

Nitrogen and fine root length dynamics in a tropical agroforestry system with periodically pruned *Erythrina poeppigiana*

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Abstract The effect of pruning all branches (complete pruning) or retaining one branch (partial pruning) on the dynamics of nitrogen cycling in aboveground biomass, nitrogen supplying power of an amended Eutric Cambisol, and fine root length, was studied in an *Erythrina poeppigiana* (Walp.) O.F. Cook—tomato (*Lycopersicon esculentum* Mill.) alley cropping practice in Turrialba, Costa Rica during 1999–2000. Over the 1 year pruning cycle, in which trees were completely or partially pruned four times, respective aboveground biomass production was 4.4 Mg or 7 Mg ha⁻¹ (2-year-old trees) and 5.5 Mg or 9 Mg ha⁻¹ (8-year-old trees); N cycled in aboveground biomass was 123 kg or 187 kg ha⁻¹ (2-year-old trees) and 160 kg or 256 kg N ha⁻¹ (8-year-old trees); mean fine root length was 489 or 821 m (2-year-old-trees), 184 or 364 m per tree (8-year-old-trees). Pruning intensity did not significantly affect net N mineralisation and net nitrification rates during the tomato-cropping season. For the tomato crop, pre-plant mean net N mineralisation rate of 2.5 mg N kg⁻¹ soil day⁻¹ was significantly lower than 16.7 or 11.6 mg N kg⁻¹ soil day⁻¹ at the end of

vegetative development and flowering, respectively. Mean net nitrification rates of 3.5, and 4.3 mg N kg⁻¹ soil day⁻¹, at pre-plant and end of vegetative development, respectively, were significantly higher than 0.3 mg N kg⁻¹ soil day⁻¹ at end of flowering. In humid tropical low-input agroforestry practices that depend on organic inputs from trees for crop nutrition, retention of a branch on the pruned tree stump appears to be a good alternative to removal of all branches for reducing N losses through higher N cycling in aboveground biomass, and for conserving fine root length for higher N uptake, although it might enhance competition for associated crops.

Keywords Aboveground biomass · Humid tropics · Mineralisation · Nitrification · Nutrient cycling

Introduction

The tomato (*Lycopersicon esculentum* Mill.) on live stake agroforestry practice has shown promise when organic inputs for crop nutrition are provided by *Erythrina poeppigiana* (Walp.) O.F. Cook trees (Chesney et al. 2000). The main input from *E. poeppigiana* is the more than 250 kg N ha⁻¹ year⁻¹ cycled in aboveground biomass (Beer 1988; Kass et al. 1993) of trees that are managed by complete shoot pruning at half-yearly intervals to enhance light supply to the associated crop. Additional N sources

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are from increased fluxes in senescent nodules (Nygren and Ramírez 1995) and fine roots (Muñoz and Beer 2001; Nygren and Campos 1995), of periodically pruned *E. poeppigiana* trees.

However, half-yearly complete pruning of *E. poeppigiana* trees delays the renewal of N₂ fixation (Vaast and Snoeck 1999) and new nodule biomass production (Nygren and Ramírez 1995) for 10–16 weeks. During this lag period, regrowing trees may reabsorb soil N (Kass et al. 1997). Research with other species has shown that complete pruning can increase N losses (Vanlauwe and Sanginga 1995), and influence other below ground processes such as net N mineralisation and net nitrification rates (Haggard et al. 1993), and distribution of nitrates (Jama et al. 1998) and fine root length (van Noordwijk et al. 1996).

Experiences with maize (*Zea mays* L.) (Kass et al. 1993) and tomato (Chesney et al. 2000) alley cropping recommend pruning of *E. poeppigiana* trees more frequently than twice a year. Complete pruning at a frequency of three times a year reduced aboveground biomass production (Russo and Budowski 1986; Romero et al. 1993) thus limiting the potential of this species to provide adequate amounts of organic inputs for crop nutrition. As a tree management alternative, pruning part of the canopy of the service tree instead of all shoots may satisfy the primary pruning function, and in addition, may increase pruning N availability (Vanlauwe and Sanginga 1995) possibly through conservation of fine roots (Nygren and Cruz 1998).

Leaving one or two branches on the pruned tree stump is a traditional partial pruning practice of *E. poeppigiana* shade trees in Costa Rican coffee (*Coffea arabica* L.) farms (Somarriba et al. 1996). This technique called 'lung branch' pruning in tea (*Camellia sinensis* (L.) O. Kuntze) culture, dates back to the 1930s (Kandiah et al. 1984). It is presumed that the retained branch ensures a supply of photosynthates to developing new shoots. The functional advantages of partial pruning of leguminous service trees over complete pruning in humid tropical agroforestry systems have been little studied. A field study was carried out to test the effects of complete and partial shoot pruning on the dynamics of soil N and fine root length in an *E. poeppigiana*—tomato live-stake agroforestry practice under humid tropical conditions in Turrialba, Costa Rica.

Materials and methods

The study environment

The study was carried out in the La Montaña experimental farm of CATIE, (Centro Agronómico Tropical de Investigación y Enseñanza), Turrialba, Costa Rica (9°53' N, 83°43' W, 602 m a.s.l.). The ecological zone is a very humid pre-montane forest (Holdridge 1987) with a medium fertility Eutric Cambisol (Kass et al. 1995) (Table 1). Meteorological variables (average ± SD) measured during field data collection from May 1999 to May 2000, were monthly precipitation 325 ± 181 mm; daily temperature maxima 30.3 ± 1.3°C; daily temperature minima 15.2 ± 1.7°C, and relative humidity 87.8 ± 2.0%.

The experimental plots were established in January 1991 to compare different maize and bean (*Phaseolus vulgaris* L.) varieties associated with *E. poeppigiana*, *Calliandra calothyrsus* Meissn., *Gliricidia sepium* (Jacq.) Kunth ex Walp. and treeless control treatments. Further description will be confined to *E. poeppigiana* plots. The initial spacing was 6 × 2 m. In 1997, row width was changed to 3 m (1,666 trees ha⁻¹) with the planting of rooted stakes, taken from the same plots. Throughout this article, the trees planted in 1991 will be referred to 8-year-old trees, and the trees planted in the original alleyways in 1997 will be referred to as 2-year-old trees.

Between 1992 and 1996, trees were managed by half-yearly complete shoot pruning carried out at the beginning of each of two cropping seasons. Pruned material was chopped into small pieces and added to the alleys and fertilised bean and maize were grown in rotation up to 1996. From 1998 onward, bean was replaced by tomato in the rotation and fertiliser use was discontinued. Pruning height of live stakes was raised from 0.75 m to 1.5 m to allow for connecting trees with wire at 1.3 m height for the staking of tomatoes.

Experimental design

The effect of complete and partial pruning on N cycling in foliar biomass, net N mineralisation rates, net N nitrification rates and fine root length was studied in a split plot in time design with three replications. Mainplot factor was pruning intensity (complete i.e. removal of all shoots; and partial i.e.

Table 1 Chemical properties of *E. poeppigiana*-amended alluvial Eutric Cambisol, Turrialba, Costa Rica, January 1999

Soil depth (cm)	pH (H ₂ O)	Extract-able acidity cmol l ⁻¹	Ca cmol l ⁻¹	Mg cmol l ⁻¹	K cmol l ⁻¹	ECEC cmol l ⁻¹	SOM %	P mg kg ⁻¹	NH ₄ -N mg kg ⁻¹	NO ₃ -N mg kg ⁻¹
0–20	5.14 ± 0.16	0.36 ± 0.19	4.75 ± 0.07	1.61 ± 0.07	0.33 ± 0.09	7.05 ± 0.06	5.12 ± 0.28	14.3 ± 7.4	1.85 ± 0.28	1.84 ± 0.27
20–40	5.26 ± 0.04	0.22 ± 0.06	4.37 ± 0.81	1.23 ± 0.1	0.2 ± 0.07	6.03 ± 0.88	3.76 ± 0.5	10.3 ± 3.0	–	–
40–60	5.51 ± 0.14	0.15 ± 0.08	4.46 ± 0.46	1.22 ± 0.18	0.16 ± 0.11	5.99 ± 0.52	2.38 ± 0.39	10.6 ± 3.3	–	–
Mean	5.3 ± 0.19	0.24 ± 0.15	4.53 ± 0.5	1.35 ± 0.23	0.23 ± 0.11	6.35 ± 0.73	3.75 ± 1.23	11.7 ± 4.7	–	–

Data are means ± standard deviations of three replications each with six composite sub-samples randomly taken. Gravimetric moisture content was 27.3%

retention of one branch corresponding to 5% of total shoot biomass). Subplot factor was pruning date (May, August, November of 1999, January and May 2000; applied without re-randomisation). Sampling and analyses were separate for tree age except for the net N mineralisation and net nitrification study. Soil N data were collected from treeless plots to compare with those from *E. poeppigiana*-amended plots.

Plot management

Cropping seasons were May–August 1999 (maize) and November 1999–January 2000 (tomato). Plots were fallowed in the intervals between crops. Crops of maize var. Diamantes 8,843 sown 15 June 1999 at a density of 26,666 plants ha⁻¹, and tomato var. Dina Panama transplanted at 22 days on 26 November 1999 at a density of 13,333 plants ha⁻¹, were established uniformly in the alleys formed by tree rows. Trees were pruned 2 weeks before planting and at crop flowering phenophase. The same branch was not retained at each pruning. Pre-plant N-containing pruned materials were chopped into small pieces; one-half (Table 2) along with dolomitic lime (0.5 Mg ha⁻¹ CaCO₃·MgCO₃) was incorporated into the planting strips while the other half was applied as mulch. Mid-season (flowering) pruned material was applied as mulch. Plots were manually weeded at monthly intervals.

Pruned biomass and N accumulation

On each pruning date, total fresh weight of pruned shoots was measured. Shoots were separated into leaves, woody and non-woody branch parts and 0.5 kg sub-samples of each part was oven-dried (65°C) to constant dry weight for dry mass determination. Composite (combined replications) dried sub-samples were analysed for total N by semi-micro kjeldahl

Table 2 Nitrogen added in *E. poeppigiana* prunings^a

Month of pruning	Tree age (years)	N (kg ha ⁻¹)
August 1999	2	24
	8	35
November 1999	2	20
	8	31

^a Composite samples were analyzed

(Weaver et al. 1994). Accumulated biomass N was computed as the sum of the products of dry weight and N concentration in each compartment.

Soil nitrogen dynamics

Net N mineralisation and nitrification rates

Mineralisation rates were studied during the tomato crop at pre-plant (2 weeks before to 2 weeks after pruning) and during vegetative (from planting to 21 days later) and flowering (end of vegetative phase to 28 days later) phases in *E. poeppigiana*-amended and treeless soil. The closed-top solid cylinder field incubation method (Hart et al. 1994) was used. At the beginning of each phase, three cylinders per plot were removed immediately after insertion. The top 20 cm of soil were mixed, extracted with 2N KCl and analysed for initial concentration of NH_4 and NO_3 (Weaver et al. 1994). The remaining tubes in the field were removed at the end dates of each phase and the process repeated. Net mineralisation and nitrification rates were calculated according to Hart et al. (1994).

Available N (NH_4 , NO_3)

During the tomato crop, sampling commenced 2 weeks after transplanting (WAT) and continued thereafter weekly for six consecutive weeks. On each sampling date, six topsoil (0–20 cm) auger samples were randomly taken from the planting rows and analysed for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ as described above.

Fine root length dynamics

Inventory coring of a modal (stem diameter) 8-year-old tree to 60 cm soil depth in September 1998 revealed that 80% of fine roots of *E. poeppigiana* was distributed in the topsoil. For the present study, 10 topsoil core (auger cylinder: $\phi = 8$ cm; $L = 25$ cm) samples were taken randomly from within the unit soil area, a rectangle measuring 1.5 m^2 with the tree in the centre of the rectangle, at 6, 10, 14 and 22 weeks after pruning (WAP) in August 1999. The sampling periods were selected based on observation of nodule dynamics by Nygren and Ramírez (1995). Sampling in the unit soil area to 20, 40 and 60 cm soil depth was carried out in May 2000 to determine the effect of pruning intensity on vertical distribution of fine roots.

Roots were washed free from soil in 0.5 mm sieves and sorted into live and dead fractions with the aid of a stereomicroscope and criteria of colour, texture and appearance of the central cylinder. Live fine roots (< 2 mm) were measured for root length using WinRHizo Pro[®] (Régent Instruments, Quebec, Canada). Fine root length was corrected from the sample area of 1.5 m^2 to the 6-m^2 area each tree occupies.

Statistical analyses

Foliar biomass, fine root length and nitrogen data were examined for homogeneity of variances and normality. For analysis of biomass data, individual trees in each plot were treated as sub-samples and diameter at 10 cm was used as co-variable. Data were analysed using SAS/GLM (SAS Institute, Cary, North Carolina) procedure for split plot in time design with three replications. Mean comparisons were by the Ryan-Elliott-Gabriel-Welch (REGWQ) test ($P < 0.05$), which limits Type 1 experiment-wise error.

Results

Pruned *E. poeppigiana* biomass

In the year following the initial pruning, partial pruning treatment significantly increased above-ground biomass by approximately 50% over complete pruning (Table 3). Total biomass production from completely versus partially pruned trees was 4.4 vs. 7 Mg ha^{-1} in 2-year-old trees, and 5.5 vs. 9 Mg ha^{-1} in 8-year-old trees, respectively. Pruned biomass decreased significantly over the observation period with lowest production in January 2000 (Table 3), when precipitation was highest and average solar radiation lowest (Fig. 1). Plots of mean pruned biomass against pruning date showed that the relationship could best be described by a quadratic orthogonal polynomial function (Fig. 2). The rate of change of biomass by time showed that for 2- and 8-year-old trees, the minimum values for significant biomass changes along the curvature were 14.7 and 15.4 months, respectively. These values correspond to the February–March 2000 dry season. The interaction between pruning intensity and pruning date was non-significant.

Table 3 Effect of shoot pruning *E. poeppigiana* trees on pruned total biomass and proportion of leaf to total biomass, Turrialba, 1999–2000

Age of stakes (years)	Pruning intensity	Pruned total biomass and the proportion that is leaf ^z					Mean ^y (Total) ^{y,x}
		May 99	Aug 99	Nov 99	Jan 00	May 00	
Total biomass (Mg ha⁻¹)							
2	Complete	4.8 ± 0.7	1.7 ± 0.4	1.2 ± 0.2	0.4 ± 0.1	1.1 ± 0.9	1.1b (4.4)
	Partial	4.2 ± 0.6	2.6 ± 0.8	1.7 ± 0.7	0.9 ± 0.4	1.8 ± 0.4	1.7a (7.0)
	Mean	4.5	2.1a	1.4b	0.6c	1.5b	1.4
8	Complete	5.7 ± 1.0	2.1 ± 0.5	1.6 ± 0.5	0.6 ± 0.2	1.2 ± 0.7	1.4b (5.5)
	Partial	6.2 ± 1.7	3.2 ± 1.0	2.7 ± 0.9	1.0 ± 0.2	2.1 ± 0.9	2.2a (9.0)
	Mean	6.0	2.6a	2.1a	0.8c	1.6b	1.8
Proportion of total biomass that is leaf biomass (%)							
2	Complete	43.9	48.5	76.1	79.2	76.1	70.0
	Partial	47.8	43.9	65.0	64.1	67.6	60.2
8	Complete	48.4	47.6	76.3	77.8	74.3	69.0
	Partial	49.1	49.5	71.9	67.2	72.7	65.3

Data are means ± standard deviations

^z Biomass at 20, 13, 12, 10 and 16 weeks regrowth corresponding to May 99, Aug 99, Nov 99, Jan 00 and May 00, respectively; ^y applies to August 99 through May 00; ^x in Mg ha⁻¹ year⁻¹

Means in the same column (pruning intensity) or in the same row (pruning period) followed by the same letter are not significantly different, REGWQ ($P \leq 0.05$)

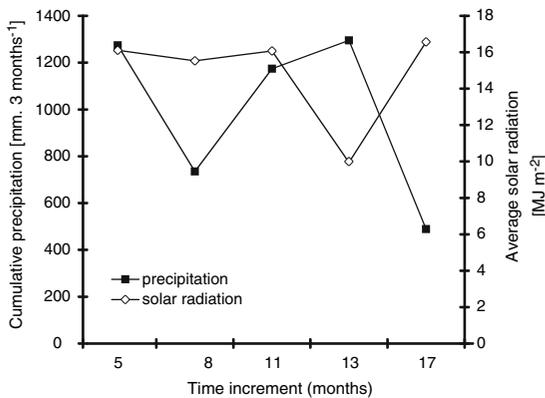


Fig. 1 Cumulative precipitation, and average solar radiation

The proportion of leaf to branch biomass increased when the preceding pruning interval was less than 20 weeks and was generally higher in completely pruned trees compared to partially pruned trees (Table 3). Completely pruned trees did not produce woody branch tissue until a regrowth period of 16 weeks; branch tissue at August 1999 to January 2000 pruning events was entirely non-lignified. Partially pruned tree developed approximately three-quarters of its new growth on the retained

branch that was lignified at all pruning events; stem borne shoots were non-lignified.

Nitrogen accumulation in pruned *E. poeppigiana* biomass

Over the 1-year pruning cycle, N cycled in total aboveground biomass of completely versus partially pruned trees was 123 vs. 187 kg ha⁻¹ (2-year-old trees) and 160 vs. 256 kg ha⁻¹ (8-year-old trees), respectively (Table 4). Nitrogen cycled in 10-week biomass regrowth cut in January 2000 was lower than the overall mean value. Differences in accumulated N were due to differences in the amounts of biomass since leaf N concentration was similar: 3.6% and 3.7% for completely and partially pruned 2-year-old tree, and 3.8% and 4% for completely and partially pruned 8-year-old tree, respectively.

Soil nitrogen dynamics

Net N mineralisation and nitrification rates

Tree pruning did not significantly affect net mineralisation and nitrification rates. Net N mineralisation rates significantly increased after crop planting to a peak of

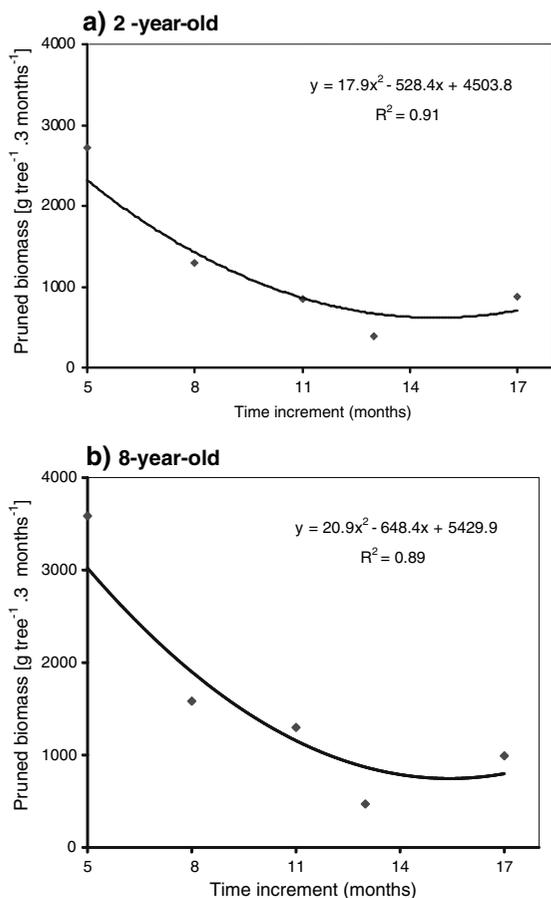


Fig. 2 Aboveground biomass with pruning date (as increments in time) of (a) 2-year-old and (b) 8-year-old *E. poeppigiana* trees over the period May 1999 to May 2000, Turrialba. Average of pruning regimes

16.7 mg N kg soil⁻¹ day⁻¹ at the end of the tomato vegetative stage, and decreased by non-significant amounts during early tomato fruit development

(Table 5). Net nitrification rate decreased by significant amounts to 0.3 mg N kg soil⁻¹ day⁻¹, during early tomato fruit development (Table 5).

Comparison of net N mineralisation and net nitrification rates in *E. poeppigiana*-amended soil and treeless soil did not show any significant differences ($P = 0.92$). Time course changes were also similar (Table 5). The interaction between soil amendment and sampling date was non-significant ($P = 0.30$).

Available N (NH_4 , NO_3)

During the tomato crop, NH_4 -N concentration at 2 WAT was about twice as high and NO_3 -N concentration was 12-fold lower than corresponding values during the maize crop earlier in the annual cropping cycle (data not shown). Soil inorganic N ($NH_4 + NO_3$) concentration decreased by non-significant quantities over the measurement period (Table 6). During the first 3 WAT, NO_3 -N concentration increased while that of NH_4 -N decreased, thereafter both N forms decreased in soil under completely pruned live stakes but fluctuated in soil under partially pruned live stakes. Soil water content remained unchanged over the observation period.

Fine root length dynamics in *E. poeppigiana*

Mean fine root length was significantly lower in completely pruned compared to partially pruned trees for both tree ages. Respective values were 489 vs. 821 m plot⁻¹ for 2-year-old-trees, and 184 vs. 364 m plot⁻¹ for 8-year-old-trees (Fig. 3). Maximum fine root length was observed between 10–14 WAP.

Table 4 Effect of shoot pruning *E. poeppigiana* trees on total nitrogen (kg N ha⁻¹) obtained from pruned biomass, Turrialba, 1999–2000

Tree age (years)	Pruning intensity	Total N ^z					Total ^y kg ha ⁻¹ year ⁻¹
		May 99	Aug 99	Nov 99	Jan 00	May 00	
2	Complete	119	42	32	13	36	123
	Partial	109	57	47	27	56	187
8	Complete	154	53	46	21	40	160
	Partial	169	82	78	29	67	256
	Mean	138	59	51	23	50	183

^z Biomass at 20, 13, 12, 10 and 16 weeks regrowth corresponding to May 99, Aug 99, Nov 99, Jan 00 and May 00, respectively;

^y applies to August 99 through May 00

Table 5 Effect of shoot pruning on *E. poeppigiana*-amended topsoil (0–20 cm) net mineralisation and nitrification rates during different stages of tomato development, Turrialba, 1999–2000

Pruning intensity	Net mineralisation rates			Net nitrification rates		
	Pre-plant mg N kg ⁻¹ d ⁻¹	Vegetative mg N kg ⁻¹ d ⁻¹	Flowering mg N kg ⁻¹ d ⁻¹	Pre-plant mg N kg ⁻¹ d ⁻¹	Vegetative mg N kg ⁻¹ d ⁻¹	Flowering mg N kg ⁻¹ d ⁻¹
Complete	2.0 ± 0.33	16.2 ± 6.63	11.4 ± 7.5	4.1 ± 1.2	1.6 ± 1.3	-0.6 ± 0.3
Partial	3.0 ± 4.23	17.2 ± 4.81	11.6 ± 3.0	2.9 ± 2.0	6.9 ± 1.0	1.2 ± 1.0
Mean ^z	2.5b	16.7a	11.5ab	3.5a	4.3a	0.3b
Treeless soil	-0.54 ± 2.1	13.7 ± 3.6	15.9 ± 4.7	1.2 ± 1.7	7.1 ± 2.3	1.3 ± 1.9
Mean ^y	1.0b	15.2a	13.7a	2.4b	5.7a	0.8b

Data are means ± SEM

Means in the same row followed by a different letter (net mineralisation rates) or superscript letter (net nitrification rates) are not significantly different, REGWQ ($P \leq 0.05$)

^z Mean values for *E. poeppigiana*-amended soil; ^y mean values for *E. poeppigiana*-amended and treeless soil

Table 6 Effects of shoot pruning *E. poeppigiana* trees on topsoil (0–20 cm) inorganic N (mg kg⁻¹) concentration, 2–7 weeks after tomato transplanting, December 1999 to January 2000, Turrialba

Weeks after planting	NH ₄		NO ₃		NH ₄ + NO ₃		Soil water (g g ⁻¹)	
	Complete	Partial	Complete	Partial	Complete	Partial	Complete	Partial
2	3.9a	4.1a	2.1a	2.1b	6.1a	6.2a	28.5a	29.7a
3	2.6ab	3.0ab	3.9a	3.4ab	6.5a	6.4a	29.7a	30.0a
4	1.8b	2.4bc	3.6a	3.5ab	5.4a	5.9a	29.7a	29.6a
5	1.9b	1.7bc	3.6a	3.9a	5.5a	6.4a	29.2a	30.8a
6	0.9b	1.2c	3.0a	2.9ab	3.9a	4.1a	29.1a	29.5a
7	1.4b	1.5bc	2.8a	3.1ab	4.2a	4.6a	29.1a	29.7a

Means in the same column followed by the same letter are not significantly different, REGWQ ($P \leq 0.05$)

Decline in root length at 22 WAP may be attributed to the effect of pruning in November 1999; the slope of the curve was steeper in completely pruned trees compared to partially pruned trees.

In May 2000, 1 year after the pruning regime was imposed, and 16 WAP, more than 90% (2-year-old trees) or 75% (8-year-old trees) of fine roots were distributed to topsoil (Fig. 4). Partially pruned trees conserved more than 2–3 times more fine roots than completely pruned trees, a difference that was significant in 2-year-old trees but non-significant in 8-year-old trees.

Discussion

Pruned *E. poeppigiana* biomass

The results of this study clearly showed that partial pruning doubled total aboveground tree biomass output

over complete pruning. The average biomass of 8 Mg ha⁻¹ year⁻¹ from 2- to 8-year-old partially pruned trees is comparable to values reported by Kass et al. (1993) for *E. poeppigiana* when pruning intensity was complete and pruning frequency, half-yearly. The decline in pruned biomass at shorter regrowth periods even when a branch was retained, confirmed that regrowth periods longer than 16 weeks (Nygren 1995) are necessary to maintain the biomass productivity of *E. poeppigiana*. Unfavourable environmental conditions of high precipitation and low solar radiation may have contributed to low values for biomass harvested in January 2000. Recovery (increasing biomass) began during February–March when environmental conditions for growth were more favourable.

The development of about 75% of new shoot growth on the retained branch may support the hypothesis that branch autonomy for C uptake and export is independent of C needs of other developing

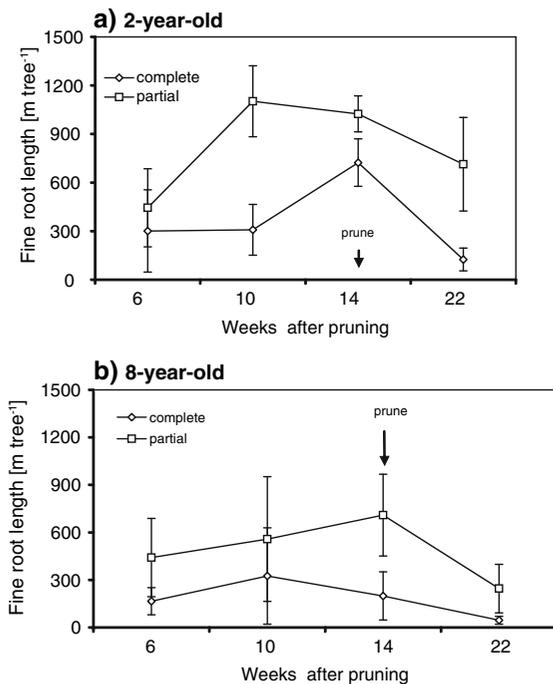


Fig. 3 Fine root length of *E. poeppigiana* in topsoil (0–20 cm) of (a) 2-year-old and (b) 8-year-old trees when pruned completely or partially, Turrialba, September 1999 to January 2000. Bars are standard errors

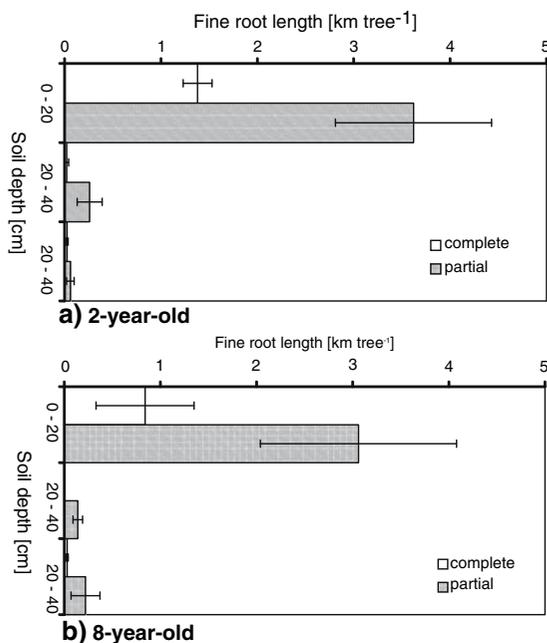


Fig. 4 Fine root length distribution of (a) 2-year and (b) 8-year old *E. poeppigiana* trees pruned after 16 weeks regrowth, May 2000. Bars are standard errors

shoots on the stem (Sprugel et al. 1991). New stem borne shoots may have met their C needs during resprouting from carbohydrate and nutrient reserves in the stem as observed in other species (Erdmann et al. 1993). Branch tissues in partially pruned trees were lignified at all regrowth periods, but branch tissue lignification in completely pruned trees did not occur until a minimum regrowth period of 4 months when a dry period occurred, further explaining the biomass difference.

N accumulation in pruned *E. poeppigiana* biomass

The accumulation of more N in partially pruned trees than in completely pruned trees may be attributed to both faster growth through branch autonomy for C and high activity NO_3^- reduction in the leaves of *E. poeppigiana* (Orebamjo et al. 1982; Muthuchelian 1993). In completely pruned trees, NO_3^- reduction may have initially taken place in roots, an energetically costly process (Marschner 1997) that may increase root and nodule turnover. Unfavourable environmental conditions of high precipitation and low solar radiation may have contributed to low values for N cycled in biomass harvested in January 2000.

Soil nitrogen dynamics

Mineralisation of organic matter is perhaps the main source of available inorganic N at the study site. The presence of microbially available C and N sources in the leaves of *E. poeppigiana* (Palm and Sanchez 1990, 1991) facilitated rapid net mineralisation of added material during the tomato vegetative phase and maintenance of high levels towards the end of tomato flowering phenophase. Mazzarino and colleagues (1993) found that after 9 years of alley cropping in Turrialba, soil C and N and microbial C and N were higher in *E. poeppigiana* alley crop plots compared to other treatments. They found that soil microbial biomass C was greatest during rapid crop growth and lowest at end of cropping period probably due to C cycling from root exudates and root mortality.

Given that the mineralisation of organic N controls the amount of N cycled in soil, higher soil $\text{NO}_3\text{-N}$ than $\text{NH}_4\text{-N}$ at the start of the rainy season in May

1999 indicates that substrate $\text{NH}_4\text{-N}$ for nitrification was not a limiting factor and that NH_4 pool was readily nitrified accounting for accumulation of NO_3 in the soil. Under low rainfall conditions, $\text{NO}_3\text{-N}$ can be used as an index of N availability for the Turrialba site. Veldkamp and colleagues (1999) made a similar observation for pasture and forest ecosystems in Costa Rica.

Lower nitrification rates during the high rainfall period in December, may be attributed to the adverse effect of environment on population and/or activity of nitrifying bacteria (Davidson et al. 1990). Also, much of the $\text{NO}_3\text{-N}$ might have been leached to lower soil depths. Under high rainfall conditions, total inorganic N may be used as an index of N availability at this site. Similar net N mineralisation and nitrification fluxes in both *E. poeppigiana*-amended and treeless soil suggest that the benefits of soil amendment were nullified by high rainfall. During the drier period in May, soil $\text{NO}_3\text{-N}$ concentration in treeless soil was one-half that in *E. poeppigiana*-amended soil.

Erythrina poeppigiana leaves decompose rapidly (Palm and Sanchez 1990, 1991) and release N even faster (Haggar et al. 1993), making it imperative that pruning management should reduce leaf: woody branch ratio if N loss under high rainfall conditions is to be reduced. In this study, partial pruning achieved this. Observations of tomato fine root distribution showed very superficial (soil depth 0–10 cm) rooting with very little horizontal spread beyond 20 cm from the base of the plant. Therefore, mid-season application of the pruned residue to the soil surface may put much of the mineralised N out of reach of tomato roots during the reproductive stage and increase potential for increased competition for nitrogen. Partially pruned trees with higher leaf biomass also had higher fine root lengths suggesting higher absorptive capacity for available N.

Fine root length dynamics of *E. poeppigiana*

Greater fine root length increases the capacity of a plant to absorb available soil N (Marschner 1997). Partial pruning, which retained some leaf area on the pruned stump, also maintained fine roots and nodules for uptake and transport (Chesney and Nygren 2002). Fine root length dynamics as affected by complete pruning approximated nodule dynamics reported by Nygren and Ramirez (1995). Partial pruning did not

change the pattern of fine root decrease after pruning and recovery at 10–14 WAP.

Frequent pruning did not result in redistribution of fine roots to greater soil depths although partially pruned 8-year-old trees had higher capacity for nutrient uptake at these depths. Superficial rooting pattern of *E. poeppigiana* may be related to better conditions for root growth in the topsoil than soil at greater depths. Topsoil had higher soil organic matter and exchangeable cations than greater soil depths (Table 1).

The retention of a branch on the pruned stump increased total aboveground biomass, N cycled in aboveground biomass, and more fine roots were conserved compared to complete removal of all shoots. The branch selected for retention should have a strong crotch to prevent breakage since most new shoots are formed on the retained branch. Frequent shoot pruning at intervals less than 16 weeks maintained the tree in perpetual renewal, and the regrowth strategy depended on the intensity of pruning. Completely pruned *E. poeppigiana* trees produced biomass with very little branch lignification, as well as fewer roots, resulting in reduced biomass production and lower recovery of internally cycled N. Partially pruned trees grew faster probably as a result of branch autonomy for C, in addition to stem borne shoot growth. More N was recovered, a process helped by higher fine root survival and production.

Per unit length of fine root (ratio of N content of pruned biomass to fine root length for November 1999, January and May 2000), older trees accumulated more N than younger trees and completely pruned trees than partially pruned trees. This observation shows that greater root length does not confer a greater advantage in terms of uptake and accumulation of N. However, partially pruned trees or juvenile trees may contribute more dry matter and nutrients to the soil organic matter pool through turnover, in addition to reducing loss of soil N. How much fine root biomass or fine root length density is required for efficient N cycling in pruned trees could not be answered from the results of this study.

On an *E. poeppigiana*-amended Eutric Cambisol in the humid tropics, the retention of a branch on the pruned tree stump (partial pruning) appears to be a good alternative to complete removal of shoots (complete pruning) for reducing N losses by cycling higher amounts of N in aboveground biomass, and for

conservation of fine root length for higher N uptake. Tomato crop N requirement during the reproductive phenophase may have to be supplemented by the use of external inputs.

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