 6.6) and ion concentrations

Table 13.11: *Estimates of pre- and post-cyclone nutrient exports (kg ha^{-1}) from the Tulasewa, Korokula and Koromani forest plots in drainage (D, in mm).*

Location	**D+Q**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Pre-cyclone period																	
Tulasewa	167	5	0.4	1.5	0.2	0.2	8	11	<1.3	<0.3	<0.1	6.1	<0.1	<0.1	<0.1	<0.2	<0.1
Korokula	194	35	<0.3	8.9	2.5	0.4	49	48	12.3	14.6	<0.1	12.7	<0.1	0.1	<0.1	0.7	0.1
Koromani	322	24	0.5	2.1	0.9	0.6	34	5	5.1	13.1	<0.1	6.1	<0.3	<0.2	<0.2	0.7	<0.1
Post-cyclone period																	
Tulasewa	877	36	1.7	10.0	<1.1	1.0	65	40	8.2	<0.7	<0.2	29.3	<0.7	<0.2	<0.2	<0.5	<0.2
Korokula	211	75	0.5	33.1	5.8	0.2	200	17	10.6	4.1	<0.1	14.4	<0.2	0.0	<0.1	0.3	<0.1
Koromani	241	30	0.6	2.3	1.7	0.4	50	3	2.4	7.0	<0.1	6.5	<0.2	<0.1	<0.1	0.3	<0.1

in soil moisture extracted from the subsoil. The results are presented in Table 13.11. The calculations suffered from various uncertainties, ranging from the errors in the ion concentrations in the soil solution discussed previously, to those in estimated amounts of water leaving the respective sites as drainage. Lateral subsurface flow is likely to occur at all sites due to the large contrast in the hydraulic conductivity of the top- and subsoils (Section 4.3.3). The composition of this lateral (subsurface) flow may differ from that of water removed by deeper drainage (Bruijnzeel, 1983a) and this will result in errors in the calculated nutrient exports whenever gradients of ion concentrations in the soil solution with depth are considerable (as in the Korokula forest plot). In addition, soil moisture passing through the weathering zone may attain higher concentrations as ions are released by weathering (Eernisse, 1993). Because the lysimeter cups could not be placed in this zone, exports of nutrients may have been underestimated further. This is supported by the fact that pre-cyclone concentrations of Na, Ca, Mg and Si in moisture collected in the subsoil just above the weathering zone in the Korokula forest plot were much higher than those at the other sites where the cups were well above the weathering zone. However, this will only be true to the extent that the water indeed travels through the zone of rotten rock rather than being deflected laterally just above it due to the associated drop in hydraulic conductivity. Therefore, although the exports of nutrients from the sites as given in Table 13.11 may be underestimated as a result of these uncertainties, the effect may be limited (*cf.* Section 13.7.2), but further work is necessary on this subject is necessary (Bruijnzeel, 1991). The annual nutrient yield values of the study plots are plotted against the annual runoff in Figure 13.3 for comparison with data obtained in tropical forests elsewhere. A short discussion is given in Section 13.7.4.

Both pre- and post-cyclone exports were highest in the Korokula forest plot. The high amount of water exported from the Tulasewa forest plot during the wet post-cyclone period resulted in high exports from this site compared to the pre-cyclone exports, although the ion concentrations in the soil solution had changed little. Post-cyclone exports from the Koromani plot were only slightly higher than pre-cyclone values (Table 13.11).

13.7.2 Nutrient Exports in Streamflow from the Oleolega Catchment

The water budget of the forested Oleolega catchment and the pre-cyclone atmospheric nutrient inputs have been discussed in Section 8.3 and 13.3, respectively. To complete the catchment nutrient input – output budget, the annual export of nutrients in streamflow for the period January 4, 1990 – January 4, 1991, will be quantified here. During this period 161 mm of water was discharged as baseflow during rainless periods, whereas another 140 mm was discharged during storms (both as base- and quickflow). The data presented in the following are largely based on the work of Schellekens (1992).

Nutrient exports in streamflow are strongly dependent on amounts of streamflow (Likens *et al.*, 1977), which in turn reflect amounts and distribution of rainfall (Section 8.3). To obtain a representative estimate of nutrient output, it is important that the rainfall regime during the observation period is comparable to the long-term average (Likens *et al.*, 1977; Bruijnzeel, 1983a). Long-term average monthly rainfall totals for Nabou Station were presented in Table 6.2. Total rainfall over the period under consideration (1875 mm) was about 11% above the long-term average (1695 mm). Furthermore, the monthly distribution differed from the long-term average as well, with below average rainfall in February (92 mm), and above average rainfall in June (140 mm), August (228 mm) and November (313 mm). The effect of such deviations from the long-term average conditions on nutrient outputs is difficult to establish, but is considered to remain within the errors associated with the discharge measurements and the analytical procedures. In addition, there may be slight topographic and orographic effects as Nabou station is situated at a lower elevation than than the Oleolega catchment. The basic hydrological data collected at the Oleolega catchment were not adjusted therefore.

The nutrient output from a catchment for a given period can be obtained by multiplying discharge with the average nutrient concentrations of the streamwater samples collected during this period, provided that fluctuations in concentrations with variations in discharge remain small (Likens *et al.*, 1977). Whilst this is generally true during baseflow conditions, much larger variations are usually observed during stormflow conditions when streamflow consists of contributions from various sources (Bruijnzeel, 1983a; Ward, 1984). Various discharge–solute concentration relationships have been proposed in the literature (Hall, 1968; Johnson *et al.*, 1968) to overcome this problem. In the following sections the chemical composition of the Oleolega Creek during baseflow and stormflow conditions will be discussed separately.

Chemical Composition of Baseflow

Baseflow samples were collected over the normal range of baseflow discharge (0.01–0.04 mm h^{-1}) and the average discharge at sampling (0.02±0.01 mm h^{-1}, range 0.009–0.030 mm h^{-1}) was similar to the weighted average for the whole period. The average concentrations obtained from these samples are presented in Table 13.12. Concentrations of PO_4, total P, Al, and to a lesser extent NO_3 and total N, were often below the detection limits and the resulting averages must therefore be too high. The dominant ion in streamflow was HCO_3, which accounted for 29% of the sum of ions, followed by Si (23%), Na (22%), Cl (9%), Mg (8%), SO_4 (4%), and Ca (3%). Contributions to the sum of ions by the other constituents were less than 1%. The standard deviations of the concentrations of the major ions were within, or close to, the range of analytical

Table 13.12: *Mean chemical composition of baseflow and stormflow (in mg* l^{-1}*; SD: standard deviation; n: number of samples) in the Oleolega catchment and the ratio of concentrations in baseflow to those in precipitation (Q/P ratio).*

	EC	**pH**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Pre-cyclone Baseflow, December 25, 1989 - November 26, 1990																		
Mean	91	6.62	10.54	0.24	3.82	2.79	0.22	6.19	36.32	7.47	0.16	0.02	13.7	0.06	0.35	0.18	0.08	0.02
SD	4	0.10	0.23	0.11	0.22	0.21	0.17	0.31	2.21	0.74	0.13	0.01	0.6	0.03	0.06	0.04	0.05	0.01
n	20	20	20	20	20	20	20	20	20	20	19	19	20	20	16	16	20	20
Q/P ratio	12.3	1.2	17.2	1.6	55.0	28.6	0.8	5.0	6.2	8.6	0.9	0.6	146	1.0	7.8	5.7	0.5	0.9
Pre-cyclone Stormflow, January 14 - November 27, 1990																		
Mean	87	6.58	9.64	0.81	3.63	2.63	0.18	6.07	31.02	6.82	0.68	0.02	12.2	0.05	0.29	0.14	0.09	0.02
SD	7	0.13	0.58	0.38	0.44	0.42	0.12	0.68	4.51	0.76	1.11	0.02	1.4	0.06	0.10	0.05	0.06	0.00
n	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23
Comparison between pre-cyclone baseflow (A) and stormflow (B) concentrations																		
A <> B	>**	>*	>***	<***	>*	>*	ns	ns	>***	>***	<**	ns	>***	ns	>**	>***	ns	ns

ns: not significant; *: significance level 0.10; **: significance level 0.05; ***: significance level 0.01

errors (Table 13.2). The baseflow composition may therefore be considered constant during the pre-cyclone period, although a seasonal trend could be observed with somewhat lower than average concentrations during the wet season, and somewhat higher concentrations during the dry season.

The ratio of concentrations in streamflow (Q) to those in rainfall (P) provides a good indication of how the composition of the water is altered when passing through the ecosystem (Likens *et al.*, 1977). Evapotranspiration reduced the amount of water leaving the Oleolega catchment by a factor 6.4 (Section 8.3) compared to rainfall input. If this would be the only process acting to change the composition of the rain water then concentrations in streamflow would all increase by a factor 6.4. The Q/P ratios for HCO_3 and Mn were fairly close to this value, but the ratios for the other ions deviated substantially, indicating that other processes (*e.g.* weathering, biogeochemical processes) were acting to change the concentrations of these ions. The Q/P ratios for K, NH_4 and total N were low, suggesting that these ions were accumulating in the catchment, presumably in the pine biomass for this actively growing forest. Similar ratios would be expected for NO_3, PO_4 and total P, as these constituents are also strongly influenced by biolological processes (Waring and Schlesinger, 1985), but no conclusions could be drawn in this respect because their concentrations were below the detection limits in both rainfall and stream water. The same was true for Al. Q/P ratios for Si, Mg, Ca and Na were high, however, indicating that these nutrients were leached from the catchment. The most likely source of these elements is weathering of the parent rock and primary minerals in the soil (Section 4.4).

Pre-cyclone data on the chemistry of the baseflow from the Oleolega catchment, and from several other forested and grassland catchments in the same area, collected during the dry season of 1990, are given in Table 13.13. The data clearly indicate that afforestation did not result in significant changes in the baseflow concentrations of K, Total N, NO_3, PO_4, Total P and Mn ($\alpha = 0.05$). Total P was just above or below the detection limit at all sites and exports of this element are therefore low both from grassland and forest catchments. Concentrations of NH_4 were significantly higher

Table 13.13: *Means and standard deviations of the EC, pH and ion concentrations in baseflow (mg l^{-1}) from samples (n= sample size) collected at various locations in and around the Oleolega catchment. Levels of significance (*Student' t *test) for differences between means added.*

Location	**EC**	**pH**	**Na**	**K**	**Mg**	**Ca**	**NH4**	**Cl**	**HCO3**	**SO4**	**NO3**	**PO4**	**Si**	**Al**	**Fe-T**	**Mn**	**N-T**	**P-T**
Pre-cyclone baseflow Oleolega Creek, Forested, A																		
Average	91	6.61	10.2	0.36	3.9	2.9	0.18	6.5	35.0	7.4	0.28	0.02	12.4	0.04	0.36	0.19	0.07	0.02
SD	*4*	*0.16*	*0.7*	*0.18*	*0.2*	*0.2*	*0.17*	*0.6*	*3.4*	*0.7*	*0.27*	*0.02*	*1.1*	*0.01*	*0.10*	*0.06*	*0.06*	*0.00*
n	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Pre-cyclone baseflow Oleolega Creek, downstream at Junction with Kubuna Creek, Forested, B																		
Average	161	6.90	12.3	0.45	8.3	12.0	0.31	9.3	82.0	7.4	0.15	0.01	9.8	0.04	0.05	0.02	0.04	0.02
SD	*10*	*0.09*	*0.7*	*0.06*	*0.5*	*0.8*	*0.23*	*0.5*	*5.4*	*0.7*	*0.09*	*0.01*	*0.4*	*0.01*	*0.03*	*0.00*	*0.02*	*0.00*
n	5	5	5	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5
Pre-cyclone Naruku Creek, Forested, C																		
Average	131	6.47	12.4	0.70	5.1	6.7	0.46	10.3	50.4	9.5	0.56	0.01	10.0	0.15	1.61	1.01	0.12	0.02
SD	*26*	*0.17*	*1.0*	*0.74*	*1.1*	*1.5*	*0.31*	*1.0*	*11.0*	*4.9*	*0.58*	*0.00*	*1.7*	*0.14*	*2.05*	*0.29*	*0.09*	*0.00*
n	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2
Pre-cyclone baseflow Ividamu Creek, Grassland, D																		
Average	137	6.39	14.4	0.57	5.9	6.2	0.16	12.6	63.5	2.4	0.25	0.04	10.1	0.07	1.22	0.71	0.11	0.02
SD	*15*	*0.21*	*0.7*	*0.47*	*1.2*	*1.8*	*0.04*	*1.2*	*12.5*	*1.3*	*0.32*	*0.02*	*1.2*	*0.07*	*1.03*	*0.65*	*0.11*	*0.00*
n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Significance of differences between means																		
A<>B	<***	<***	<***	ns	<***	<***	ns	<***	<***	ns	ns	ns	>***	ns	>***	>***	ns	ns
A<>C	<**	ns	<***	ns	<**	<***	<*	<***	<**	ns	ns	ns	>**	<*	ns	<***	ns	ns
A<>D	<***	>*	<***	ns	<***	<***	ns	<***	<***	>***	ns	ns	>**	ns	<*	<*	ns	ns
C<>D	ns	ns	<***	ns	ns	ns	>**	<**	ns	>**	ns	<*	ns	ns	ns	ns	ns	ns

ns: not significant; *: significance level 0.10; **: significance level 0.05; ***: significance level 0.01

in baseflow from the forested Naruku catchment than from the Ividamu grassland catchment. However, this may reflect local factors because the difference between the means for the Oleolega and Ividamu catchments were not significant. Differences in the Mg and Ca concentrations from the Naruku and Ividamu catchments were not significant, suggesting again that the impact of afforestation on the concentrations of these nutrients in baseflow was negligible, and that the observed differences for the other sites must be due to differences in geology, rather than vegetation.

However, concentrations of SO_4 in baseflow from the forested catchments were significantly higher than those from the grassland catchment, whereas concentrations of Na and Cl were significantly lower. These differences could not be attributed to differences in geology and must therefore reflect differences in the biogeochemical processes in forest and grassland. Whilst the rise in SO_4 concentration might be related to higher bacteriological activity in the forested areas the drop in Na and Cl is more difficult to explain. After all, a positive change would have been expected in view of the larger trapping efficiency for maritime aerosols of the forest canopy (*cf.* Section 13.4 on throughfall chemistry). The only explanation that one is left with at present would be accumulation of Na and Cl in the biomass of the forest but we lack the data to substantiate this supposition.

A seasonal trend was observed in the pre- and post-cyclone baseflow concentrations of PO_4, Total N and K from the grassland catchment, with relatively high levels at the end of the dry season, and low levels at the end of the wet season. The pattern corresponded with the seasonal growth pattern of the grassland vegetation (Chapter 10). No such trends were observed for the forested catchments.

13.7.3 Chemical Composition of Stormflow

The average chemical composition of stormflow is much harder to establish, because stormflow is a mixture of baseflow, channel precipitation and various other contributions from the hillslope (*e.g.* saturated and Hortonian overland flow, subsurface stormflow). Furthermore, the contribution of each of these components is likely to change with antecedent moisture conditions, storm size, rainfall intensity, and the areal distribution of rainfall, resulting in relatively large variations in streamflow ion concentrations during a storm. To complicate the matter further, the various ions respond differently to changes in the discharge, and ion concentrations for a specific discharge in the rising limb of the hydrograph may be different from those at the same discharge in the falling limb (hysteresis, Hall, 1968).

During the pre-cyclone period insufficient stormflow samples were collected to express ion concentrations as a function of discharge or EC, for which continuous records were available. Assenberg (1993) observed that stormflow concentrations of Na, Mg, Ca, NH_4, Cl, HCO_3, Si and Mn at Oleolega were lower than those in baseflow, and attributed this to dilution of the streamwater by precipitation and overland flow. On the other hand, concentrations of K and NO_3, and to a lesser extent Cl, seemed to increase during the rising stage, reaching maximum values at discharges below 10 mm h^{-1}, followed by a decrease at higher discharges. This behaviour was attributed to leaching of the litter layer and topsoil. Concentrations of SO_4 did not show a clear dependency on the discharge. Although the data set of Assenberg (1993) consisted of samples collected shortly after the passage of cyclone Sina and during the subsequent harvesting of the destroyed plantation (December, 1990 – May, 1991), the observed relationships may generally hold for the pre-logging period as well, since the impact of logging at that stage was limited (see also Section 15.6).

Table 13.14: *Annual export of nutrients from the Oleolega catchment in baseflow and stormflow, as well as the total. The totals were obtained by multiplying the total amounts of base- and stormflow (mm) over the period January 4, 1990 – January 4, 1991, with the corresponding pre-cyclone ion concentrations (mg l^{-1}.*

	Q	Na	K	Mg	Ca	NH4	Cl	HCO3	SO4	NO3	PO4	Si	Al	Fe-T	Mn	N-T	P-T
Annual Export in Baseflow [kg ha-1]																	
Total	160.9	17.0	0.39	6.1	4.5	0.36	10.0	58.4	12.0	<0.26	<0.03	22.0	<0.10	0.57	0.30	<0.12	<0.03
SD		0.4	0.17	0.4	0.3	0.27	0.5	3.6	1.2	0.20	0.02	0.9	0.05	0.09	0.07	0.08	0.01
Annual Export in Stormflow [kg ha-1]																	
Total	140.1	13.5	1.13	5.1	3.7	0.25	8.5	43.5	9.6	0.95	<0.02	17.1	<0.07	0.41	0.19	<0.13	<0.03
SD		0.8	0.54	0.6	0.6	0.17	1.0	6.3	1.1	1.56	0.02	1.9	0.09	0.13	0.07	0.08	0.00
Total Annual Export [kg ha-1]																	
	301.0	30.5	1.52	11.2	8.2	0.61	18.5	101.9	21.6	<1.21	<0.05	39.1	<0.17	0.98	0.49	<0.25	<0.06

Average EC, pH and ion concentrations for pre-harvesting stormflow samples are given in Table 13.12. The samples were collected mostly at relatively low discharges, averaging 0.06±0.08 mm h^{-1} (range 0.01–0.3 mm h^{-1}), as it was too dangerous to collect samples during the two cyclone events when 77% of the annual stormflow total was produced (besides, the area was inaccessible at that time). The weighted average stormflow discharge amounted to 0.25 mm h^{-1} including cyclone events, but only 0.08 mm h^{-1} when these were excluded. As such, the concentrations of ions that were positively correlated with discharge have probably been overestimated, whereas those for K and NO_3 may have been underestimated.

Comparison of the average ion concentrations in pre-cyclone stormflow with those in the pre-cyclone baseflow confirmed the findings of Assenberg (1993), with significantly lower concentrations of Na, Mg, Ca, HCO_3, Si and Mn, and significantly higher concentrations of K and NO_3 in the former. The stormflow concentration of SO_4 was significantly lower than the baseflow concentration suggesting that SO_4 was also subject to dilution by channel precipitation or hillslope runoff.

13.7.4 Nutrient Exports from the Oleolega Catchment

The baseflow composition may be considered relatively constant, and a fairly reliable estimate of the associated nutrient output from the catchment can thus be obtained by multiplying the average pre-cyclone concentrations with the baseflow total, excluding the baseflow component of stormflow events. In view of the limited number of pre-cyclone stormflow samples, stormflow exports were calculated by simply multiplying total stormflow volume with the average stormflow concentrations given in Table 13.13. This, of course, is a rather crude method, and the stormflow exports may therefore be more or less seriously in error. The resulting annual exports of nutrients in baseflow, stormflow and total streamflow are presented in Table 13.14. Exports in baseflow were generally larger than in stormflow, with the exception of those for K and NO_3. Due to the low concentrations, nutrient exports were fairly low when compared with losses from other tropical catchments. Because the total export is a composite of the exports in base- and stormflow, any errors in the latter (N, P and K) tend to produce (relatively small) changes in the nutrient export these important nutrients. Bruijnzeel

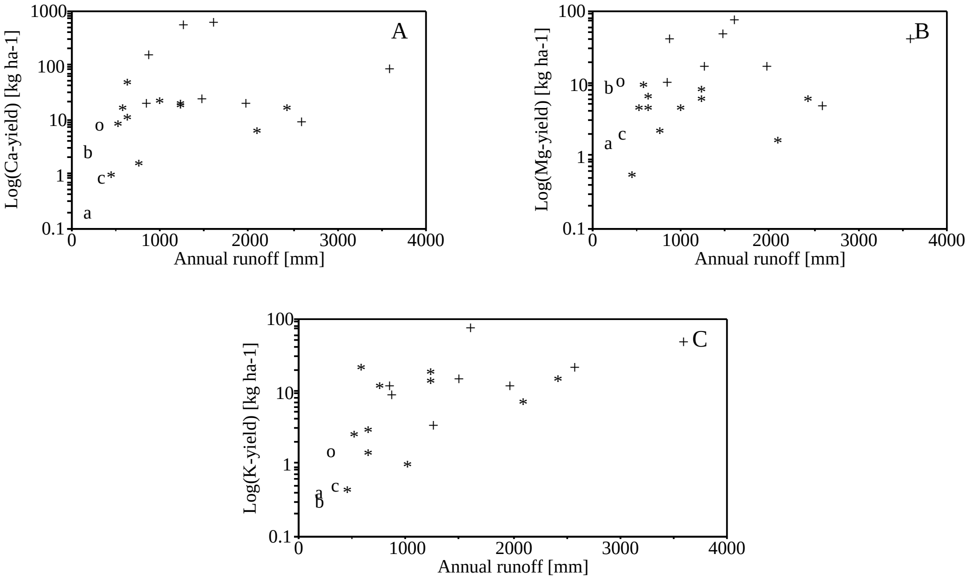

Figure 13.3: *Scatter plots of annual runoff* versus *yields of Ca (A), Mg (B) and K (C) for tropical forest ecosystems differentiated according to soil type (*: oxisols/ultisols; +: mollisols/vertisols) or location (a: Tulasewa; b: Korokula; c: Koromani; o: Oleolega). After Bruijnzeel (1990) and Malmer (1993).*

(1990; Table 3) reviewed the annual water yield and corresponding nutrient export data from a number of studies in tropical forests and grouped them according to their soil type and elevation (lowland/montane).

The nutrient exports in streamflow from the Oleolega catchment were larger than those calculated from soil moisture samples and drainage from the forest plots. This could only partly be due to differences in drainage totals and parent rock. The high exports of Na, Mg, Ca and Si from the catchment, compared to those from the forest plots (Table 13.11), suggest that these elements may well have been underestimated in the latter case due to the impossibility to sample moisture within or below the zone of active weathering (*cf.* Eernisse, 1993).

Additional data for lowland tropical rain forest was obtained by Malmer (1993) in Sabah, Malaysia. The annual nutrient exports obtained from the catchment and forest plots presently studied has been plotted in Figure 13.3 together with the lowland data (excluding spodosols and inceptisols) obtained by Bruijnzeel (1990) and Malmer (1993). The annual runoff values from the study sites in SW Viti Levu fall are lower than those obtained in the studies reviewed by Bruijnzeel (1990) and that of Malmer (1993), and the relatively low annual yields of Ca and K confirm the observed decreasing trend of the yield of these nutrients with annual runoff. However, annual yields of Mg at our study sites were relatively high in view of the low annual runoff.

Table 13.15: *Average post-cyclone concentrations and standard deviations (SD) of baseflow samples (n= 11) collected in the forested Oleolega catchment (between December 2, 1990, and January 7, 1991), as well as for baseflow samples collected in the grassland Ividamu catchment (January – September, 1991; n= 10). Levels of significance (*Student's t*) for differences between means of pre- and post-cyclone compositions added for comparison.*

Location	EC	pH	Na	K	Mg	Ca	NH4	Cl	HCO3	SO4	NO3	PO4	Si	Al	Fe-T	Mn	N-T	P-T
Oleolega pine forest (1)																		
Mean	94	6.65	11.23	0.89	4.35	3.04	0.21	7.05	38.72	5.94	0.15	0.02	13.8	0.10	0.35	0.14	0.15	0.02
SD	4	0.06	0.23	0.39	0.14	0.12	0.13	1.40	2.34	1.02	0.19	0.01	0.3	0.03	0.10	0.03	0.13	0.00
Ividamu grassland (2)																		
Mean	179	6.67	15.14	0.58	9.24	9.92	0.23	13.37	97.83	1.74	0.06	0.12	12.0	0.07	3.51	1.41	0.19	0.05
SD	33	0.13	1.19	0.58	1.65	1.94	0.10	1.26	22.92	0.84	0.02	0.16	1.4	0.03	4.51	0.85	0.20	0.06
Comparison between pre- (A) and post-cyclone (B) baseflow concentrations																		
(1) A <> B	<***	ns	<***	<***	<***	<***	ns	<***	<***	>***	ns	ns	ns	<***	ns	>***	<**	ns
(2) A <> B	<**	<***	ns	ns	<***	<***	<*	ns	<***	ns	>**	ns	<**	ns	ns	<*	ns	ns

ns: not significant; *: significance level 0.10; **: significance level 0.05; ***: significance level 0.01

13.8 Impact of Cyclone Sina on the Baseflow Composition

The impact of cyclone Sina on the chemical composition of baseflow was evaluated from 11 samples collected between December 2, 1990 and January 7, 1991. Logging of cyclone damaged trees had started in the catchment in December, but less than 10% of the catchment area had been logged at the beginning of January. As such the effect of harvesting on baseflow composition could be considered negligible and any differences between the pre- and post-cyclone baseflow composition could be attributed to the cyclone event. The average post-cyclone baseflow composition is shown in Table 13.15. Because the discharges at which the baseflow samples were collected were not significantly different for the pre- and post-cyclone periods, the observed changes may be due entirely to cyclone effects. As would be expected from the deposition of sea spray and the transfer of large amounts of debris by the cyclone, concentrations of most constituents increased significantly after the event. However, the mean concentration of SO_4 in post-cyclone baseflow was significantly lower than the pre-cyclone average. This is consistent with the relatively low contribution of SO_4 in cyclone rain water ($Cl/SO_4= 7.1$) compared to pre-cyclone rain water ($Cl/SO_4= 1.4$; Table 13.3). Mn concentrations decreased as well after the cyclone event. The significant increase of Al reflects a change in the detection limit from 0.05 mg l^{-1} to 0.10 mg l^{-1}, rather than a real change since this element fell below the detection limits for both periods.

Asbury and Scatena (pers. comm.) also observed increased concentrations of K, Ca, and Mg in streamflow from a small watershed in the Bisley area in Puerto Rico after the above-ground biomass of the natural rain forest had been reduced by 50% (Scatena *et al.*, 1993) during the passage of hurricane Hugo in 1989.

Post-cyclone concentrations of Mg, Ca, HCO_3 in the baseflow from the grassland Ividamu catchment were significantly higher than corresponding pre-cyclone values (Table 13.15) but, unlike those in the forested Oleolega catchment, pre- and post-cyclone concentrations of Na, K, Cl and SO_4 were not significantly different, which may reflect differences in the trapping efficiency for cyclone sea spray between grass and pine forest. A possible explanation for the increased post-cyclone concentrations of Ca and Mg may be that cyclone depositions of Na and K were exchanged against Ca and Mg in the soil, which were subsequently leached at a higher rate. The grassland biomass in November 1990 (dead grass) was not likely to be affected much by the cyclone and observed differences in pre- and post-cyclone NO_3 and NO_4 concentrations, and possibly also in pH values, may reflect seasonal variations.

Since there had been little rainfall in the period between cyclone Sina and the start of harvesting, the effect of the cyclone on the chemical composition of stormflow could not be studied. The effects of harvesting and subsequent burning on baseflow and stormflow chemistry will be discussed in Chapter 15, although some of the changes reported therein must be attributed to the impact of the cyclone.

Chapter 14

Summary of Forest Nutrient Cycles

14.1 Introduction

From the nutrient point of view, the sustainability of plantation forestry depends on whether the nutrient losses associated with harvesting at the end of a rotation, as well as with site preparation (burning of slash) and plantation establishment (enhanced leaching), can be minimized in such a way that the soil remains capable of providing the required nutrients for uptake in subsequent rotations (Bruijnzeel, 1992b). One of the goals of the present study was to quantify these requirements for a chronosequence of pine forests, so as to provide information on whether future rotations in SW Viti Levu were likely to suffer from nutrient deficiencies. Plantation nutrient requirements change with the age of the forest, and may be approximated by studying an age series of sites as a substitute for a long-term study in a single forest (Hase and Fölster, 1982). The transfer of nutrients from the soil into the biomass at the various stages of forest development may be evaluated from nutrient budgets, provided that all other components of the budget are known.

The nutrient contents of the various compartments of the ecosystem (vegetation, litter layer, soil) and amounts of nutrients cycling through the ecosystem in water (precipitation, throughfall and stemflow, litter percolate and soil moisture) and litterfall have been quantified in the previous chapters. Nutrient budgets can now be compiled for the forest chronosequence to identify the period of maximum uptake as well as to quantify the uptake of nutrients from soil reserves. As indicated earlier, differences existed between soil chemical and physical properties at the various sites, which made a direct comparison difficult for some nutrients (*e.g.* K; *cf.* Section 4.4).

Although it is recognised that mineral weathering also constitutes an important input of nutrients for these deep-rooted pine forests, it is not possible at this stage to quantify contributions by mineral weathering. This will be done in Chapter 16 which discusses the overall nutrient budget for a *Pinus caribaea* plantation throughout a rotation period. Furthermore, estimates for the amounts of nutrients transferred from the soil to the forest ecosystem in the study plots are presented in Section 14.2.1.

Nutrient losses associated with the removal of merchantable timber at the end of a rotation period, and those by increased leaching following harvesting and burning of the slash will be discussed separately in Chapter 15.

More or less complete nutrient budgets could only be calculated for the macronutrients, because micronutrients had not been analysed in the soil (Zn, Mn, B) and water samples (Zn, B). The budgets presented for N are obviously incomplete due to the exclusion of the gaseous phase and the effects of various biochemical processes on the cycling of this nutrient (including fixation by bacteria, denitrification during wet conditions *etc.*). No corrections were applied to the nutrient contents of the forests to account for differences in stocking, since a reduction in stocking with increasing forest age resulting from cyclone damage must be considered the norm in Fiji. However, pre-cyclone and post-cyclone nutrient budgets will be presented in the following sections to illustrate the impact of cyclone Sina.

14.2 Pre-cyclone Nutrient Cycling Patterns

14.2.1 Nutrient Input – Output Budgets at Ecosystem Level

Information on whether nutrients are accumulating or being lost at ecosystem level can be obtained by comparing inputs with outputs. The net annual nutrient gains or losses at the Tulasewa, Korokula and Koromani forest plots, as well as those at the forested Oleolega catchment were calculated as the difference between annual atmospheric inputs and the corresponding exports in water leaving the ecosystems either as drainage or streamflow (*cf.* Chapter 13). Effects of cyclone Sina were excluded by using pre-cyclone concentrations in rainfall and drainage (Tables 13.4, 13.11 and 13.14). Data for Korokula and Koromani forests were collected during an 11-month period in 1990 and were linearly extrapolated on a time basis to obtain annual estimates. The results are presented in Table 14.1.

Inputs of N were calculated as the sum of N-NH_4 and N-NO_3 inputs in bulk precipitation, whereas that of P was taken equal to that of P-PO_4 only, as total N and total P had not been analysed in rain water samples collected before July 1990. However, the sum of N-NH_4 and N-NO_3 concentrations was often higher than the concentration of total N in rainfall and because both PO_4 and total P in subsequent samples were below the respective detection limits the results will not have been influenced much by this practice.

The atmospheric nutrient inputs for the forests in Fiji were rather low compared to those observed in various tropical countries elsewhere (Bruijnzeel, 1989a, 1991), which is in accordance with the absence of sources of polution and the rather low annual rainfall in the region. The high inputs of K at Tulasewa forest, and of P at the Oleolega catchment, are somewhat suspect and may be due to analytical errors as K and P inputs at the surrounding sites were consistently lower (Table 13.3).

Annual nutrient losses by leaching from the forest plots were also low, which may partly be due to the high water use of the forests which tends to restrict the occurrence of drainage to relatively short periods after heavy rainfall. Furthermore, uptake of nutrients from the soil solution by the rapidly growing pines may have reduced the nutrient concentrations in water percolating through the rooting zone, in which the water samples were collected, and on which the calculations of exported nutrients were based. Somewhat larger exports of nutrients released by weathering would be expected in water percolating through the weathering zone, as suggested by the exports of Ca,

Table 14.1: *Atmospheric nutrient inputs (based on actual precipitation amounts), outputs with drainage, and net gains or losses cyclones in pine plantations at various stages of development. Weathering inputs and in- and outputs associated with cyclone Sina not included.*

Location	**Age**	**N**	**P**	**K**	**Ca**	**Mg**	**Mn**	**Zn**	**B**
Annual Atmospheric Input [kg ha-1], Pre-cyclone 1990									
Tulasewa Forest	6	<4.2	<0.09	<6.1	<2.3	<1.1	<0.30		
Korokula Forest	11	<3.5	<0.07	<1.9	<1.4	<1.1	<0.30		
Koromani Forest	15	<2.5	<0.08	<1.8	<1.5	<1.2	<0.30		
Oleolega Catchment	15	<4.0	<0.55	<2.2	<2.1	<1.3	<0.84		
Annual Output with Drainage or Streamflow [kg ha-1], Pre-cyclone 1990									
Tulasewa Forest	6	<0.2	<0.01	0.4	0.2	1.5	<0.10		
Korokula Forest	11	0.8	0.02	0.4	2.8	9.8	<0.10		
Koromani Forest	15	0.8	<0.01	0.6	1.0	2.3	<0.20		
Oleolega Catchment	15	<0.3	<0.06	1.5	8.2	11.2	0.49		
Net Annual Gains (+) or Losses (-) [kg ha-1], Pre-cyclone 1990									
Tulasewa Forest	6	4.0	0.08	<5.7	<2.1	<-0.4	0.20		
Korokula Forest	11	<2.7	<0.05	<1.5	<-1.4	<-8.7	0.20		
Koromani Forest	15	<1.5	0.07	<1.2	<0.5	<-1.1	0.10		
Oleolega Catchment	15	3.7	0.49	<0.7	<-6.1	<-9.9	<0.35		

Mg and Mn in streamflow from the Oleolega catchment (*cf.* Table 14.1).

Comparison of the overall annual inputs and outputs suggested that N, P, K and Mn accumulated at all sites, although at (very) low rates. However, this conclusion must be looked upon with caution as the nutrient concentrations in both rain water and water leaving the sites were close to, or below, the detection limits. Losses of Mg were observed at all sites, whereas Ca was lost from the Korokula forest plot and the Oleolega catchment, but accumulated in the Tulasewa and Koromani forest plots. Because pine roots penetrated the zone of active weathering in all sites, with the possible exception of Koromani, these losses of Mg, and to a lesser extent of Ca, suggest that these elements were released by weathering in excess of amounts taken up by the vegetation (see also Chapter 16).

In spite of the different techniques used to obtain estimates of the nutrient exports from the respective sites, nutrient gains and losses from the catchment compared reasonably well with those from the forest plots (Sections 13.7.1 and 13.7.2), lending confidence to the results.

14.2.2 Intra-System Nutrient Cycling

Nutrients cycle continuously within the ecosystem and this cycle has been called the intra-system cycle (*cf.* Figure 1.2, Likens *et al.*, 1977). The various components of the intra-system cycle for the forest chronosequence under study have been quantified in Table 14.2. The net annual uptake by the vegetation (*sensu* Gholz *et al.*, 1985) was calculated as the sum of nutrients accumulating in the above-ground living pine biomass, and those returned to the forest floor in pine litterfall and canopy wash. The canopy wash may have contained some nutrients leached from the undergrowth

Table 14.2: *Quantification of the components of the intra-system nutrient cycle of Pinus caribaea at various ages and various indices of 'nutrient use efficiency'.*

Location	Age	N	P	K	Ca	Mg	Mn	Zn	B
Annual Accumulation in Pine Biomass [kg ha-1], Pre-cyclone 1990									
Tulasewa Forest	6	35.1	4.8	22.4	18.4	8.8	1.70	0.24	0.03
Korokula Forest	11	9.2	1.8	4.2	5.8	3.1	0.45	0.08	0.01
Koromani Forest	15	10.8	1.2	6.6	8.5	2.7	0.65	0.10	0.01
Annual Returns in Throughfall and Stemflow [kg ha-1], Pre-cyclone 1990									
Tulasewa Forest	6	0.9	0.0	9.9	0.4	1.5	-0.10		
Korokula Forest	11	-0.6	0.1	11.0	1.8	3.6	-0.10		
Koromani Forest	15	0.2	0.1	16.8	2.0	2.5	-0.10		
Annual Returns in Pine Litter Fall [kg ha-1], Pre-cyclone 1990 #									
Tulasewa Forest	6	19.0	0.8	4.6	43.1	9.7	2.50	0.12	0.04
Korokula Forest	11	34.2	1.9	8.9	56.9	24.7	3.70	0.19	0.06
Koromani Forest	15	20.6	0.9	5.5	33.1	10.4	1.90	0.08	0.03
Net Annual Uptake by Pines [kg ha-1], Pre-cyclone 1990									
Tulasewa Forest	6	55.0	5.6	36.9	61.9	20.0	4.10	>0.36	>0.07
Korokula Forest	11	42.8	3.8	24.1	64.5	31.4	4.05	>0.27	>0.07
Koromani Forest	15	31.6	2.2	28.9	43.6	15.6	2.45	>0.18	>0.04
Fraction of Net Annual Uptake Provided by Internal Cycling [%]									
Tulasewa Forest	*6*	*36*	*14*	*39*	*70*	*56*	*59*	*>33*	*>55*
Korokula Forest	*11*	*79*	*53*	*83*	*91*	*90*	*89*	*>70*	*>83*
Koromani Forest	*15*	*66*	*45*	*77*	*81*	*83*	*73*	*>44*	*>68*
Ratio of Net Primary Production to Net Annual Uptake by Pines									
Tulasewa Forest	*6*	*500*	*4930*	*745*	*444*	*1375*	*6709*	*76408*	*392957*
Korokula Forest	*11*	*394*	*4435*	*699*	*261*	*537*	*6796*	*62419*	*234069*
Koromani Forest	*15*	*473*	*6797*	*517*	*343*	*959*	*11234*	*83072*	*339841*
Ratio of Annual Litter Fall Mass to Nutrient Returns to the Forest Floor									
Tulasewa Forest	*6*	*264*	*6426*	*1090*	*116*	*517*	*2005*	*41767*	*125300*
Korokula Forest	*11*	*271*	*4886*	*1043*	*163*	*376*	*2509*	*48863*	*154733*
Koromani Forest	*15*	*260*	*5957*	*975*	*162*	*515*	*2822*	*67013*	*178700*
Annual Accumulation in Litter Layer [kg ha-1], Pre-cyclone 1990									
All sites	0-15	2.5	0.1	0.3	4.4	1.4	0.20	0.00	0.01
Mean Annual Release (+) or Uptake (-) by the Undergrowth Vegetation [kg ha-1]									
Tulasewa Forest+	0-6	0.0	0.0	0.0	0.0	0.0	0.00	0.00	0.00
Korokula Forest+	6-11	6.2	0.6	17.7	3.0	3.2	0.37	0.02	0.01
Koromani Forest+	11-15	-2.0	-0.2	-5.7	-1.0	-1.0	-0.12	-0.01	-0.00
Net Annual Uptake (+) or Return of Soil Nutrients [kg ha-1], Pre-cyclone 1990*									
Tulasewa Forest	6	33.6	4.8	17.0	20.7	10.6	1.70	0.24	0.04
Korokula Forest	11	3.0	1.3	-14.6	8.6	10.0	0.08	0.06	0.01
Koromani Forest	15	13.8	1.4	11.4	13.3	6.2	0.87	0.11	0.02

#: Trace elements for foliage only; *: Annual gains or losses assumed zero for Zn and B

+: Obtained from the mean annual decrease in undergrowth mass, using nutrient concentrations in grass vegetation, and this may have led to a slight overestimation of the computed net annual uptake by the pines. The mean annual release of nutrients as a result of changes in the undergrowth biomass was calculated from the difference in the nutrient content of the undergrowth vegetation (Tables 11.14 – 11.16) from one age class to the next, divided by the number of years between observations. Although the composition of the undergrowth vegetation changed during the course of a rotation, its nutrient content had to be calculated using nutrient concentrations obtained for grassland vegetation. As such the estimates for the older forests may contain relatively large errors.

The annual production rates of foliage and woody tissue were high in the young Tulasewa forest, which therefore accumulated nutrients at a high rate (Table 14.2). The canopy was fully developed at age 11, represented by Korokula forest, and from then on nutrient accumulation occurred mainly in the form of nutrient-poor woody tissue and at a much lower rate. Biomass production was some 20% lower in the Korokula forest plot than that in the Koromani forest plot (Table 11.7), resulting in slightly lower accumulation rates for N, K, Ca, Mn, Zn and B, but not for P and Mg. The higher P and Mg accumulation in the pine biomass of the former may be attributed to higher nutrient concentrations in plant material (Table 11.11), possibly as a result of differences in available Mg and P between the two soils (Section 11.5.3).

The annual return of nutrients to the forest floor occurred predominantly in litterfall, with contributions by throughfall and stemflow amounting to less than 20% of the total for Mg, and less than 5% for N, P, Ca and Mn at all sites. However, the larger part of K was returned to the forest floor in throughfall and stemflow, contributing 55%, 68% and 73% to the total in the Tulasewa, Korokula and Koromani forest plots, respectively. Nutrients returned in throughfall and stemflow are mainly in ionic form and are therefore directly available for uptake by plants, whereas those in litterfall become available only slowly during decomposition of the litter. The cycling of K through the ecosystem must therefore be considered much more rapid than those of the other nutrients. This holds both for natural and plantation forests in the tropics (Bruijnzeel, 1983a; Parker, 1983; Vitousek and Sanford, 1986; Burghouts, 1993). Litter production was considerably higher in the Korokula forest plot than in the Tulasewa and Koromani plots, which resulted in high annual nutrient returns at the former site. The difference in litter production between Korokula forest on the one hand, and Koromani and Tulasewa forests on the other hand must be attributed to differences in the soils (particularly soil depth, texture and water holding capacity, *cf.* Sections 4.3 and 6.5).

The net annual uptake of nutrients was largest early in the rotation period due to the high accumulation rate in the pine biomass, but generally decreased with forest age after age 6. The high net uptakes of Ca and Mg in Korokula forest should be attributed to the high rate of litter production, rather than to accumulation in pine biomass. Internal cycling constituted between 13% (P) and 63% (Ca) of the net annual uptake in Tulasewa forest. Higher proportions were found in the older forests, with values ranging between 51% (P) and 86% (Mg) in Korokula forest, and 43% (P) and 76% (K) in Koromani forest. The relative amounts of P in internal cycling were much lower than those of the other nutrients at all sites. This suggests that P is strongly retained within the biomass, possibly through retranslocation before abscission of old foliage. The relatively low percentages for N indicate that retranslocation may be important for this nutrient as well (*cf.* Vitousek, 1984). This contention was supported by the higher concentrations of N and P in fresh needles compared to those in needle fall (see Tables 11.8–11.10 and 12.2).

The 'nutrient use efficiency' of a forest ecosystem may be evaluated using the ratio of the net primary production (NPP, taken as the sum of the CAI of biomass and the annual litter production) to the net annual uptake (Vitousek, 1982; Gholz *et al.*, 1985). Alternatively, the ratio of litterfall mass to the nutrient returns to the forest floor in litterfall and canopy wash may be used (Vitousek, 1984). Both indices were calculated for Tulasewa, Korokula and Koromani forests and have been included in Table 14.2. Vitousek (1982) examined the relationship between 'nutrient use efficiency' and nutrient cycling for a wide range of forests and observed that the 'nutrient use efficiency' of forests on nutrient-poor soils was higher than on nutrient-rich sites. Comparison of the indices published by Vitousek (1984) for N, P and Ca in 62 natural tropical forests older than 25 years with those presently obtained indicated that the pine plantations in Fiji were very efficient in their use of N and P, exceeding the range for N (50-180) and with values near the upper range for P (1000–7500). The nutrient use efficiency of Ca was low (Tulasewa) to normal. Gholz *et al.* (1985) presented ratios of NPP to net annual nutrient uptake of N, P, K, Ca and Mg for a chronosequence of slash pine plantation forests (2–34 years) on a nutrient-poor soil in Florida and found that the nutrient use of their stands was highly efficient for P and K, and to a lesser extent for N and Ca, whereas nutrient use efficiency increased greatly with the forest age. They attributed the high efficiency for P in the older forests to reductions in the availability of P in the soil, which forced the trees to retranslocate increasingly larger amounts of P in order to sustain growth. The indices for N, P, K, Ca and Mg for Tulasewa and Korokula forests, and those for N, P and Ca in Koromani forest, were considerably higher than those found by Gholz *et al.* (1985) in stands of corresponding age (5, 8 and 14 years old). In spite of the high 'nutrient use efficiencies', biomass production was high in the Fiji plantations and no evidence was found that growth was limited by the availability of nutrients in the soil at any stage.

Lugo (1992) compared the dynamics of *Pinus caribaea* (age 4 and 18.5 years) and mahogany plantation forests (age 17 and 49 years) with those of paired secondary forests of the same age on volcanic soils in Puerto Rico, and observed higher 'nutrient use efficiencies', particularly for P, for the plantation forests than for the paired secondary forests using the two indices discussed above. His NPP/Uptake ratios for P in the pine plantation forests were of similar magnitude (3677–4719) as those calculated for Tulasewa and Korokula forests. However, his ratios for N were lower (131–157), whereas his ratios for K were higher (950–839). Because the plantation forests were on the same soils as the paired secondary forests, Lugo (1992) concluded that the high nutrient use efficiency by the plantation forests for P was a characteristic of the species, rather than an indicator of the nutrient status of the soil. The higher 'nutrient use efficiency' of the plantation forests could be explained by the fact that in the plantations a greater proportion of the nutrients needed for sustained growth was derived from retranslocation than in the paired secondary forests (Lugo, 1992). The 'nutrient use efficiency' of N and P increased with forest age in the Puerto Rican plantation forests (Lugo, 1992), which suggested that the demands for nutrient uptake from the soil were likely to decrease since nutrients taken up earlier were increasingly retranslocated. This is supported by the data obtained during the present study. A decrease in the 'nutrient use efficiency' of K was observed in the Puerto Rican forests, as well as in the forests presently studied. This may be related to the fact that K is very mobile, and is being leached increasingly from the canopy as the forests grow older and increase their foliage biomass (Table 14.2).

The net annual uptake or return of soil nutrients (Table 14.2) was calculated as the difference between net gains and losses to and from the ecosystem (Table 14.1) and the respective uptake and returns by and from the vegetation and litter layer.

The demands on the soil were highest early in the rotation period and decreased sharply after canopy closure, when considerable amounts of nutrients (*e.g.* K, N, Mn) must have been released from the dissapearing undergrowth vegetation. The release of K from the undergrowth vegetation between age 6 and 11 exceeded uptake by the pine trees and the accumulation in the litter layer, resulting in a net input of K to the soil. The undergrowth biomass increased again after age 11 due to the more open character of the older, cyclone damaged, forest. Nutrient demands from the soil increased correspondingly, but remained much lower than those early in the rotation (Table 14.2).

Comparison of the nutrient demands of the vegetation with the nutrient reserves in the soils (Section 4.4) suggested that the pools of Ca and Mg were sufficiently large to sustain plantation forestry at all sites. Amounts of K available in the soils would also be sufficient, provided that nutrient losses associated with harvesting would be minimized. As some of the nitrogen may be obtained by the forest by fixation of gaseous N, deficiencies for this nutrient are also unlikely. As for P, the estimates of 'available' P obtained with the Ca-Lactate method were much lower than those obtained with the Bray II method. If the latter are taken as representative for the availability of P, no deficiencies would be expected in the Tulasewa and Korokula forest plots. However, Bray-II 'available' P was fairly low in Koromani forest (24 kg ha^{-1}), and deficiencies may be expected in the next rotation if losses of P during and after harvesting would not be minimized (see also Chapter 16).

Requirements of Na, K, Ca, and Mg the by forest in Tulasewa (and Korokula) could for the most part be supplied by weathering of the substrate as the base saturation of the soil remained above 85% throughout the profile, suggesting that no depletion occurred in spite of the high nutrient uptake by the trees.

14.3 Post-Cyclone Nutrient Cycling

The impact of cyclone Sina will be evaluated in this section by comparing post-cyclone nutrient budgets with the pre-cyclone budgets presented earlier for the Tulasewa, Korokula and Koromani forest plots. Because logging in the Oleolega catchment started soon after the event cyclone effects could not be separated from those as a result of harvesting, and input – output budgets for the Oleolega catchment will therefore be presented here separately. Atmospheric inputs at all forest plots during cyclone Sina and in the period following the event, the corresponding exports in water leaving the forests, and the net gains or losses are presented in Table 14.3. Data collected during the post-cyclone period (306 days) were extrapolated linearly on a time basis to obtain annual estimates. The influence of cyclone Sina on the inputs of N, P and Mn was negligible, because concentrations in cyclone rain water were close to (total N) or below (total P, Mn) the respective detection limits. The higher N inputs observed for the post-cyclone period, compared to those during the pre-cyclone period, reflected the higher concentrations of total N in rainfall during the former period (Table 13.3). Nutrient inputs of Mg, and to a lesser extent of K and Ca, reflected the deposition of sea spray by the cyclone. The errors in the estimates of the atmospheric nutrient inputs given in Table 14.3 may be considerable due to uncertainties in the amounts of nutrients deposited by cyclone Sina (see discussion in Section 13.4), which almost certainly must have been underestimated. The annual inputs presented for the post-cyclone period remained within the lower ranges of those presented by Vitousek and Sanford (1986) and Bruijnzeel (1989a, 1991).

Table 14.3: *Annual atmospheric nutrient inputs, corresponding outputs in water leaving the forests, and net gains or losses at the Tulasewa, Korokula and Koromani forest plots, including those resulting from the passage of cyclone Sina. Annual values obtained by linear extrapolation on a time basis.*

Location	**Age**	**N**	**P**	**K**	**Ca**	**Mg**	**Mn**	**Zn**	**B**
Annual Atmospheric Input [kg ha-1], Cyclone and Post-cyclone 1991									
Tulasewa Forest*	7	3.6	<0.5	<5.6	<1.8	<3.0	<0.4		
Korokula Forest	12	9.1	<0.2	<3.2	3.3	<4.3	<0.2		
Koromani Forest	16	5.2	<0.2	<4.2	<2.6	<5.4	<0.2		
Annual Export with Drainage [kg ha-1], Cyclone and Post-cyclone 1991									
Tulasewa Forest	7	<0.6	<0.2	2.0	<1.3	11.8	<0.2		
Korokula Forest	12	0.4	<0.1	0.6	6.9	39.1	<0.1		
Koromani Forest	16	0.4	<0.1	0.7	2.0	2.7	<0.1		
Net Annual Gains (+) or Losses (-) [kg ha-1], Cyclone and Post-cyclone 1991									
Tulasewa Forest	7	>3.0	0.3	<3.6	0.5	<-8.8	0.20		
Korokula Forest	12	8.7	0.1	<2.8	-3.6	<-33.8	0.10		
Koromani Forest	16	4.8	0.1	<3.5	<0.6	<2.7	0.10		

*: Cyclone rainfall inputs taken as 0.5 times those at Korokula Forest

Post-cyclone outputs of Mg, Ca and K in drainage, and possibly those of P (concentrations often below the detection limit), were larger than pre-cyclone outputs, whereas that of N was lower. However, outputs of N, P, K and Mn did not exceed the atmospheric inputs and small net annual gains were therefore observed for these nutrients at all sites. Small gains of Ca were calculated for Tulasewa and Koromani forest, whereas a small loss was derived for Korokula forest. In the year after the passage of cyclone Sina, Mg was exported from Korokula forest in much larger quantities than in the year before, which was due to increased concentrations of Mg in the soil moisture (Table 13.10). Larger exports of this nutrient were also observed at Tulasewa forest due to a combination of higher concentrations and increased drainage following the cyclone event. However, a small gain in Mg was observed at Koromani forest. A large proportion of the exchange places in the subsoils of Tulasewa and Korokula forests was occupied by Mg (Section 4.4) and some of these ions may have been exchanged against Na, which was deposited in large quantities on the soils by cyclone Sina. The CEC and base saturation of the soil in Koromani forest were much lower, and this may have prevented the release of Mg at this site.

In Puerto Rico, Asbury and Scatena (pers. comm.) also observed higher concentrations of nutrients in streamflow from the small Bisley catchments after hurricane Hugo reduced the above-ground biomass with 50% (Scatena *et al.*, 1993). However, since rainfall amounts were below average in the period following the event (Scatena and Larsen, 1991) no increase in the annual nutrient export was observed compared to the previous year.

The impact of cyclone Sina on the intra-system nutrient cycle was large as the cyclone downed more than 40%, 14% and 10% of the above-ground tree biomass in the Tulasewa, Korokula and Koromani forest plots, respectively. The damage to the nutrient-rich canopy was severe at all sites, leading to the transfer of large amounts of nutrients to the forest floor (Tables 12.10–12.12) and therefore eventually to the soil.

The post-cyclone sources, sinks and transfers of nutrients are presented in Table 14.4. The biomass of the forests immediately after the cyclone event was unknown, which made the calculation of the annual post-cyclone nutrient uptake by the vegetation from the biomass data difficult. Furthermore, uncertainties in the nutrient returns in cyclone litterfall, as well as in the accumulation of nutrients in the litter layer, were large due to the high spatial variation and the inability to include large wood in the samples (see Sections 12.3.3 and 12.5.3). Hence the following assumptions were made to obtain the estimates for post-cyclone nutrient uptake presented in Table 14.4:

- Post-cyclone diameter increments were only slightly lower than the pre-cyclone rates in the Tulasewa forest plot (Section 11.3.4) and post-cyclone annual nutrient uptake was therefore assumed equal to pre-cyclone uptake, multiplied by a correction factor to account for the reduction in stocking.
- Diameter increments in the Korokula and Koromani forest plots were zero during the nine months following the cyclone event, suggesting that nutrients taken up by the trees were exclusively used for the regeneration of foliage. Here the post-cyclone uptake was therefore approximated by the mean annnual pre-cyclone nutrient increment in branches, twigs and foliage, again after corrections were made for reductions in stocking.

Due to these and other uncertainties, the data presented in Table 14.4 may be relatively inaccurate. However, they may serve as a rough indication of the changes in the forest nutrient cycle after severe damage by a cyclone.

The cyclone transferred large amounts of nutrients from the canopy to the forest floor, the greater part of which were deposited as litterfall (Tables 12.4–12.6). The amounts of nutrients leached from the canopy and stem during cyclone Sina were presumably small, and the amounts in canopy and stem wash (Table 13.7) were probably overestimated as a consequence of the underestimation of atmospheric inputs during the cyclone event. The release of nutrients from the litter layer by decomposition is a slow process, and a large proportion of the nutrients deposited on the forest floor in litterfall remained immobilised in the litter layer, which resulted in a large accumulation of nutrients in the litter layer in the year following the cyclone event. The values presented in Table 14.4 represent only 8 months of post-cyclone data, and the actual accumulation rates will have been somewhat lower due to continued decomposition between August and November 1991, for which no data were available.

The 'nutrient use efficiency' of the forests for the post-cyclone period was evaluated using the litterfall – nutrient return index (Vitousek, 1984). Comparison of post-cyclone ratios with pre-cyclones ratios showed that the 'nutrient use efficiency' decreased considerably after the cyclone for P, K and Mg, with smaller decreases for the other nutrients at most of the forest sites. The low post-cyclone nutrient use efficiency could be attributed to less efficient retranslocation of nutrients in the cyclone damaged canopy before abscission of the foliage. This resulted in relatively high nutrient concentrations in post-cyclone litterfall compared to those in the pre-cyclone period, until several months after the cyclone event (Section 12.3.2).

The damage afflicted to the forests by cyclone Sina resulted in an enrichment of most soil nutrients a year after the event (Table 14.3) as indicated by higher nutrient concentrations in the soil moisture (see Section 13.6). Net returns to the soil were high for K and Ca, a large part of which were presumably retained in the soil on cation exchange places as the large inputs did not result in similar losses via drainage (Tables 14.3 and 14.4). Small net losses were observed for Mg in Tulasewa and Korokula forests due to increased outputs of Mg in drainage, but not in Koromani forest. Rain-

Table 14.4: *Quantification of the components of the intra-system nutrient cycle in the year following the passage of cyclone Sina. Note that the estimates for nutrient accumulation in the litter layer pertain to an 8-month period.*

Location	**Age**	**N**	**P**	**K**	**Ca**	**Mg**	**Mn**	**Zn**	**B**
Return in Cyclone Throughfall and Stemflow [kg ha-1]									
Tulasewa Forest+	7	-0.1	0.0	3.3	7.3	2.9	0.06		
Korokula Forest	12	-0.2	0.0	6.6	14.5	5.8	0.12		
Koromani Forest*	16	-0.2	0.0	6.6	14.5	5.8	0.12		
Return in Cyclone Litter fall [kg ha-1] #									
Tulasewa Forest	7	75.8	9.0	47.3	66.3	22.4	3.35	0.17	0.05
Korokula Forest	12	108.6	7.5	35.1	71.7	38.7	3.73	0.15	0.15
Koromani Forest	16	91.2	6.5	32.0	71.3	23.1	4.29	0.15	0.08
Accumulation in Pine Biomass [kg ha-1], Post-cyclone 1991*									
Tulasewa Forest	7	20.9	2.9	13.3	11.0	5.2	1.01	0.14	0.02
Korokula Forest	12	12.6	1.0	4.8	4.2	3.6	0.21	0.03	0.01
Koromani Forest	16	9.1	0.7	5.8	4.0	1.6	0.33	0.02	0.01
Return in Throughfall and Stemflow [kg ha-1], Post-cyclone 1991									
Tulasewa Forest	7	-1.7	0.0	11.2	1.2	1.2	-0.04		
Korokula Forest	12	-7.7	0.0	5.6	1.4	1.9	-0.02		
Koromani Forest	16	-3.4	0.0	7.1	1.4	1.4	-0.02		
Return in Litter Fall [kg ha-1], Post-cyclone 1991 #									
Tulasewa Forest	7	15.6	1.2	3.8	29.4	8.0	2.31	0.11	0.04
Korokula Forest	12	20.1	3.8	3.6	26.5	13.2	1.44	0.08	0.05
Koromani Forest	16	19.9	0.8	4.1	23.9	6.8	2.63	0.09	0.04
Net Annual Uptake by Pines [kg ha-1], Post-cyclone 1991									
Tulasewa Forest	7	34.8	4.1	28.3	41.5	14.4	3.28	0.25	0.06
Korokula Forest	12	25.0	4.8	14.0	32.1	18.7	1.63	0.11	0.07
Koromani Forest	16	25.6	1.5	17.0	29.3	9.8	2.94	0.11	0.05
Ratio of Annual Post-cyclone Litter Fall Mass to Nutrient Returns to the Forest Floor									
Tulasewa Forest	*7*	*259*	*2909*	*241*	*118*	*393*	*1587*	*33491*	*99953*
Korokula Forest	*12*	*325*	*1066*	*439*	*144*	*267*	*2841*	*50524*	*73809*
Koromani Forest	*16*	*227*	*4417*	*335*	*149*	*457*	*1440*	*42533*	*92791*
Accumulation in Litter Layer [kg ha-1], Cyclone and Post-cyclone period, Nov ’90 - Aug ’91									
Tulasewa Forest	7	62.2	5.3	13.5	43.3	12.2	1.99	0.07	0.02
Korokula Forest	12	66.4	3.1	8.3	20.5	12.7	0.89	0.11	-0.01
Koromani Forest	16	82.4	5.2	8.9	28.8	14.2	0.16	0.04	0.00
Net Annual Uptake (+) or Return (-) of Soil Nutrients [kg ha-1] in the year after the passage of Cyclone Sina @									
Tulasewa Forest	7	4.4	-1.1	-27.4	-19.8	1.0	-0.61	0.04	-0.01
Korokula Forest	12	-38.1	-3.5	-31.4	-57.9	5.6	-2.85	-0.01	-0.15
Koromani Forest	16	-4.3	-0.7	-27.4	-53.6	-15.7	-4.02	-0.09	-0.07

+: Cyclone canopy wash assumed 0.5 times that at Korokula forest
*: Cyclone canopy wash taken equal to that at Korokula forest
#: Trace elements totals for foliage only; @: Totals of Zn and B in moisture fluxes assumed zero

fall amounts during the post-cyclone period (Table 6.9) at the Korokula and Koromani plots were 7–10% lower than the corresponding long-term average for Nabou station (Table 6.2), which will have limited nutrient losses via drainage to some extent at these sites compared to those that would have occurred with more representative rainfall conditions. The converse was true for nutrient losses via drainage at the Tulasewa site, where post-cyclone rainfall was 42% higher than the corresponding long-term average.

The nutrient enrichment of the soil one year after the cyclone event, in combination with the further release of nutrients accumulated in the litter layer, seems sufficient to balance the forest nutrient uptake for at least another year. As such the effect of a major cyclone on the intra-system nutrient cycle may last several years, depending on the amount of damage afflicted to the forest (decrease in stocking) and the rate of decomposition of the cyclone debris.

Such disruptions of the intra-system nutrient cycles as a result of severe wind damage to natural rain forests were also observed in Puerto Rico after hurricane Hugo transferred large amounts of nutrients from the forest canopy to the soil surface (Lodge *et al.*, 1991; Steudler *et al.*, 1991; Scatena *et al*, 1993).