

# **The use of vascular plant densities to estimate the age of undated lava flows in semi-arid areas of Fogo Island (Cape Verde, Atlantic Ocean)**

Sébastien Larrue, Raphael Paris, Samuel Etienne

## **To cite this version:**

Sébastien Larrue, Raphael Paris, Samuel Etienne. The use of vascular plant densities to estimate the age of undated lava flows in semi-arid areas of Fogo Island (Cape Verde, Atlantic Ocean). Journal of Arid Environments, 2020, 173, pp.104042.  $10.1016/j.jaridenv.2019.104042$ . hal-02367322

# **HAL Id: hal-02367322 <https://hal.science/hal-02367322v1>**

Submitted on 24 Jan 2025

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*camara* densities explained significantly lava ages (adjusted  $R^2 = 0.733$ , P < 0.0001). PCA demonstrated similar plant species densities on lavas were related to similar year-old lavas. Model age-predictions were congruent with PCA result supporting that vascular plant species densities may provide useful information about the relative age of undated lava flows in arid environment.

 Keywords: Fogo Island, semi-arid lava flows, vascular plants, chronosequence, Cape Verde, island biogeography.

#### **Introduction**

 Fresh mineral material deposited at the surface of the Earth offer the opportunity to study the pattern and the timing of colonization of volcanic substrate by vascular plant species.

Volcanic lava flows are especially unique as they are sterile material recovering a preexisting

landscape where volcanic eruption acts as a reset factor for plant colonization (e.g. Whittaker

1984, Thornton et al. 1992). Hence, plant colonization on lava flows is mainly limited by the

suitable conditions for establishment and it is well known that such conditions evolve mainly

with time and climatic conditions (e.g. Whittaker et al. 1984, Fenner 1987, Drake 1992, Drake

and Dombois 1993, Aplet et al. 1998, Cutler et al. 2008).

Primary plant succession in island volcanic environment has been studied by many workers

and the increase of plant diversity with the age of lava flow seems quite expected (e.g.

Whittaker et al. 1992, Partomihardjo et al. 1992, and Thornton et al. 1992, on Anak Krakatau

Island; Aplet et al. 1998 on Hawaii Island; Cutler et al. 2008 on Iceland; Magnússon et al.

23 2014 on Surtsey Island), although the exact shape of the age-diversity might differ (Cutler

2010). Furthermore, in volcanic environments where historic effusive products create new

sterile land surfaces, lava flows can be used as chronosequences to study plant population

 development (Drake and Dombois 1993, Cutler et al. 2008, 2010). Indeed, plant succession has been investigated by comparing sites that differ in age but were geologically and climatically similar (e.g. Drury and Nisbet 1973, Miles 1979, Drake and Dombois 1993). Usually, historical lavas represent an opportunity to study plant succession within a well- constrained chronological framework, and lava flow ages were used as variable to explain plant densities and species composition (e.g. Aplet 1998). Conversely, plant densities and composition on lava flows might provide useful information for the distinction of undated lavas. Indeed, where land surface ages is unknown, geo-ecological successions have been used formerly as relative-age dating of glacial foreland (Matthews 1992). Here, plant densities in semi-arid conditions were assigned as variables to explain lava flow ages and such approach is still very poorly documented. On the east-north-east coast of Fogo Island (Cape Verde), the ages of some lava flows remain 13 unknown due notably to the lack of charcoal beneath these lava flows, preventing  $^{14}$ C dating to be applied (Ribeiro 1960, Machado 1965, Torres et al. 1997, Day et al. 1999, Foeken et al. 2009), while this information may be relevant for a retrospective analysis of volcanic hazard evaluation and prevention for local authorities. We argue that vascular plant species densities may be used as indicator to provide information on the relative age of volcanic eruptions, as complementary methodology or in case of non-applicability of the conventional methods such 19 as  ${}^{14}$ C. We hypothesized that similar plant species densities in comparable semi-arid environment on lava flows might be related to similar year-old lavas.

**Materials & Methods**

*Study area*

The Cape Verde Archipelago includes ten ocean islands stretching in the eastern Atlantic

Ocean between 14°51'13'' – 17°03'29''N and 22°41'38'' – 25°10'31''W at *c*. 580 km from the

 nearest African mainland and 1,300 km south of the Canary Islands. With a land surface of 476 km², Fogo Island is the fourth largest island of the Archipelago and the highest, reaching 2,829 m a.s.l. at *Pico do Fogo* volcano (Machado 1965). Fogo is one of the most active volcano of the Atlantic Ocean and the only active volcano of the Cape Verde archipelago for the last centuries (Machado 1965a-b, Torres et al. 1997, Dionis et al. 2015). The island is a shield volcano truncated by an 8 km-wide horseshoe-shaped caldera opened to the east. The caldera is related to a massive collapse of the eastern flank of the island (Day et al. 1999), the latter being mostly covered by historical lava flows (Dionis et al. 2015, Paris et al. 2017). The semi-arid climate of Fogo Island experiences two seasons: a cool dry season (November to June) with very low rainfall and cool temperatures, and a warmer season with occasional rainfalls (July to October) (Soares 1956, Amaral 1991). Fogo Island has a mean annual 12 temperature of  $24.2^{\circ}$ C and rainfall of 272 mm year<sup>-1</sup> at São Filipe, southwestern coast (https://en.climate-data.org/). However, rainfall experience high variability due to elevation range, influence of the continental Sahel zone, and exposure to the trade winds (Soares 1956, Amaral 1991, Ribeiro 1997, Olehowski et al. 2008). Annual precipitation ranges from *c*. 150 mm at sea level to > 600 mm in higher elevation. Fogo Island has a leeward dry south-west coast and a windward wetter north-east coast exposed to the dominant maritime trade winds 18 (Amaral 1991). Thus, rainfall ranges from 150-200 mm year<sup>-1</sup> at sea level on the leeward 19 coast to 200-250 mm year<sup>-1</sup> on the windward coast. 20 Since the  $15<sup>th</sup>$  century, native vegetation cover of Fogo Island has changed widely due to

human colonization (Chevalier 1935). However, despite human settlements and activities

such as deforestation, agriculture and farmland, overgrazing, and the spread of many

naturalized species (Duarte & Moreira 2009, Siegmund et al. 2005), 41 endemics species still

 observed among a total of 373 vascular plants on Fogo Island (Duarte et al. 2008, Romeiras et al. 2015).

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#### *Lava flows sampled*

 We selected 11 basaltic lava flows as a chronosequence located in semi-arid climate on the eastern coast of Fogo Island (Fig.1). The year of eruption (AD) was documented by using reports and geological maps for nine lava flows (Torres et al. 1997; revisited by Paris et al. 2017), while the date of one eruption was uncertain (proposed as "1664?" in Torres et al. 1997, here named Nd.10 (1664?)). The age of dated lava flows ranged from 67 to *c*. 350 yrs old (defined as "historical" lavas). Two other lava flows locally covered by 1769 lava remained undated (Nd.1 and Nd.9; Nd.1 being younger than Nd.9 as evidenced by the map of Paris et al. 2017). All of the 11 lava flows sampled shared similar field characteristics: they were identify as a'a lavas, i.e. rough lavas with a chaotic surface made of blocks formed during the fragmentation of the cooling crust during lava emplacement. These lavas were also similar in geology as all of the historical eruptions on Fogo Island produced alkali basalts classified as basanites in

terms of major-element composition, with clinopyroxene and olivine as dominant phenocrysts

(Machado 1965; Gerlach 1988, Doucelance et al. 2003, Cornu 2017). According to field

observation, these rough lava flows were not cultivated.

### *Plant count on lava flows*

 When using a chronosequence, replicate sites of a given age are often unavailable, making 23 statistical analysis difficult (Drake and Dombois, 1993). Here, three replicate plots of 314 m<sup>2</sup> (each) were delineated in the central part of the 11 lava flow sampled (i.e. not at the flow front or lateral levees where environmental conditions and accessibility to successional plant

 species might be different). The distance between the three replicate plots per lava flow ranged between 5 and 15 m (not shown). A total of 33 314 m² plots were delineated. In addition, one replicate of 140 m² per lava flow (n=11) was performed using vertical aerial photographs at ~ 4 m above ground acquired with a DJI Phantom 2 drone (Plot 4, Table 1). We then identified and counted plant species in laboratory. Note that this additional drone replicate was done to improve the whole sample and save time during field survey. All plots were selected in order to maximize homogeneity of environmental parameters such as geology, elevation, terrain roughness, and climatic conditions. General plot characteristics are given in Table 1. In these plots, vascular plant species including (i) natives (i.e. indigenous and endemic species), and (ii) naturalized species (i.e. formerly introduced, since naturally dispersed in environment) were investigated. We recorded species richness, abundance (i.e. the total number of plants), and species abundance (i.e. the number of individuals per species). Fieldwork was led at the rainy season (in September) in the exposure 14 rainfall zone of 200-300 mm year<sup>-1</sup> (Olehowski et al. 2008). In order to homogenise plot area, we calculated the density of every species per 314 m² and 140 m² plots (i.e. the number of individuals per species divided by plot area; here after species density per m²). Thus, we obtained (i) the density of every species per plot and (ii) the density of every species per lava flow (by summing species, divided by total plot area 1-4). 

*Statistical analysis*

 First, we used the simple Sørensen Index to confirm similarity of the three replicate plots on each lava flow sampled (Plots 1-3, Table 1). Note that Sørensen Index was not calculated for the 1951 lava flow (lack of vascular species on this lava).

 Second, linear regression was used to observe the relationships between plants abundance and species richness versus age of lava flows, while Spearman's correlation was used to provide



*Plant species composition on lava flows*

In the 44 plots, we found a total of 27 vascular plant species representing an abundance of

- 3,092 individual plants. Abundance per lava flow ranged from 1 to 663 individuals while
- species richness ranged from 1 to 19 species. Species richness per plot ranged from 0 to 16
- while abundance ranged from 0 to 135 (Table 2). We encountered 15 shrubs, 5 trees, 2



 Among the nine vascular plant species age-correlated, stepwise model showed a better fit of species density versus age of lavas by using mostly *S. daltonii* with *L. camara* (Table 4). 3 According to stepwise model equation, Nd.1 and Nd.9 lavas would be  $\sim$  249 and 256  $\pm$  40 yr-old, respectively.

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*Lava flows comparaison*

 Significant relationships were found between species densities and similar years of volcanic 13 eruption (PCA, Fig. 6). Spearman's correlation values ranged from 0.497 to 0.778,  $P \le 0.01$  (Table 5). Lava flows were clearly distinguished with two groups: Nd.10 (1664?)-1785 and 1799-1857 (Fig. 6). Species densities of undated Nd.1 and Nd.9 lava flows were linked and 16 fitted with the 17<sup>th</sup>-18<sup>th</sup> century lava flows (Table 5 & Fig. 6). Nd.1 lava was linked with 1769 and 1785 lavas while Nd.9 lava was linked with Nd.10 (1664?) and 1769 lavas. The lava flow Nd.10 (1664?) was significantly linked with 1785 lava (Table 5). PCA axis F1 explained a large part of the total inertia of the dataset (44.63%, Fig. 6). This axis was controlled mostly by *S. daltonii* (127.8%), *Dryopteris* sp. (11.1%), and *Polypodium*  sp. (2.5%) (Table 6). Axis F2 explained 18.5% of the total inertia; *Dryopteris* sp. (23.5%), *Polypodium* sp. (9.2%), and *E. tuckeyana* (3.8%) were the most important explanatory

- 23 variables for this axis (Table 6).
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#### **Discussion**

#### *Trend in species and age of lava flows*

 On Fogo Island, plant species richness and abundance are related to the age of lava flows. Thus, colonization of the sampled lava flows by vascular plants is characterised by a temporal evolution related to the age of lava flows with successive stages of vegetation development. This result is congruent with many studies. For example, Drake and Dombois (1993) demonstrated, on Hawaii Island, an increase in plants density on a chronosequence of six lava flows aged between 47 and ~3,000-yr-old with changes in dominant species on the oldest lavas. In Iceland, similar result was obtain from Cutler et al. (2008) whose defined, with a 850-yr chronosequence on seven lava flows, the stages of vegetation development as "Pioneer colonization stage", then "Pioneer expansion stage", and "Higher plant colonization stage" including additional species growing within the pioneer matrix. On Fogo Island, the increase of plant species number with time appears to be very slow on the semi-arid lava flows sampled. Indeed, we found only five and one species on the 1852 and 1951 lava flows, respectively. So, a period of at least 65 years is required for plant colonization, namely by *S. daltonii*. This result is in agreement with Chevalier (1935) who reported only one species (*S. daltonii*) on the 1852 lava flow, which was 83-yr-old in time of observation. First, this time lapse before pioneer plants start to colonize lava may be explain by changes of lava environment, here with a weak alteration of lava due to poor chemical weathering of basic volcanic rock in such semi-arid conditions (Barros 1998, Karthe and Siegmund 2004) leading to slow plant colonisation. For example, Anak Krakatau Island (where vascular plants were extirpated due to major eruption in 1952) supports an extensive

 forest along the wet eastern/north-eastern coastline, while the xeric island interior lavas remain sparsely colonized by vascular plants (Partomihardjo et al. 1992). Second, plants colonization on lava is controlled by the time required for random seeds dispersal from adult plants. Indeed, it has long been demonstrated that during primary ecological succession on lava flows, no seed bank exists in the sterile new substrate. Thus, all pioneer plants must be recruited from the seed rain, involving wind dispersed taxa as well as mammal and bird-dispersers availability (e.g. Drake 1992, Whittaker et al. 1992).

 Our findings show that some vascular plant species led the relationships between species density and the age of lava flows, among which *S. daltonii*, *E. tuckeyana*, *J. curcas*, and *L. camara* are significant species. The endemic species *S. daltonii* is the most abundant species observed on the lava flows sampled and the dominant pioneer on lavas of this area. It may refer to early "Pioneer colonization stage" on lava flows < 160 yr-old. We then also observed a significant increase density with time for species *E. tuckeyana*, supporting a "Pioneer expansion stage" on 160-230 yr-old lava flows. Here, we also found naturalized species *J. curcas*, and the well-known island invasive species *L. camara*. Moreover, stepwise model confirms that density of *S. daltonii* associated with that of *L. camara* is the best indicator to explain the age of lava flows sampled. Overall, the presence of natives and naturalized species on the same lava might be viewed as a

bio-indicator of the oldest lava flows sampled and interpreted as "Higher plant colonization

stage" on > *c*. 230 yr-old lava flows. However, because a chronosequence assumes a

substitution of space for time, result provides only a partial assessment of succession (see

Drake and Dombois, 1993).

#### *Some references to invasive species*

 On Fogo Island, the invasive species *L*. *camara* represents a potential threat for native species established on the same lava flows, especially for the native *E. tuckeyana, L. jacobaeus* and *L. purpureus*. Indeed, Chevalier (1935) reported that *E. tuckeyana*, *L. jacobaeus* and *L. purpureus* were mostly found on the oldest lava flows on Fogo Island but *L. camara* was never mentioned by the botanist among these natives. Here, *L. jacobaeus* and *L. purpureus*  were barely linked with the age of lava flows, while a strong significant relationship was observed for the invasive *L. camara*. Similar result was found for the naturalized *J. curcas*. Thus, our results suggest that *L. camara* and *J. curcas* seem to occupy habitat colonized by *L. jacobaeus* and *L. purpureus* previously. We argue that *J. curcas* should be also viewed as an invasive species on the northeast coast of Fogo Island. Finally, we also observed some adults *A. precatorius*, only on the oldest sampled lava flows. Formerly, this vine was reported as invasive species in numerous tropical islands, e.g. in the Caribbean Islands (Holm et al. 1979), New Caledonia (MacKee 1994), Hawaiian Islands (Wagner et al. 1999), and French Polynesia (Florence et al. 2007). Although not studied here, it is possible that *A. precatorius* also become a dominant alien species on the oldest lava flows of Fogo Island.

*Species densities fit period of eruption*

 Plant species densities of the Nd.10 (1664?)-1785 lava flows group are clearly different from the 1799-1857 lava flows group. This finding confirms the hypothesis that similar plant species densities in comparable semi-arid environment on lava flows are related to similar year-old lavas.

 However, significantly-linked density group encompasses lavas with large age range (several decades), e.g. Nd. 10 (1664?) linked with 1785, or 1799 linked with 1857. This confirms that

 species composition and densities might remain similar during at least several decades on Fogo Island. Thus, a range of several decades is necessary to detect a significant gap in plant

species densities and composition among semi-arid lava flows.

 Species densities of the Nd.10 (1664?) lava flow are significantly correlated with those of 1785 lava flow. There is no doubt that Nd.10 (1664?) lava is older than 1785 lava, as available maps of lava flows show that the Nd.10 lava is locally below the 1785 lava (Torres et al. 1997; Paris et al. 2017). Torres et al. (1997) tentatively linked the Nd.10 lava flow to the 1664 eruption (Ribeiro 1997). Our results support that the Nd.10 (1664?) eruption occurred 9 lately in the  $17<sup>th</sup>$  century or early in the  $18<sup>th</sup>$  century. There are indeed several historical accounts of eruptions during this period, including 1664, 1695, and 1721-25 (Ribeiro 1997). Surprisingly, although species densities on the Nd.10 (1664?) and 1769 lavas were strongly linked with 1785 lava, species densities of the Nd.10 (1664?) and 1769 lavas were not linked. This might be explained by (i) the distance between Nd.10 (1664?) and 1769 lava (see Fig. 1) leading to possible geographic disjunction in plants accessibility between sampled sites or (ii) related to human disturbances. Indeed, while we assume that lava flows sampled were not cultivated, Fogo Island is inhabited by more than 37,000 people with a mean density of 77 people per m²; hence the most part of the island is cultivated mainly by subsistence rainfed farming (Barros 1998). Thus, human impacts such goats grazing, fire, or human picking landscape plants on the lava flows sampled might disturb plant densities and colonization. This may explain some lack of correlation as well as different levels of similarity (Sørensen) observed among replicate plots, especially for *S. daltonii*, *Dryopteris* sp. *Polypodium* sp., and *E. tuckeyana* which are the most important species to discriminate lavas on the east-north-east coast of Fogo Island (PCA).

#### *Undated lavas*

2 Model age-prediction suggest that Nd.9 lava might be related to an eruption around  $1761 \pm 40$  yr, and PCA shows that species densities of undated Nd.9 lava are linked with the former 1664-1769 lava flows. Accordingly, these findings lead us to classify Nd.9 lava as early  $18<sup>th</sup>$  century lava flow, possibly related to 1721-25 eruption. Similarly, model age-prediction 6 supports that Nd.1 lava might be related to an eruption around  $1768 \pm 40$  yr. Species densities of Nd.1 lava is linked with the 1769 lava, supporting a similar or slightly older period of 8 eruption in the  $18<sup>th</sup>$  century.

#### **Conclusion**

 Species densities are significantly related to the age of lava flows on Fogo Island. Moreover, similar plant species densities in comparable semi-arid environment on lava flows were related to similar year-old lavas. However, species densities may provide only an estimate of year-old lavas with a gap of several decades on Fogo Island. Nevertheless, vascular plant densities are helpful to detect the period of eruption. Consequently, when lava flow ages are unknown because of non-applicability of the conventional dating methods, vascular plant species densities may provide useful information on the relative age of volcanic eruptions. Although not extended here, our results support that plant densities and composition might represent another input for volcanic hazard evaluation, establishing a reliable chronological framework of volcanic eruptions for the evaluation of volcanic hazard, especially for probabilistic models.











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### **Figure and caption**



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 Figure 1. Study area with location of the sampling sites (black squares) on eleven lava flows of the east-north-east coast of Fogo (Cape Verde, Atlantic Ocean). Bold numbers on the surveyed lava flows refer to year of eruption (AD). The year of eruption of lava flows named "Nd.10 (1664?)" was uncertain, while "Nd.1" and "Nd.9" were not documented. 

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Figure 3. Vascular plant species composition (%) on the 11 lava flows (Fogo Island, Cape

- Verde).
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 the age of lava flows in 27 plots (314 m² each). Plots on undated lavas Nd.1 (grey circle) and Nd.9 (black circle) have been added as supplementary information.

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 *tuckeyana* (colorless bar) and the naturalized species *Lantana camara* and *Jatropha curcas* (black bar) on the semi-arid surveyed lavas (Fogo Island, Cape Verde). The undated lavas Nd.1 and Nd.9 have been added as supplementary information. Error bars refer to standard deviation.







based on vascular plant species densities and composition in the 44 plots (Fogo, Cape Verde).

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### **Table and caption**

 Table 1. Characteristics of the 44 plots surveyed on 11 lava flows of the east-north-east coast of Fogo Island (Cape Verde, Atlantic Ocean). Sørensen Index (plant similarity) is calculated for the three field plot replicates of 314 m² (plot numbers 1-3). Drone plot area: 140 m² (plot number 4). Numbers in brackets refer to mean value. px: pyroxene; ol: olivine.



\* field observations

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- Table 2. Vascular plant species observed in the 44 plots surveyed with species richness and total number of plants (Fogo Island, Cape Verde). Biogeographical status has been added with (I) indigenous (i.e. native but not endemic), (E) endemic, and (Ntz) naturalized species.
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 () = Range per plot



 Table 3. Relationships between species density and age of lava flows in the plots (Spearman's coefficient correlation).



 $P^{***}$  < 0.0001; 0.001\*\* < P < 0.01; \*P < 0.05



- Table 4. Plant species densities versus age of lava flows sampled (Stepwise regression
- model). Equation model is provided with the table.



Age of lava flows = (136.263974515594 + 7337.7542282911 x L. camara) + (396.447385251673 x S. daltonii) 

## Table 5. Relationships between the 11 lava flows based on 27 vascular plant species densities

- (Spearman's correlation with PCA).
- 





 Table 6. Principal Component Analysis (PCA). Contribution of the species per axis (%) to the total inertia of the dataset. 

Vascular plants (n=27)	F <sub>1</sub>	F <sub>2</sub>	F <sub>3</sub>	F <sub>4</sub>	F <sub>5</sub>	F <sub>6</sub>	F7	F <sub>8</sub>	F <sub>9</sub>	F10
Abrus precatorius	0.65	0.03	0.06	0.04	0.02	0.25	0.03	0.04	0.10	0.00
Abutilon pannosum	0.55	0.06	0.00	0.36	0.00	0.17	0.02	0.03	0.30	0.07
Acacia spirobis	0.73	0.00	0.03	0.13	0.00	0.03	0.02	0.04	0.08	0.26
Asparagus sp.	0.64	0.03	0.09	0.04	0.02	0.28	0.05	0.06	0.05	0.00
Catharanthus roseus	0.71	0.00	0.02	0.02	0.00	0.00	0.07	0.01	0.07	0.34
Coniza varia	0.72	0.00	0.01	0.18	0.00	0.08	0.01	0.00	0.06	0.29
Desmodium tortuosum	0.70	0.01	0.05	0.06	0.01	0.11	0.03	0.04	0.08	0.06
Dichrostachys cinerea	0.64	0.04	0.03	0.04	0.04	0.18	0.01	0.01	0.14	0.10
Diplotaxis irta	0.70	0.00	0.01	0.21	0.01	0.12	0.01	0.00	0.05	0.26
Dryopteris sp.	11.17	24.78	33.55	6.76	57.42	24.77	0.34	8.21	1.06	1.31
Euphorbia tuckeyana	0.23	3.37	0.27	1.11	0.09	2.00	0.46	0.02	24.82	2.33
<b>Ficus thonningii</b>	0.71	0.00	0.03	0.04	0.00	0.03	0.05	0.02	0.07	0.23
Forsskaolea procridifolia	0.69	0.00	0.00	0.13	0.00	0.05	0.01	0.26	0.08	0.46
Furcraea gigantea	0.23	0.44	0.10	5.42	1.47	1.42	3.42	0.97	0.12	0.12
Globularia amygdalifolia	0.75	0.00	0.03	0.12	0.00	0.04	0.02	0.03	0.07	0.30
Grewia villosa	0.61	0.02	0.10	0.14	0.00	0.05	0.05	0.06	0.68	0.08
Paronychia illecebroides	0.02	2.27	5.26	0.21	2.74	1.80	37.91	0.01	0.01	5.18
Jatropha curcas	0.56	0.08	0.01	0.02	0.12	0.04	0.01	0.04	0.24	0.85
Kalanchoe pinnata	0.61	0.02	0.03	0.32	0.40	0.02	0.45	0.00	0.11	0.25
Lantana camara	0.46	0.11	0.05	0.03	0.16	0.06	0.02	0.01	0.17	0.68
Lavandula rotundifolia	0.04	0.65	0.16	6.50	0.92	1.42	0.71	0.93	0.00	0.03
Leucaena leucocephala	0.75	0.00	0.03	0.12	0.00	0.04	0.02	0.03	0.07	0.30
Lotus jacobaeus	0.52	0.07	0.11	0.09	0.00	0.11	0.07	0.07	0.02	0.01
Lotus purpureus	0.37	0.18	0.01	0.29	0.00	0.07	0.03	0.01	0.01	0.02
Polypodium sp.	2.53	8.26	9.60	6.43	0.18	30.75	0.38	3.11	33.61	54.05
Sarcostemma daltonii	127.89	0.37	10.61	5.27	49.47	3.22	0.69	32.22	47.80	5.53
Senna bicapsularis	0.64	0.03	0.01	0.20	0.00	0.00	0.02	0.04	0.03	0.00