



Communication

# Stem Carbon Dioxide Efflux of Lignophytes Exceeds That of Cycads and Arborescent Monocots

Thomas E. Marler

Western Pacific Tropical Research Center, University of Guam, Mangilao, GU 96923, USA; marler.uog@gmail.com

**Abstract:** Tree stem CO<sub>2</sub> efflux (Es) can be substantial and the factors controlling ecosystem-level Es are required to fully understand the carbon cycle and construct models that predict atmospheric CO<sub>2</sub> dynamics. The majority of Es studies used woody lignophyte trees as the model species. Applying these lignophyte data to represent all tree forms can be inaccurate. The Es of 318 arborescent species was quantified in a common garden setting and the results were sorted into four stem growth forms: cycads, palms, monocot trees that were not palms, and woody lignophyte trees. The woody trees were comprised of gymnosperm and eudicot species. The Es did not differ among the cycads, palms, and non-palm monocots. Lignophyte trees exhibited Es that was 40% greater than that of the other stem growth forms. The Es of lignophyte gymnosperm trees was similar to that of lignophyte eudicot trees. This extensive species survey indicates that the Es from lignophyte tree species do not align with the Es from other tree growth forms. Use of Es estimates from the literature can be inaccurate for understanding the carbon cycle in tropical forests, which contain numerous non-lignophyte tree species.

**Keywords:** conservation physiology; secondary cambium; stem respiration



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## 1. Introduction

The efflux of carbon dioxide (CO<sub>2</sub>) from tree stem surfaces (Es) has been extensively studied to answer various questions and more fully understand the global carbon cycle [1,2]. As with many aspects of biology research, the Es literature is biased toward one subset of biodiversity. Most case studies of tree Es have focused exclusively on lignophyte species with stems comprised mostly of wood constructed by true bifacial secondary cambium. This expansive literature contains only a few examples in which pachycaulous tree species with stems devoid of bifacial secondary cambium were represented [3–6].

A major contributor to Es is stem tissue respiration. However, numerous interacting factors coalesce to define Es in space and time. For example, CO<sub>2</sub> from root respiration can be transported to stems by way of xylem, and this CO<sub>2</sub> can exit xylem within stems to increase the Es above that of stem tissue respiration [7,8]. This transported CO<sub>2</sub> is under the influence of diel variations in sap flow [9,10]. The movement of CO<sub>2</sub> from the internal tissues to stem surfaces can also be under the control of temporal storage or re-fixation [11]. These and other interacting factors can cause the Es to be heavily influenced by CO<sub>2</sub> that was respired from tissues that are distant from the site of efflux [12].

A recent study designed to understand the diel patterns of Es for arborescent cycads, monocots, and lignophytes [6] included only six species of each growth form. Other studies that compared different stem tissue anatomy and its influence in Es were restricted to lignophyte species [13–15]. An extensive survey to compare the Es of trees with disparate stem growth forms has not been conducted to date in a single forest or garden. I hypothesized that Es from an extensive range of tree species would sort into significantly different groups, based on stem design. The objective of this study was to use the large living collection in a common garden setting to compare the Es of four growth forms used to design and construct tree stems.

## 2. Materials and Methods

This study was conducted at Nong Nooth Tropical Botanical Garden in Sattahip, Thailand. The location and characteristics of this living collection have been described [6]. The dates of measurements were 8–15 July 2019. In this setting and this time of year, the Es of non-lignophyte trees was not influenced by the time of day, but the lignophyte trees exhibited greater Es during midday [6]. Therefore, the measurements for this extensive species survey were restricted to the hours of 900–1500 h on each day of measurement.

A total of 99 cycad species were included (Table A1). There were 96 lignophyte species included (Table A2). The arborescent monocot species were separated into two groups. A total of 17 arborescent monocot taxa that were not palm species were included (Table A3). Finally, there were 106 palm species in the study (Table A4).

The Es was measured, as previously described [4–6]. Vigorous trees with no obvious wounds or decay on the stems were selected. A CIRAS EGM-4 analyzer fitted with a SRC-1 close system chamber (PP Systems, Amesbury, MA, USA) was used to quantify the Es from the stem surfaces. The chamber was secured using modeling clay as the sealant at a stem height of 30–40 cm above the root collar. The EGM-4 recorded the air temperature, and the chamber's increase in CO<sub>2</sub> concentration above ambient was quantified after a 2 min period. The change in CO<sub>2</sub> concentration was used to calculate the flux by dividing by area and time. Three periods of efflux were recorded at different radial locations for each sampling period for each tree.

The stem surface temperature was measured with an infrared thermometer (Milwaukee Model 2267-20, Milwaukee Tool, Brookfield, WI, USA). The relative humidity was determined with a sling psychrometer every hour during the periods of measurements. The stem diameter at the height of measurements and total stem height were measured for each tree.

Two sampling periods were applied to each species. For taxa with more than one large tree, this included two trees. For taxa with a single large tree, the two samples were from the same tree but separated by at least three days. The data were sorted according to four stem growth forms: cycad species, palm species, arborescent non-palm monocot species, and lignophyte species. The data were subjected to ANOVA using the PROC MIXED model (SAS Institute, Cary, NC, USA) with unequal replications. There were 636 observations in the data set, two per species. The two observations were treated as subsamples in the analysis. The means separation was conducted by Tukey's HSD test.

## 3. Results and Discussion

The cycad trees were represented by 53 Cycadaceae and 46 Zamiaceae species (Table A1). The stem circumference ranged from 51–169 cm with a mean of 96 cm. The mean stem temperature was 31.8 °C and the concomitant mean air temperature was 32.6 °C. Individual Es measurements ranged from 0.5–6.2 µmol·m<sup>-2</sup>·s<sup>-1</sup>. The lignophyte trees were represented by 34 families (Table A2). The stem circumference ranged from 51–156 cm with a mean of 84 cm. The mean stem temperature was 31.3 °C and concomitant mean air temperature was 32.0 °C. Individual Es measurements ranged from 0.2–7.6 µmol·m<sup>-2</sup>·s<sup>-1</sup>. The monocot trees that were not palm species were represented by five families (Table A3). The stem circumference ranged from 51–175 cm with a mean of 82 cm. The mean stem temperature was 31.5 °C and the concomitant mean air temperature was 32.1 °C. The individual Es measurements range from 0.8–4.7 µmol·m<sup>-2</sup>·s<sup>-1</sup>. The palm species representing the Arecaceae family exhibited a stem circumference ranging from 48–182 cm with a mean of 71 cm (Table A4). The mean stem temperature was 31.7 °C and the concomitant mean air temperature was 32.4 °C. The individual Es measurements ranged from 0.7–7.5 µmol·m<sup>-2</sup>·s<sup>-1</sup>. The relative humidity ranged from 56% to 69% and did not change substantially among the hours and dates of the study.

The stem CO<sub>2</sub> efflux differed among the four stem growth forms ( $F_{3,314} = 10.64$ ,  $p < 0.001$ ). The means separated into two groups, with the lignophyte species exhibiting greater Es than the other three stem growth forms (Table 1). The lignophyte trees exhibited

$E_s$  that was 40% greater than the mean of the other growth forms. No differences in the  $E_s$  occurred among the cycad, palm, and non-palm monocot stem forms.

**Table 1.** Stem carbon dioxide efflux ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) of arborescent species as influenced by the stem growth form.

Stem Growth Form	n	Efflux
Lignophyte <sup>1</sup>	96	$3.421 \pm 0.140$ a <sup>2</sup>
Palm	106	$2.593 \pm 0.133$ b
Cycad	99	$2.415 \pm 0.138$ b
Monocot (non-palm)	17	$2.321 \pm 0.332$ b

<sup>1</sup> The lignophyte species were eudicot and gymnosperm trees that produce true wood from secondary bifacial vascular cambium. <sup>2</sup> Growth form with the same letter not different according to Tukey's HSD test.

Cycads and monocot trees often produce thick primary growth constructed by a primary thickening meristem, and do not possess bifacial secondary cambium to increase stem diameter at distances away from the stem tip [16–22]. For all of these trees, the peripheral tissues are ground tissue with vascular tissues embedded closer to the stem center. One of the factors that influences  $\text{CO}_2$  efflux from a stem surface is the diffusion and conductance constraints imposed by tissues that are peripheral to tissues that serve as the greatest internal source of  $\text{CO}_2$ , such as sap flow in xylem [23]. The substantial radial distance of xylem tissues and other major sources of  $\text{CO}_2$  from the stem surface of these pachycaulous trees can account for the greater mean  $E_s$  for lignophyte trees, which has been shown herein.

Considering the prominence of these pachycaulous trees in tropical forests, the historical exclusion of them from  $E_s$  studies is unfortunate. Indeed, the  $\text{CO}_2$  derived from stem efflux can represent up to 40% of the  $\text{CO}_2$  contributed to by vegetation [1,24]. This survey, represented by 222 pachycaulous tree species, confirms the earlier findings based on a limited number of species [6], and indicates that attempts to use the  $E_s$  literature based on the lignophyte species can over-estimate the  $E_s$  in regions that are represented by these tree species.

Cycads comprise the most threatened contemporary plant group [25]. Conservation physiology has emerged as a critical component of the suite of conservation strategies, because an understanding of the physiological responses of threatened organisms to their escalating biotic and abiotic threats is required for successful species recovery [26,27]. For federally listed endangered cycad species in the United States, such as *Cycas micronesica* K.D. Hill (see Table A1), understanding the physiology of the taxa is crucial for developing effective federal recovery plans [28]. Clearly, the pursuit of more cycad physiology studies will advance the nascent discipline of conservation physiology.

Future research on the  $E_s$  of cycad and monocot trees will be required to fully understand the reasons that mean  $E_s$  is less than the mean  $E_s$  of lignophyte trees. The design of cycad stems is fairly homogeneous, with vascular cylinders inserted between the persistent living pith and cortex [29]. The design of palm stems is also fairly homogeneous with vascular bundles scattered through the ground tissue [19,22]. However, the design of the non-palm arborescent monocot tree stems is heterogeneous among the families. A closer look at this group of pachycaulous species can yield interesting findings about what endogenous factors mostly control the  $E_s$  of these non-lignophyte trees.

In conclusion, the many factors that interact to control the magnitude of  $\text{CO}_2$  efflux from tree stem surfaces are differentially expressed among various tree stem designs. The results herein suggest that the traits of stem peripheral tissues can be among the defining factors that cause the differences in  $E_s$  among various tree growth forms.

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## Appendix A

**Table A1.** List of cycad species included in the carbon dioxide efflux study. Circ = circumference, Air T = air temperature, and Stem T = surface temperature of stems.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Ceratozamia delucana</i> Vázq.Torres, A.Moretti and Carvajal-Hern.	Zamiaceae	84	32	32.9	2.6222	2.3290
<i>Ceratozamia latifolia</i> Miq.	Zamiaceae	72	31	32.9	2.3227	2.0197
<i>Ceratozamia robusta</i> Miq.	Zamiaceae	112	31	33.1	2.2501	1.9566
<i>Cycas angulata</i> R.Br.	Cycadaceae	107	32	32.8	5.7745	5.1166
<i>Cycas apoa</i> K.D.Hill	Cycadaceae	76	33	32.5	4.8633	4.2288
<i>Cycas badensis</i> K.D.Hill	Cycadaceae	82	32	31.1	1.7512	1.5148
<i>Cycas beddomei</i> Dyer	Cycadaceae	78	33	31.7	1.7819	1.5508
<i>Cycas bougainvilleana</i> K.D.Hill	Cycadaceae	65	32	31.1	4.1522	3.6103
<i>Cycas cairnsiana</i> F.Muell.	Cycadaceae	101	31	31.4	2.0749	1.8051
<i>Cycas campestris</i> K.D.Hill	Cycadaceae	93	32	30.4	2.4442	2.1251
<i>Cycas chamaoensis</i> K.D.Hill	Cycadaceae	101	32	31.8	1.8463	1.5969
<i>Cycas changjiangensis</i> N.Liu	Cycadaceae	81	33	31.7	1.0225	2.2722
<i>Cycas clivicola</i> K.D.Hill	Cycadaceae	87	33	31.7	2.0377	1.7805
<i>Cycas couttsiana</i> K.D.Hill	Cycadaceae	95	33	32.1	0.9089	1.1361
<i>Cycas curranii</i> (J.Schust.) K.D.Hill	Cycadaceae	103	32	30.1	5.1493	4.4800
<i>Cycas debaoensis</i> Y.C.Zhong and C.J.Chen	Cycadaceae	110	32	30.9	1.5203	1.3191
<i>Cycas diannanensis</i> Z.T.Guan and G.D.Tao	Cycadaceae	84	33	32.1	5.6678	4.9231
<i>Cycas edentata</i> de Laub.	Cycadaceae	68	32	29.8	1.9212	1.6663
<i>Cycas elongata</i> (Leandri) D.Y.Wang	Cycadaceae	103	32	31.9	2.1460	1.7042
<i>Cycas falcata</i> K.D.Hill	Cycadaceae	89	33	31.8	2.8403	1.4517
<i>Cycas furfuracea</i> W.Fitzg.	Cycadaceae	108	34	34.5	2.5564	2.2217
<i>Cycas glauca</i> Miq.	Cycadaceae	92	33	32.2	4.0045	3.5346
<i>Cycas hainanensis</i> C.J.Chen ex C.Y.Cheng, W.C.Cheng and L.K.Fu	Cycadaceae	91	33	31.4	2.5496	2.2217
<i>Cycas hongheensis</i> S.Y.Yang and S.L.Yang	Cycadaceae	82	32	30.8	2.2847	2.1165
<i>Cycas inermis</i> Lour.	Cycadaceae	109	33	32.1	6.1934	5.4154
<i>Cycas javana</i> (Miq.) de Laub.	Cycadaceae	112	33	32.7	2.7945	2.4300
<i>Cycas macrocarpa</i> Griff.	Cycadaceae	75	31	31.2	4.1164	3.6103
<i>Cycas media</i> R.Br.	Cycadaceae	82	33	31.9	2.1964	1.8996
<i>Cycas megacarpa</i> K.D.Hill	Cycadaceae	62	33	31.8	2.1114	1.8380
<i>Cycas micronesica</i> K.D.Hill	Cycadaceae	62	33	32.5	1.3764	1.1992
<i>Cycas natherstii</i> J.Schust.	Cycadaceae	102	32	31.9	1.7446	1.5148
<i>Cycas nongnoochiae</i> K.D.Hill	Cycadaceae	88	33	31.9	2.9513	2.5689
<i>Cycas ophiolitica</i> K.D.Hill	Cycadaceae	115	33	32.1	1.1846	1.0225
<i>Cycas pachypoda</i> K.D.Hill	Cycadaceae	98	32	30.8	4.4112	3.8482
<i>Cycas papuana</i> F.Muell.	Cycadaceae	86	31	30.7	5.3312	4.6517
<i>Cycas pectinata</i> Buch.-Ham.	Cycadaceae	93	32	33.4	2.0547	1.7805
<i>Cycas petrae</i> A.Lindstr. and K.D.Hill	Cycadaceae	69	33	32.1	1.7965	2.3353
<i>Cycas platyphylla</i> K.D.Hill	Cycadaceae	116	33	31.7	0.6817	1.5905
<i>Cycas pranburiensis</i> Yang, Tang, Hill and Vatcharakorn	Cycadaceae	78	33	32.5	1.5115	1.3210
<i>Cycas revoluta</i> Thunb.	Cycadaceae	85	32	32.8	2.2223	1.9314

**Table A1.** Cont.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Cycas riuminiana</i> Porte ex Regel	Cycadaceae	65	33	33.1	3.7784	3.2821
<i>Cycas rumphii</i> Miq.	Cycadaceae	84	30	32.1	4.0561	3.5346
<i>Cycas seemannii</i> A.Br.	Cycadaceae	63	32	31.1	3.0296	2.1523
<i>Cycas semota</i> K.D.Hill	Cycadaceae	84	33	30.2	3.4865	3.0296
<i>Cycas shanyaensis</i> G.A.Fu	Cycadaceae	68	32	32.1	2.4690	3.0296
<i>Cycas siamensis</i> Miq.	Cycadaceae	79	32	31.9	3.4431	2.9867
<i>Cycas silvestris</i> K.D.Hill	Cycadaceae	69	33	32.2	1.6679	1.4517
<i>Cycas sphaerica</i> Roxb.	Cycadaceae	92	32	30.4	3.4155	2.9867
<i>Cycas taitungensis</i> Shen, Hill, Tsou and Chen	Cycadaceae	83	32	31.8	4.4478	3.8880
<i>Cycas tansachana</i> K.D.Hill and S.L.Yang	Cycadaceae	113	33	31.8	1.1864	1.0099
<i>Cycas thouarsii</i> R.Br.	Cycadaceae	82	31	30.9	1.1968	1.0225
<i>Cycas tropophylla</i> K.D.Hill and P.K.Lôc	Cycadaceae	94	33	32.1	2.0312	1.7673
<i>Cycas tuckeri</i> K.D.Hill	Cycadaceae	95	32	30.8	1.7157	1.4933
<i>Cycas wadei</i> Merr.	Cycadaceae	83	32	31.3	2.1113	1.8380
<i>Cycas yorkiana</i> K.D.Hill	Cycadaceae	94	33	32.1	2.1564	1.8746
<i>Cycas zeylanica</i> (J.Schust.) A.Lindstr. and K.D.Hill	Cycadaceae	78	33	30.8	2.3312	2.0103
<i>Dioon argenteum</i> Gregory, Chemnick, Salas-Morales and Vovides	Zamiaceae	93	33	31.1	4.9455	4.4308
<i>Dioon caputoi</i> De Luca, Sabato and Vázq.Torres	Zamiaceae	91	32	34.8	2.4857	2.1523
<i>Dioon edule</i> Lindl.	Zamiaceae	155	32	33.1	3.7795	3.2821
<i>Dioon mejiae</i> Standl. and L.O. Williams	Zamiaceae	98	33	31.6	1.9594	1.7042
<i>Dioon merolae</i> De Luca, Sabato and Vázq.Torres	Zamiaceae	110	32	32.7	4.9132	4.2920
<i>Dioon spinulosum</i> Dyer ex Eichl.	Zamiaceae	91	33	32.2	2.2561	1.9566
<i>Encephalartos aemulans</i> Vorster	Zamiaceae	138	33	31.9	4.4466	3.9976
<i>Encephalartos altensteinii</i> Lehm.	Zamiaceae	116	34	32.2	2.2504	2.4679
<i>Encephalartos arenarius</i> R.A.Dyer	Zamiaceae	97	33	32.2	1.4495	1.5905
<i>Encephalartos bubalinus</i> Melville	Zamiaceae	125	33	31.7	1.0569	1.1614
<i>Encephalartos chimanmaniensis</i> R.A.Dyer and I.Verd.	Zamiaceae	121	33	31.8	1.5948	1.7420
<i>Encephalartos concinnus</i> R.A.Dyer and Verdoorn	Zamiaceae	114	33	32.1	4.9765	5.4465
<i>Encephalartos dyerianus</i> Lavranos and D.L.Goode	Zamiaceae	124	34	32.9	3.5004	3.8501
<i>Encephalartos equatorialis</i> P.J.H.Hurter	Zamiaceae	127	34	32.9	1.7764	1.9314
<i>Encephalartos eugene-maraisii</i> Verd.	Zamiaceae	116	33	32.1	2.2465	2.4679
<i>Encephalartos inopinus</i> R.A.Dyer	Zamiaceae	121	34	32.2	2.3611	2.5878
<i>Encephalartos lebomboensis</i> I.Verd.	Zamiaceae	97	33	32.3	1.6564	1.8146
<i>Encephalartos mackenziei</i> L.E.Newton	Zamiaceae	111	33	32.2	0.8645	0.9089
<i>Encephalartos macrostrobilus</i> S.Jones and Wyants	Zamiaceae	125	34	32.8	1.7946	1.9566
<i>Encephalartos manikensis</i> (Gilliland) Gilliland	Zamiaceae	133	33	31.7	1.5946	1.7420
<i>Encephalartos msinganus</i> Vorster	Zamiaceae	108	33	32.1	2.9764	3.2663
<i>Encephalartos murchii</i> R.A.Dyer and I.Verd.	Zamiaceae	134	33	32.2	2.3331	2.5562
<i>Encephalartos natalensis</i> R.A.Dyer and I.Verd.	Zamiaceae	109	34	32.9	1.1915	1.3065
<i>Encephalartos paucidentatus</i> Stapf and Burtt Davy	Zamiaceae	120	33	32.5	1.7764	1.9314
<i>Encephalartos princeps</i> R.A.Dyer	Zamiaceae	113	33	32.8	2.0645	1.8947
<i>Encephalartos pterogonus</i> R.A.Dyer and I.Verd.	Zamiaceae	119	33	33.1	2.4465	2.6986
<i>Encephalartos sclavoi</i> De Luca, D.W.Stev. and A.Moretti	Zamiaceae	101	33	32.1	1.5959	1.7420
<i>Encephalartos senticosus</i> Vorster	Zamiaceae	107	32	30.9	0.8465	0.8710
<i>Encephalartos septentrionalis</i> Schweinf.	Zamiaceae	119	34	32.9	1.6694	3.7239
<i>Encephalartos tegulaneus</i> Melville	Zamiaceae	124	33	32.1	3.6915	4.0647
<i>Encephalartos transvenosus</i> Stapf and Burtt Davy	Zamiaceae	128	33	31.2	4.5121	4.9357
<i>Encephalartos whitelockii</i> P.J.H.Hurter	Zamiaceae	163	32	31.1	2.7154	2.9865
<i>Lepidozamia hopei</i> (W.Hill) Regel	Zamiaceae	64	32	29.1	1.4896	1.2623
<i>Lepidozamia peroffskyana</i> Regel	Zamiaceae	92	32	33.8	1.6765	1.8304

**Table A1.** Cont.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Macrozamia moorei</i> F.Muell.	Zamiaceae	169	32	32.7	1.8686	1.6663
<i>Microcycas calocoma</i> (Miq.) A.DC.	Zamiaceae	91	32	32.1	2.0644	1.8304
<i>Zamia elegantissima</i> Schutzman, Vovides and R.S.Adams	Zamiaceae	51	33	30.9	1.3312	1.4517
<i>Zamia furfuracea</i> L.f.	Zamiaceae	91	33	32.1	1.7154	1.8746
<i>Zamia gentryi</i> Dodson	Zamiaceae	63	33	30.5	2.0105	2.1999
<i>Zamia imperialis</i> A.S.Taylor, J.L.Haynes and Holzman	Zamiaceae	59	32	31.1	1.3866	1.5148
<i>Zamia lindenii</i> Regel ex André	Zamiaceae	78	30	29.9	2.0166	2.1998
<i>Zamia obliqua</i> A.Braun	Zamiaceae	51	32	30.2	2.7626	2.9965
<i>Zamia skinneri</i> Warsc.	Zamiaceae	58	32	30.2	2.3465	2.5765

**Table A2.** List of the lignophyte species included in the carbon dioxide efflux study. Circ = circumference, Air T = air temperature, and Stem T = surface temperature of stems.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Acacia auriculiformis</i> A.Cunn. Ex Benth.	Fabaceae	92	32	29.3	3.5566	3.7944
<i>Adansonia digitata</i> L.	Malvaceae	71	31	31.4	3.9465	3.5346
<i>Adansonia madagascariensis</i> Baill.	Malvaceae	69	33	32.3	2.0566	1.8304
<i>Afrocarpus gracilior</i> (Pilg.) C.N. Page	Podocarpaceae	72	32	31.3	6.4465	6.3748
<i>Agathis dammara</i> (Lamb.) Rich.	Araucariaceae	85	33	32.2	2.3465	2.5698
<i>Agathis moorei</i> (Lind.) Mast.	Araucariaceae	52	33	30.9	1.3255	1.8304
<i>Agathis robusta</i> (C.Moore ex F.Muell.) Bailey	Araucariaceae	55	32	30.9	1.7198	1.8935
<i>Albizia saman</i> (Jacq.) Merr.	Fabaceae	156	32	30.6	1.2765	1.3886
<i>Amherstia nobilis</i> Wall.	Fabaceae	68	32	31.4	2.1894	1.9566
<i>Annona squamosa</i> L.	Annonaceae	62	31	30.8	1.6768	1.8746
<i>Araucaria bidwillii</i> Hook.	Araucariaceae	91	32	31.2	5.0032	4.4813
<i>Araucaria columnaris</i> J.R.Forst. Hook	Araucariaceae	69	30	30.2	6.2264	5.6237
<i>Araucaria cunninghamii</i> Mudie	Araucariaceae	58	31	29.4	2.3631	2.0829
<i>Araucaria heterophylla</i> (Salisb.) Franco	Araucariaceae	96	32	33.2	2.8403	2.7771
<i>Araucaria luxurians</i> (Brongn. and Grisb.) de Laub.	Araucariaceae	64	31	30.1	6.0021	5.4281
<i>Araucaria montana</i> Brong. and Gris	Araucariaceae	54	32	31.8	2.9034	2.6643
<i>Araucaria nemorosa</i> de Laub.	Araucariaceae	93	33	31.8	2.0829	2.0197
<i>Artocarpus altilis</i> (Parkinson) Fosberg	Moraceae	88	33	32.1	3.6625	3.9986
<i>Artocarpus heterophyllus</i> Lam.	Moraceae	74	31	30.8	2.4689	2.7140
<i>Averrhoa bilimbi</i> L.	Oxalidaceae	72	33	32.3	4.2165	4.6647
<i>Averrhoa carambola</i> L.	Oxalidaceae	69	31	30.1	4.4465	3.9865
<i>Bougainvillea</i> sp. Comm. Ex Juss.	Nyctaginaceae	51	33	32.1	1.9955	2.1133
<i>Brachychiton acerifolius</i> (A.Cunn ex G.Don) F.Muell.	Malvaceae	53	31	31.7	2.2566	2.0134
<i>Brachychiton rupestris</i> (T.Mitch. Ex Lindl.) K.Schum.	Malvaceae	54	30	30.3	4.4656	4.0269
<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae	51	32	30.8	0.8119	0.9026
<i>Callistemon viminalis</i> (Sol. Ex Gaertn.) G.Don	Myrtaceae	77	30	30.7	6.0022	5.4154
<i>Callistriis baileyi</i> C.T. White	Cupressaceae	59	31	30.8	2.6644	2.3984
<i>Calophyllum sil</i> Lauterb.	Clusiaceae	103	30	30.9	3.3186	3.0107
<i>Cananga odorata</i> (Lam.) Hook.f. and Thomson	Annonaceae	121	32	31.1	4.4212	4.8766
<i>Casuarina equisetifolia</i> L.	Casuarinaceae	102	33	33.4	3.5564	3.8965
<i>Cavanillesia hylotelephitton</i> Ulbr.	Malvaceae	111	33	32.8	2.8845	2.5562
<i>Cecropia obtusifolia</i> Bertol.	Urticaceae	88	31	30.3	5.1114	4.6012
<i>Cecropia peltata</i> L.	Urticaceae	113	32	31.6	3.6266	3.2265
<i>Ceiba pentandra</i> (L.) Gaertn.	Malvaceae	123	33	31.9	4.3489	3.9196
<i>Clusia rosea</i> Jacq.	Clusiaceae	61	33	31.3	3.1153	3.5642
<i>Delonix decaryi</i> (R.Vig.) Capuron	Fabaceae	82	32	31.7	1.3349	1.1992

**Table A2.** Cont.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Delonix regia</i> (Hook.) Raf.	Fabaceae	72	32	31.2	3.6644	3.2947
<i>Dimocarpus longan</i> Lour.	Sapindaceae	126	33	32.3	2.8844	2.5649
<i>Diospyros discolor</i> Willd.	Ebenaceae	129	33	31.7	0.5116	0.4418
<i>Diospyros nigra</i> (J.F.Gmel.) Perrier	Ebenaceae	99	30	28.9	4.1445	4.5444
<i>Elaeocarpus hygrophilus</i> Kurz	Elaeocarpaceae	53	31	30.8	3.9787	3.5699
<i>Euphorbia kamponii</i> Rauh and Petignat	Euphorbiaceae	53	33	33.2	1.1899	1.3065
<i>Euphorbia laeta</i> Aiton	Euphorbiaceae	81	34	33.5	4.8011	4.2920
<i>Fernandoa madagascariensis</i> (Baker) A.H.Gentry	Bignoniaceae	51	31	30.3	2.0645	1.8304
<i>Ficus benjamina</i> L.	Moraceae	151	30	29.8	3.2233	2.9034
<i>Ficus elastica</i> Roxb. ex Hornem.	Moraceae	94	33	32.2	3.6151	3.2663
<i>Ficus lyrata</i> Warb.	Moraceae	104	32	31.4	6.1184	5.8793
<i>Ficus natalensis</i> Hochst.	Moraceae	56	31	29.8	5.6112	5.0083
<i>Garcinia cymosa</i> (K.Schum.) I.M.Turner and P.F.Stevens	Clusiaceae	64	32	31.3	3.2311	2.9760
<i>Guaiacum officinale</i> L.	Zygophyllaceae	74	32	30.5	4.3365	3.8956
<i>Inga edulis</i> Mart.	Fabaceae	64	33	32.2	1.0848	0.9650
<i>Kopsia arborea</i> Blume	Apocynaceae	78	31	30.8	1.1323	0.9976
<i>Lagerstroemia indica</i> L.	Lythraceae	66	33	31.9	5.7112	5.1125
<i>Lagerstroemia speciosa</i> (L.) Pers.	Lythraceae	78	33	32.1	6.3054	5.6616
<i>Leucaena leucocephala</i> (Lam.) de Wit	Fabaceae	51	32	30.8	2.0202	2.2091
<i>Litsea elliptica</i> Blume	Lauraceae	62	32	31.3	2.1132	1.8935
<i>Magnolia × alba</i> (D.C.) Figlar	Magnoliaceae	145	32	31.8	1.6650	1.5148
<i>Mallotus barbatus</i> Müll.Arg.	Euphorbiaceae	82	30	30.3	5.7765	5.1347
<i>Mangifera foetida</i> Lour.	Anacardiaceae	57	33	33.4	7.4986	6.9429
<i>Mangifera indica</i> L.	Anacardiaceae	61	33	33.5	4.0065	3.5847
<i>Melaleuca bracteata</i> F. Muell.	Myrtaceae	96	31	30.2	1.0065	1.4466
<i>Morinda citrifolia</i> L.	Rubiaceae	61	30	30.7	1.3389	1.4678
<i>Moringa hildebrandtii</i> Eng.	Moringaceae	82	32	31.2	4.1132	3.6608
<i>Moringa oleifera</i> Lam.	Moringaceae	75	33	32.1	0.2211	0.1894
<i>Muntingia calabura</i> L.	Muntingiaceae	66	32	31.1	1.5644	1.3886
<i>Nephelium lappaceum</i> L.	Sapindaceae	128	33	32.3	1.8686	1.6663
<i>Nerium oleander</i> L.	Apocynaceae	52	32	30.8	1.2234	1.1321
<i>Pachira aquatica</i> Aub.	Malvaceae	105	33	32.1	2.0044	1.7988
<i>Pachira insignis</i> (Sw.) Savigny	Malvaceae	95	30	30.6	5.2123	5.8068
<i>Persea americana</i> Mill.	Lauraceae	126	33	32.5	1.5590	1.3232
<i>Phyllanthus acidus</i> (L.) Skeels	Phyllanthaceae	86	32	31.1	1.4391	1.5565
<i>Pithecellobium dulce</i> (Roxb.) Benth.	Fabaceae	96	32	31.8	1.6265	1.4517
<i>Plumeria rubra</i> L.	Apocynaceae	73	33	31.6	5.3795	5.9764
<i>Podocarpus nerifolius</i> D.Don	Podocarpaceae	85	30	29.8	4.3035	4.7965
<i>Polyalthia longifolia</i> (Sonn.) Thwaites	Annonaceae	93	33	32.1	3.1138	2.7105
<i>Pouteria campechiana</i> (Kunth.) Baehni	Sapotaceae	138	32	30.7	1.1133	2.0197
<i>Pseudobombax septenatum</i> (Jacq.) Dugand	Malvaceae	66	31	30.7	0.9922	0.8836
<i>Psidium guajava</i> L.	Myrtaceae	52	30	30.8	4.9597	5.5416
<i>Robinia hispida</i> L.	Fabaceae	66	33	31.8	2.4465	2.2247
<i>Sandoricum koetjape</i> (Burm.f.) Merr.	Meliaceae	141	33	32.1	1.9322	1.7042
<i>Saraca asoca</i> (Roxb.) Willd.	Fabaceae	72	31	30.3	4.1645	4.5679
<i>Saraca declinata</i> Miq.	Fabaceae	75	32	30.1	3.0111	3.3452
<i>Saraca thaipingensis</i> Prain	Fabaceae	89	31	30.7	1.0946	1.1992
<i>Schizolobium parahyba</i> (Vill.) S.F.Blake	Fabaceae	91	32	31.1	0.9955	0.8836
<i>Senegalnia polyacantha</i> (Willd.) Siegler and Ebinger	Fabaceae	81	33	31.8	3.7989	4.2265
<i>Sterculia foetida</i> L.	Malvaceae	141	33	32.4	3.4844	3.8877
<i>Syzygium cumini</i> (L.) Skeels	Myrtaceae	151	32	30.2	4.6075	3.9764
<i>Syzygium forte</i> (F.Muell.) B.Hyland	Myrtaceae	113	31	31.5	1.2134	1.3255
<i>Syzygium malaccense</i> (L.) Merr. and L.M.Perry	Myrtaceae	91	33	31.8	2.2233	2.4616

**Table A2.** Cont.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Tamarindus indica</i> L.	Fabaceae	119	33	32.2	6.6644	7.5740
<i>Tecoma stans</i> Griseb.	Bignoniaceae	61	33	31.9	2.1645	2.3984
<i>Tectona grandis</i> L.f.	Lamiaceae	65	33	32.2	0.6566	0.6943
<i>Terminalia catappa</i> L.	Combretaceae	53	30	30.5	2.4844	2.7771
<i>Terminalia ivorensis</i> A.Chev.	Combretaceae	69	33	31.9	3.5467	3.9865
<i>Triplaris americana</i> L.	Polygonaceae	97	32	31.1	2.5546	2.8403
<i>Xanthostemon chrysanthus</i> (F.Muell.) Benth.	Xanthorrhoeaceae	96	33	32.2	3.6134	4.0395

**Table A3.** List of non-palm arborescent monocot species included the in carbon dioxide efflux study. Circ = circumference, Air T = air temperature, and Stem T = surface temperature of stems.

Species	Family	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Beaucarnea recurvata</i> Lem.	Asparagaceae	84	31	30.2	3.1848	2.8466
<i>Dasyliion wheeleri</i> S.Watson ex Rothr.	Asparagaceae	99	33	32.6	4.4489	4.0032
<i>Dracaena cochinchinensis</i> (Lour.) S.C.Chen	Asparagaceae	117	32	31.5	2.9441	2.6509
<i>Dracaena dereminis</i> Engl.	Asparagaceae	58	33	32.5	1.2234	1.0730
<i>Dracaena floribunda</i> Baker	Asparagaceae	101	33	32.2	2.0498	1.8304
<i>Dracaena fragrans</i> (L.) Ker Gaw.	Asparagaceae	66	33	32.1	3.4899	3.0927
<i>Ensete ventricosum</i> (Welw.) Cheesman	Musaceae	175	33	31.8	4.7003	4.2099
<i>Musa x paradisiaca</i> L.	Musaceae	75	31	30.5	2.4468	2.6798
<i>Pandanus dubius</i> Spreng.	Pandanaceae	73	32	31.7	3.5564	3.9888
<i>Pandanus rabaiensis</i> Rendle.	Pandanaceae	64	33	32.1	3.9166	3.4714
<i>Pandanus tectorius</i> Parkinson ex Du Roi	Pandanaceae	71	31	31.2	3.0865	3.4470
<i>Pandanus utilis</i> Bory	Pandanaceae	58	32	31.8	0.7658	0.8205
<i>Pandanus vandermeeschii</i> Balf.f.	Pandanaceae	68	31	30.3	3.8465	4.2920
<i>Pandanus veitchii</i> Mast.	Pandanaceae	72	33	32.2	2.1779	2.3984
<i>Ravenala madagascariensis</i> Sonn.	Strelitziaceae	85	31	30.6	1.0044	0.9468
<i>Strelitzia alba</i> (L.f.) Skeels	Strelitziaceae	51	32	31.1	3.5668	4.0547
<i>Xanthorrhoea glauca</i> D.J.Bedford	Xanthorrhoeaceae	78	31	31.5	1.4465	1.5779

**Table A4.** List of the Arecaceae species included in the carbon dioxide efflux study. Circ = circumference, Air T = air temperature, and Stem T = surface temperature of stems.

Species	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Adonidia merrillii</i> (Becc.) Becc.	66	33	31.9	1.4868	1.3255
<i>Aiphanes minima</i> (Gaertn.) Burret	53	33	31.8	3.3622	3.6797
<i>Allagoptera caudescens</i> (Mart.) Kuntze	52	32	30.8	1.6623	1.8051
<i>Archontophoenix myolensis</i> Dowe	87	31	32.8	2.4465	2.1460
<i>Archontophoenix purpurea</i> Hodel and Dowe	51	32	31.2	4.1657	3.6645
<i>Areca catechu</i> L.	59	32	31.8	1.8165	2.0134
<i>Areca macrocarpa</i> Becc.	61	33	32.1	3.7799	4.3046
<i>Areca parens</i> Becc.	59	33	33.9	3.2136	3.5649
<i>Astrocaryum mexicanum</i> Leibm. Ex Mart.	51	32	31.1	2.5644	2.2722
<i>Beccariophoenix alfredii</i> Rakotoarin., Ranariv. and J.Dransf.	182	33	32.9	1.1165	0.9864
<i>Beccariophoenix madagascariensis</i> Jum. and H.Perrier	103	32	31.2	3.6645	4.0031
<i>Bentinckia nicobarica</i> (Kurz.) Becc.	65	32	31.8	3.1619	3.4466
<i>Borassodendron machadonis</i> Becc.	127	33	31.2	2.8645	3.1165
<i>Brassiophoenix schumannii</i> (Becc.) Essig	52	33	32.1	1.7115	1.5274
<i>Burretokentia dumasi</i> Pintaud and Hodel	51	32	31.1	2.7654	3.0031
<i>Burretokentia grandiflora</i> Pintaud and Hodel	52	32	31.7	4.2958	4.7799
<i>Burretokentia vieillardii</i> (Brongn. and Gris) Pic.Serm.	51	33	31.9	0.8286	0.8898

**Table A4.** Cont.

Species	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Calyptrocalyx spicatus</i> (Lam.) Blume	52	34	32.9	1.2989	1.1361
<i>Calyptronoma rivalis</i> (O.F.Cook) L.H.Bailey	66	33	31.7	2.6798	2.9765
<i>Carpentaria acuminata</i> (H.Wendl. and Drude) Becc.	52	33	32.2	2.2722	1.7042
<i>Carpoxylon macrospermum</i> H.Wendl. and Drude	67	32	30.9	0.9346	0.9979
<i>Caryota ophiopellis</i> Dowe	81	32	31.1	3.9966	4.9643
<i>Chambeyronia macrocarpa</i> (Brongn.) Vieill. Ex Becc.	51	33	32.1	1.8879	1.6410
<i>Chelyocarpus chuco</i> (Mart.) H.E.Moore	51	32	31.1	3.6626	4.0033
<i>Chelyocarpus ulei</i> Dammer	51	33	31.8	4.7474	5.2646
<i>Clinostigma ponapense</i> (Becc.) H.E.Moore and Fosberg	62	33	32.1	3.6264	3.9986
<i>Clinostigma samoense</i> H.Wendl.	68	33	31.8	4.8946	5.3970
<i>Cocos nucifera</i> L.	105	32	31.4	3.7764	4.1133
<i>Colpothrinax wrightii</i> Griseb. and H.Wendl. ex Voss	101	33	32.2	1.8445	1.6474
<i>Copernicia baileyana</i> León	162	32	31.5	0.9631	0.9987
<i>Copernicia hospita</i> Mart.	61	31	30.3	3.0844	3.4125
<i>Copernicia prunifera</i> (Mill.) H.E.Moore	64	33	32.1	4.9497	5.4895
<i>Copernicia</i> sp. Mart. ex Endl.	68	32	31.6	1.3346	1.4653
<i>Corypha utan</i> Lam.	105	33	32.1	3.0888	3.4102
<i>Cryosophila warscewiczii</i> (H.Wendl.) Bartlett	61	33	31.9	4.0054	3.6103
<i>Cryosophila williamsii</i> P.H.Allen	52	32	31.1	5.4986	5.0896
<i>Cyphophoenix elegans</i> (Brongn. and Gris) H.Wendl. ex Salomon	51	33	32.1	2.7298	2.3755
<i>Cyphophoenix nucele</i> H.E.Moore	52	32	31.6	3.1959	3.0296
<i>Cyrtostachys elegans</i> Burret	58	32	31.1	4.1121	3.6570
<i>Cyrtostachys loriae</i> Becc.	52	33	32.1	3.1645	2.8165
<i>Dictyosperma album</i> (Bory) Scheff.	58	32	31.3	1.3896	1.2497
<i>Dypsis arenarium</i> (Jum.) Beentje and J.Dransf.	63	34	33.1	5.1132	4.5547
<i>Dypsis cabadae</i> (H.E.Moore) Beentje and J.Dransf.	52	33	32.7	3.3132	2.9765
<i>Dypsis carlsmithii</i> J.Dransf. and Marcus	77	33	32.9	4.6002	4.1165
<i>Dypsis decaryi</i> (Jum.) Beentje and J.Dransf.	81	32	31.2	3.4497	3.1133
<i>Dypsis hovomantsina</i> Beentje	62	33	33.7	1.3886	3.1349
<i>Dypsis ifanadianae</i> Beentje	58	33	33.1	4.1546	3.8845
<i>Dypsis lastelliana</i> (Baill.) Beentje and J.Dransf.	77	33	33.2	6.1132	5.6068
<i>Dypsis madagascariensis</i> (Becc.) Beentje and J.Dransf.	55	34	33.5	5.7746	5.1770
<i>Dypsis mananjarensis</i> (Jum. and H.Perrier) Beentje and J.Dransf.	65	34	31.9	3.8465	3.4545
<i>Dypsis montana</i> (Jum.) Beentje and J.Dransf.	65	33	32.2	4.0064	3.6699
<i>Dypsis pembana</i> (H.E.Moore) Beentje and J.Dransf.	68	29	28.1	4.5959	4.2236
<i>Dypsis plumosa</i> Hodel, J.Marcus and J.Dransf.	62	32	31.5	1.9976	2.8965
<i>Dypsis robusta</i> Hodel, Marcus and J.Dransf.	69	34	33.9	1.8465	1.6410
<i>Dypsis saintelucei</i> Beentje	55	34	33.1	1.9292	1.7042
<i>Elaeis guineensis</i> Jacq.	118	33	32.2	1.1645	1.0235
<i>Euterpe precatoria</i> Mart.	51	32	31.4	2.4265	2.1775
<i>Heterospathe elata</i> Scheff.	64	33	32.1	2.3164	2.1050
<i>Heterospathe intermedia</i> (Becc.) Fernando	51	32	31.2	4.3465	3.9133
<i>Heterospathe sibuyanensis</i> Becc.	74	34	31.9	2.0065	1.8304
<i>Hydriastele moluccana</i> (Becc.) W.J.Baker and Loo	84	34	33.1	3.8844	3.4466
<i>Hyophorbe lagenicaulis</i> (L.H.Bailey) H.E.Moore	151	31	30.4	2.8897	2.5878
<i>Itaya amicorum</i> H.E.Moore	55	32	30.9	2.4246	2.1460
<i>Kentiopsis piersoniorum</i> Pintaud and Hodel	55	33	32.1	1.4465	1.3255
<i>Kentiopsis pyriformis</i> Pintaud and Hodel	65	32	31.2	3.6611	3.2821
<i>Laccospadix australasicus</i> H.Wendl. and Drude	51	33	32.7	1.7996	1.5969
<i>Licuala bayana</i> Saw	51	32	30.8	2.1132	1.8935
<i>Licuala peltata</i> Roxb.	58	32	31.3	1.0054	0.8836
<i>Licuala salliehana</i> Saw	69	30	29.1	1.6632	1.5148
<i>Livistona lanuginosa</i> Rodd	97	33	32.1	2.8277	2.5247

**Table A4.** Cont.

Species	Circ (cm)	Air T	Stem T	Sample 1	Sample 2
<i>Livistona mariae</i> F.Muell.	88	33	32.3	1.1312	0.9957
<i>Livistona muelleri</i> F.M.Bailey	74	32	31.5	1.8486	1.6410
<i>Livistona victoriae</i> Rodd	79	31	30.9	1.6645	1.5148
<i>Lodoicea maldivica</i> (J.F.Gmel.) Pers.	98	34	34.6	1.1132	0.9720
<i>Medemia argun</i> (Mart.) Wurtténb. ex H.Wendl.	117	32	30.3	2.7918	2.5878
<i>Neonicholsonia watsonii</i> Drammer	52	32	30.8	1.7765	1.5148
<i>Neoveitchia brunnea</i> Dowe	55	33	31.8	2.0021	1.8051
<i>Neoveitchia storckii</i> (H.Wendl.) Becc.	73	32	31.2	1.2345	1.1109
<i>Nephrosperma van-houtteanum</i> (H.Wendl. ex Van Houtte) Balf.f.	52	33	32.3	2.7711	2.4657
<i>Oenocarpus mapora</i> H.Karst	51	32	31.1	5.5056	4.9231
<i>Orania moluccana</i> Becc.	68	29	28.6	1.6465	1.4391
<i>Pelagodoxa henryana</i> Becc.	67	32	31.3	1.4215	1.6410
<i>Phoenix sylvestris</i> (L.) Roxb.	109	31	32.9	3.7164	4.1132
<i>Pinanga batanensis</i> Becc.	68	34	32.9	3.6134	4.0066
<i>Pinanga insignis</i> Becc.	48	33	31.9	2.0311	1.8304
<i>Pinanga javana</i> Blume	51	34	32.8	2.1798	1.9566
<i>Pinanga urosperma</i> Becc.	61	33	31.9	0.9554	0.8205
<i>Ponapea hosinoi</i> Kaneh.	62	33	31.8	5.4165	6.0023
<i>Prestoea acuminata</i> (Willd.) H.E.Moore	52	32	30.8	4.0154	4.4651
<i>Pritchardia thurstonii</i> F.Muell. and Drude	66	29	28.6	0.7879	0.6943
<i>Ptychosperma elegans</i> (R.Br.) Blume	53	32	31.2	6.3897	7.1322
<i>Ravenea madagascariensis</i> Becc.	52	34	33.2	0.9498	1.1021
<i>Rhopaloblaste augusta</i> (Kurz.) H.E.Mllre	58	33	32.2	1.6355	1.4517
<i>Rhopaloblaste ceramica</i> (Miq.) Burret	72	32	31.1	1.6899	1.5148
<i>Sabal mauritiiformis</i> (H.Karst.) Griseb. and H.Wendl.	71	32	31.4	3.1134	3.2265
<i>Sabal palmetto</i> (Walter) Lodd. ex Schult. and Schult.f.	95	31	31.3	1.3444	1.2231
<i>Saribus rotundifolius</i> (Lam.) Blume	105	30	30.1	1.1314	1.0099
<i>Satakentia liukiuensis</i> (Hatus.) H.E.Moore	68	32	31.5	7.5109	6.3365
<i>Schippia concolor</i> Burret	51	33	32.4	0.7544	0.7547
<i>Syagrus botryophora</i> (Mart.) Mart.	76	32	32.6	1.7655	1.5779
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	63	33	32.1	1.2615	1.1165
<i>Syagrus sancona</i> (Kunth.) H.Karst.	78	32	31.8	1.6311	1.4517
<i>Syagrus schizophylla</i> (Mart.) Glassman	56	32	31.1	1.5644	1.3886
<i>Veitchia joannis</i> H.Wendl.	59	33	32.2	1.3433	1.1992
<i>Washingtonia robusta</i> H.Wendl.	154	32	31.3	4.6899	4.2288
<i>Wodyetia bifurcata</i> A.K.Irvine	99	30	31.6	4.4454	3.9764

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