IMPACT OF *Clethra arborea* AITON (CLETHRACEAE) IN A SPECIAL PROTECTION AREA OF SÃO MIGUEL ISLAND, AZORES

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MONIZ, J. & L. SILVA. Impact of *Clethra arborea* Aiton (Clethraceae) in a Special Protection Area of São Miguel Island, Azores. *Arquipélago*. Life and Marine Sciences. 20A: 37-46.

Clethra arborea Aiton (Clethraceae) is a tree endemic to Madeira Island, and a recent introduction to São Miguel Island at Tronqueira/Pico da Vara, a Special Protection Area (SPA) included in Natura 2000, habitat of the endemic bird *Pyrrhula murina* Godman (Aves: Fringillidae). In this work the impact of *C. arborea* on the native vegetation was evaluated. Microhabitats associated with *C. arborea* and with native trees, and areas with different degrees of infestation by *C. arborea* were compared for soil pH, soil conductivity, soil macronutrient availability, leaf litter production, number of seedlings and vegetation structure. There were no clear differences in soil pH, conductivity and macronutrient availability, either between micro-habitats associated with *C. arborea* and with native trees, or between areas with different degrees of infestation by *C. arborea*. Leaf litter production was significantly higher in micro-habitats associated with *C. arborea* and higher still in areas with high levels of infestation. The number of seedlings and the percentage of endemic seedlings differed significantly between microhabitats associated with *C. arborea* and those associated with endemic trees. Invasion by *C. arborea* modified vegetation structure, especially biovolume, which was much higher in invaded areas. By considerably decreasing the proportion of biovolume allocated to native trees, *C. arborea* infestations may have a negative impact on the conservation efforts at the SPA.

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INTRODUCTION

The increase of biological invasions caused by human activities is a global phenomenon but of greatest significance in isolated islands and archipelagos (LOOPE & MUELLER-DOMBOIS 1989). Invasive plants can alter several community properties, including diversity, primary productivity, species interactions, community stability and ecological successions (VITOUSEK & WALKER 1989).

Non-indigenous plants are an important component of the Azorean vascular plant flora. Among 1002 taxa cited for the archipelago, 69 % are considered as introduced (SILVA et al. 2000, SILVA 2001).

Clethra arborea Aiton (Clethraceae) is a tree endemic to Madeira Island, where it is found in the *Clethro-Laurion* alliance (SJÖGREN 1972). It is a recent introduction to São Miguel Island (Azores), where it was first recorded in 1960 (FRANCO 1984). Later, it was found invading high altitude native vegetation in conservation areas (LE GRAND 1982, BIBBY & CHARLTON 1991). *Pyrrhula murina* Godman (Aves: Fringillidae), the Azorean bullfinch, is an endemic bird, largely confined to the native vegetation found in the eastern part of São Miguel Island (Tronqueira/Pico da Vara Special Protection Area of Natura 2000). This habitat has been considerably altered by the expansion of non-indigenous plants, especially *C. arborea* (RAMOS 1995; SILVA 2001). According to SJÖGREN (1973), the vegetation at Tronqueira belongs to the *Juniperion brevifolii* alliance, with the potential to form three vegetation layers, including 13 differential species when fully developed. This forest remains, if fully preserved, would correspond to typical Azorean Mesic or Humid Laurel Forests (DIAS 1996).

Early work with *C. arborea*, suggested the possibility of impacts on the vegetation structure of the invaded communities (SILVA 2001). In this work, the impact of *C. arborea* in high altitude native vegetation at Tronqueira was evaluated. In particular, three areas with different *C. arborea* abundances, on one hand, and microhabitats associated to *C. arborea*, *Laurus azorica* Seub. (Franco) (Lauraceae) and *Ilex perado* Aiton ssp. *azorica* (Loesener.) Tutin (Aquifoliaceae), on the other hand, were compared. We tested the following hypotheses: i) soil parameters are different in areas with different levels of infestation by *C. arborea*; ii) leaf litter production is highest in invaded areas; iii) the pool of seedlings differs between microhabitats; and iv) vegetation structure differs between areas with different infestation levels.

MATERIAL AND METHODS

Microhabitats

Native and introduced trees: Microhabitats associated with *C. arborea* and two native species, *L. azorica* and *I. perado* ssp. *azorica* were compared. In September 2000, 30 trees of each species were marked. Under the canopy of each tree, soil, seedlings, and leaf litter were sampled in three different seasons: Winter (December 2000), Spring (April 2001) and Summer (June 2001).

Soil: Under the canopy of each tree and for each sampling season, three soil cores (5 cm diameter by 15 cm deep) were collected and pooled. Soil pH, conductivity and macronutrient availability (K, P, Ammonia and Nitrate) were estimated using LAMOTTE Soil Analysis Lab (LAMOTTE 1996).

Leaf litter: Leaf litter was collected under the canopy of each marked tree using a 50 x 50 cm metal frame. Litter was dried at 70ºC up to a constant dry weight. The accumulation of leaf litter per square metre was calculated (WILLIAMS-LINERA & TOLOME 1996).

Seedlings: Seedlings were sampled within a one metre radius circle, around the tree trunk. Species diversity and equitability were calculated according to GREIG-SMITH (1983).

Invaded areas

Selection of the areas: Three areas were selected which by visual inspection appeared to have different degrees of infestation by *C. arborea*. This included an area with a high degree of infestation in which *C. arborea* greatly outnumbered other trees (HIGH), a partially invaded area (MEDIUM) and one with only a few, scattered individuals of *C. arborea* (LOW). All the areas were located in the Tronqueira region in the eastern part of São Miguel, and were only about 500 m apart. Three rounds of sampling were performed at each area (February, May and July 2001).

Soil and leaf litter: At each of 30 random points selected for the study of vegetation structure, soil and leaf litter were sampled as previously.

Vegetation structure: A distance method was used (T-Square Sampling) to evaluate vegetation structure, with thirty random points per area (KREBS 1989). According to this method, the distances from a random point to the nearest tree and from this to its nearest neighbour were measured. Tree species was recorded as well as upper and lower canopy limits, canopy diameter, and basal diameter of the trunk. Tree density was calculated using the two measured distances (KREBS 1989). Projected biovolume (Bp) was calculated according to DIAS (1996), based on canopy height (c) and mean canopy diameter (d), such that: $Bp = c\pi(d/2)^2$.

Statistical analysis: Data analysis followed ZAR (1996), using SPSS 10.0. All variables were checked for normality with the Kolmogorov-Smirnov test. For normal soil data (conductivity) and leaf litter dry weight, one factor ANOVA was used, followed by the HSD Tukey test, when three determinations were made, or a t test when only two determinations were available (ammonia, nitrate, phosphorus and potassium). Non-normal data were transformed using log(x). When transformation was insufficient to normalize data (soil pH), the Kruskal-Wallis test followed by the Nemenyi test (when three determinations were made) or the Mann-Whitney test (when two determinations were made) were used. For seedlings, the mean number of species was calculated, as well as diversity, equitability and percentage of endemic seedlings. The Friedman test was used for comparisons between microhabitats. Regarding vegetation structure, one factor ANOVA followed by the HSD Tukey test were used for normal data and the Kruskal-Wallis test followed by the Nemenyi test were used for non-normal data.

RESULTS

Microhabitats

Soil ph: Values of soil pH varied from 5.4 to 5.6 (Table 1). Significant differences were found between microhabitats and sampling occasions (Table 2). In particular, significant differences were found between *I. perado* ssp. *azorica* and the other trees and between winter and the other two seasons (Table 3).

Soil conductivity: This parameter varied considerably, from about 25 up to 79 ppm (Table 1). The effect of sampling season was clearly more significant than the effect of the microhabitat (Tables 2 and 3), with conductivity levels in Spring greatly exceeding those in the other seasons.

Soil nutrients: Phosphorus concentration varied from about 0.9 up to 2.1 kg/ha (Table 1). Phosphorus concentration showed significant differences between microhabitats (Table 2), with lower values for *Ilex* (Table 3), but not between sampling seasons (Table 2). Potassium concentration varied from 168 to 253 kg/ha (Table 1) and was significantly different between sample seasons but not between microhabitats (Table 2). Ammonia concentration varied between 36 and 65 kg/ha (Table 1), with significant differences only between microhabitats (Table 2), namely between *Ilex* and the other species (Table 3). For nitrate, although concentration varied from 5 to 7 kg/ha (Table 1), no significant differences were found for either factor (Table 2).

Table 1
Soil pH and conductivity (ppm), phosphorus, potassium, nitrate and ammonia concentrations in soil (kg/ha), for samples collected under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores), in different sampling seasons. (Mean ± SE).

Variable	Microhabitat		
Season	*Clethra arborea*	*Laurus azorica*	*Ilex perado*
pH			
Winter	5.58 ± 0.04	5.49 ± 0.04	5.59 ± 0.05
Spring	5.49 ± 0.05	5.41 ± 0.04	5.58 ± 0.05
Summer	5.41 ± 0.04	5.39 ± 0.04	5.42 ± 0.06
Conductivity			
Winter	39.83 ± 2.43	46.30 ± 4.05	43.01 ± 3.65
Spring	55.70 ± 3.65	79.14 ± 2.65	76.14 ± 3.01
Summer	26.22 ± 0.88	25.34 ± 1.25	29.38 ± 1.02
Ammonia			
Winter	36.03 ± 6.00	39.58 ± 8.23	49.07 ± 10.93
Spring	35.70 ± 3.38	40.72 ± 3.52	65.12 ± 11.14
Nitrate			
Winter	6.17 ± 1.00	6.92 ± 1.00	5.47 ± 0.88
Spring	5.90 ± 0.38	4.85 ± 0.55	7.23 ± 0.67
Phosphorus			
Winter	1.77 ± 0.79	0.86 ± 0.13	0.86 ± 0.26
Spring	2.10 ± 0.43	1.33 ± 0.41	1.18 ± 0.35
Potassium			
Winter	170.37 ± 11.32	168.33 ± 7.69	179.13 ± 26.02
Spring	185.03 ± 11.01	252.50 ± 31.88	215.72 ± 24.92

Table 2
Comparison of pH, conductivity, phosphorus, potassium, nitrate and ammonia concentrations in soil samples collected under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores). Effect of microhabitat and sampling season. Kruskal-Wallis test ($\chi 2$, test statistic; p, probability; n, number of soil samples); Mann-Whitney test (U, test statistic); one factor ANOVA (F, test statistic); t - test (t, test statistic).

Variable	Microhabitat			Season		
	$\chi 2$	p	n	$\chi 2$	p	n
pH	9.90	0.0071	180	17.92	0.0001	180
Condutivity	6.52	0.0384	180	113.65	<0.0001	180
	$\chi 2$	p	n	U	p	n
Potassium	1.57	0.4546	120	1286.5	0.0007	120
Phosporous	8.51	0.0142	120	1765.0	0.8496	120
	F	p	n	t	p	n
Nitrate	0.20	0.8153	120	0.40	0.6900	120
Ammonia	7.70	0.0007	120	-0.48	0.6340	120

Table 3
Comparison of soil conductivity (ppm), pH, phosphorus, potassium, nitrate and ammonia concentrations (kg/ha) in soil samples collected under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores). Only for those variables which showed significant differences in ANOVA or Kruskal-Wallis test (Table 2). Different letters indicate significant differences (Nemenyi test for soil conductivity, pH and phosphorus concentration; Tukey HSD test for ammonia concentration; α= 0.05). (Mean ± SE).

Variable	Factor					
	Season					
	Winter		Spring		Summer	
Soil conductivity	43.05 ± 3.38	a	70.33 ± 3.10	b	26.98 ± 1.05	c
Soil pH	5.55 ± 0.04	a	5.49 ± 0.04	b	5.41 ± 0.04	b
	Microhabitat					
	Clethra		*Ilex*		*Laurus*	
Soil conductivity	40.58 ± 2.32	a	49.51 ± 2.56	a	50.26 ± 1.98	a
Soil pH	5.49 ± 0.04	a	5.53 ± 0.05	b	5.43 ± 0.04	a
Phosphorus	1.29 ± 0.61	a	1.02 ± 0.31	b	1.10 ± 0.27	a
Ammonia	35.87 ± 20.19	a	42.10 ± 11.04	b	40.15 ± 5.88	a

Leaf litter: Leaf litter accumulated in different microhabitats varied considerably, from 29 up to 163 g/m2 (Table 4). There were significant differences between microhabitats (ANOVA: F=29.41; p<0.0001; n=180) and between sampling seasons (ANOVA: F=30.41; p<0.0001; n=180). In particular, significant differences were found between C. arborea and the other trees, and between winter and the other seasons (Table 5).

Table 4
Leaf litter (dry weight in g/m^2) accumulated under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores), during three sampling seasons. (Mean ± SE).

Season	Microhabitat		
	Clethra arborea	*Laurus azorica*	*Ilex perado*
Winter	162.96 ± 14.11	107.23 ± 15.90	92.98 ± 10.07
Spring	87.19 ± 10.70	38.92 ± 6.03	29.96 ± 6.76
Summer	80.34 ± 4.32	46.22 ± 5.12	28.73 ± 3.39

Seedlings: Five species were more frequent in the three microhabitats: *C. arborea*, *Myrsine africana* L. (Myrsinaceae), *Viburnum tinus* L. ssp. *subcordatum* P. Silva (Caprifoliaceae), *I. perado* ssp. *azorica* and *L. azorica*. Less frequent species included *Pittosporum undulatum* Ventenat (Pittosporaceae), *Erica azorica* Hochst. ex Seub. (Ericaceae) and *Juniperus brevifolia* (Seub.) Antoine (Cupressaceae). Regarding the number of taxa, this averaged one or two species (Table 6), and there were no significant differences between sampling seasons (Friedman test: χ2=3.68; p=0.159). Regarding microhabitats, the differences were not clear (Table 7), since they were not confirmed by Nemenyi test (Table 8). The number of seedlings varied between about two and nine per sample (Table 6), and differed between seasons (Friedman test: χ2=7.11; p=0.028). In winter and spring significant differences were found between *C. arborea* and the other trees (Tables 7 and 8). The percentage of native seedlings varied from 40 up to 83%, but did not differ significantly between sampling seasons (Friedman test: χ2=2.44; p=0.295). *C. arborea* microhabitats showed a significantly lower percentage of native seedlings (Tables 7 and 8). Although with some variation (Table 6), no significant differences were found for species diversity between sampling seasons (Friedman test: χ2=4.53; p=0.104). Differences between microhabitats were not clear, since they were not confirmed by the Nemenyi test (Tables 7 and 8). Regarding equitability, no significant differences were found between sampling seasons (Friedman test: χ2=5.50; p=0.0640), but significant differences were found between microhabitats (Table 7 and 8).

Table 5
Leaf litter (dry weight in g/m^2) accumulated under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores). Different letters indicate significant differences (Tukey HSD test; α= 0.05) between species (Microhabitat) or between sampling seasons (Season). (Mean ± SE).

Factor	Leaf litter	
Microhabitat		
C. arborea	110.16 ± 9.71	a
I. perado	64.12 ± 9.01	b
L. azorica	50.55 ± 6.74	b
Season		
Winter	121.05 ± 13.36	a
Spring	52.02 ± 7.83	b
Summer	51.76 ± 4.28	b

Table 6
Seedlings growing under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores), during three sampling seasons. (Mean ± SE).

Variable	Microhabitat		
Season	*Clethra arborea*	*Ilex perado*	*Laurus azorica*
Number of taxa			
Winter	2.00 ± 0.14	1.67 ± 0.21	2.27 ± 0.27
Spring	1.40 ± 0.15	2.40 ± 0.29	2.20 ± 0.32
Summer	1.40 ± 0.13	1.87 ± 0.34	1.20 ± 0.35
Number of seedlings			
Winter	3.47 ± 0.28	8.00 ± 2.87	8.07 ± 1.50
Spring	2.46 ± 0.34	8.93 ± 2.60	5.86 ± 1.12
Summer	2.73 ± 0.32	4.33 ± 1.19	3.13 ± 1.08
% of native taxa			
Winter	57.00 ± 6.60	72.00 ± 9.89	66.00 ± 8.48
Spring	56.00 ± 8.18	61.00 ± 8.10	83.00 ± 4.91
Summer	40.00 ± 7.93	75.00 ± 9.24	70.00 ± 9.46
Diversity			
Winter	0.58 ± 0.06	0.37 ± 0.08	0.61 ± 0.10
Spring	0.30 ± 0.07	0.68 ± 0.11	0.81 ± 0.12
Summer	0.26 ± 0.07	0.58 ± 0.12	0.33 ± 0.11
Equitability			
Winter	0.89 ± 0.02	0.80 ± 0.07	0.82 ± 0.05
Spring	0.96 ± 0.02	0.81 ± 0.07	0.90 ± 0.03
Summer	0.96 ± 0.02	0.89 ± 0.03	0.81 ± 0.09

Table 7
Seedlings growing under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores), during three sampling seasons. Kruskal-Wallis test ($\chi 2$, test statistic; p, probability; n, number of soil samples). For the number of seedlings, each season was analysed separately, since Freedman test showed significant differences between sampling seasons (see text).

Variable	$\chi 2$	p	n	Samples
Number of seedlings	8.36	0.0150	60	Winter
Number of seedlings	16.33	0.0003	60	Spring
Number of seedlings	0.94	0.6265	60	Summer
Number of taxa	6.41	0.0405	180	All
% of native taxa	8.87	0.0119	180	All
Diversity	6.43	0.0402	180	All
Equitability	7.89	0.0194	180	All

Invaded areas

Soil pH: The values for pH varied between 5.3 and 5.6 (Table 9) although with no significant differences both between areas and sampling seasons (Table 10).

Soil conductivity: This parameter varied from 27 up to 52 ppm (Table 9), with significant differences between sampling seasons but not between areas (Tables 10 and 11).

Table 8
Seedlings growing under *Clethra arborea*, *Ilex perado* ssp. *azorica* and *Laurus azorica* trees at Tronqueira (São Miguel Island, Azores). Different letters indicate significant differences between species (Nemenyi test; α= 0.05). Only for those variables showing significant differences according to the Kruskal-Wallis test (Table 7). (Mean ± SE).

Variable	Microhabitat		
	Clethra	*Ilex*	*Laurus*
Number of taxa	1.60 ± 0.27 a	1.98 ± 0.28 a	1.89 ± 0.46 a
Number of seedlings (winter)	3.47 ± 1.05 a	8.00 ± 2.97 b	8.07 ± 2.97 b
Number of seedlings (spring)	2.46 ± 0.81 a	8.93 ± 3.63 b	5.86 ± 1.45 b
% of native taxa	51.00 ± 7.33 a	69.33 ± 5.56 b	73.00 ± 6.67 b
Diversity	0.38 ± 0.13 a	0.54 ± 0.12 a	0.58 ± 0.17 a
Equitability	0.94 ± 0.06 a	0.83 ± 0.04 b	0.84 ± 0.04 b

Table 9
Soil pH, conductivity (ppm), phosphorus, potassium, nitrate and ammonia concentrations (kg/ha) in soil samples collected in different seasons and in areas with different degrees of infestation (High, Medium, Low) by *Clethra arborea* at Tronqueira (São Miguel Island, Azores). (Mean ± SE).

Variable	Area		
Season	HIGH	MEDIUM	LOW
pH			
Winter	5.49 ± 0.07	5.26 ± 0.06	5.49 ± 0.09
Spring	5.57 ± 0.06	5.36 ± 0.07	5.51 ± 0.08
Summer	5.52 ± 0.06	5.40 ± 0.06	5.35 ± 0.04
Conductivity			
Winter	33.60 ± 5.64	29.89 ± 2.51	30.52 ± 2.54
Spring	32.13 ± 2.80	52.27 ± 6.02	46.90 ± 5.66
Summer	29.12 ± 2.11	28.00 ± 1.51	27.44 ± 1.01
Ammonia			
Winter	108.10 ± 18.41	65.10 ± 19.18	79.95 ± 16.45
Spring	42.90 ± 5.46	90.30 ± 14.21	57.40 ± 11.24
Nitrate			
Winter	5.70 ± 1.01	3.20 ± 0.51	4.70 ± 0.71
Spring	5.90 ± 0.56	3.50 ± 0.63	6.30 ± 1.14
Phosphorus			
Winter	0.73 ± 0.24	0.50 ± 0.16	0.51 ± 0.16
Spring	6.73 ± 0.22	0.94 ± 0.34	0.78 ± 0.08
Potassium			
Winter	139.11 ± 9.81	189.80 ± 17.80	174.50 ± 29.46
Spring	130.26 ± 13.83	166.29 ± 10.04	178.07 ± 22.78

Soil nutrients: Phosphorus concentration oscillated between 0.5 and 0.9 kg/ha (Table 9) but without significant differences both between areas or seasons (Table 10). On the other hand, potassium concentration ranged from 130 up to 190 kg/ha (Table 9), with significant differences between areas, but not between seasons (Table 10). Area HIGH showed a lower potassium concentration (Table 11). Nitrate concentration varied between about 3 and 6 kg/ha (Table 9), with significant differences between areas, but not between seasons (Table 10 and 11). Ammonia concentration varied from 43 up to 108 kg/ha (Table 9), however, without significant differences both between areas or seasons (Table 10).

Table 10
Comparison of soil pH and conductivity, phosphorus, potassium, nitrate and ammonia concentrations in soil samples collected in different seasons and in areas with different degrees of infestation by *Clethra arborea* at Tronqueira (São Miguel Island, Azores). Effect of area and sampling season. Kruskal-Wallis test ($\chi 2$, test statistic; p, probability; N, number of soil samples); Mann-Whitney test (U, test statistic); one factor ANOVA (F, test statistic); t - test (t, test statistic).

Variable	Area			Season		
	$\chi 2$	p	n	$\chi 2$	p	n
pH	10.30	0.0580	90	1.50	0.4720	90
Conductivity	2.05	0.3577	90	19.18	0.0001	90
	$\chi 2$	p	n	U	p	n
Potassium	5.03	0.0097	60	0.69	0.4930	60
Phosphorus	2.53	0.2817	60	448.50	0.9485	60
	F	p	n	t	p	n
Nitrate	9.37	0.0092	60	388.50	0.3540	60
Ammonia	0.01	0.9861	60	0.66	0.5150	60

Leaf litter: Leaf litter accumulated in different areas varied considerably (Table 12). Significant differences were found between areas with different infestation levels (ANOVA: F=4.68; p=0.012) but not between sampling seasons (ANOVA: F=1.17; p=0.316). Significant differences were found between HIGH (91.9 ± 15.64) and MEDIUM (91.4 ± 16.27) relative to LOW (59.43 ± 11.97).

Vegetation structure: As expected, *C. arborea* was the most frequent tree in HIGH and MEDIUM, followed by *L. azorica* (Fig. 1). *E. azorica* was the most frequent tree in LOW, followed by *L. azorica*, *I. perado* ssp. *azorica* and *C. arborea*. Global tree densities were estimated at 9061, 5533 and 15741 per hectare for HIGH, MEDIUM and LOW, respectively. As expected, *C. arborea* showed a high density at HIGH while, at LOW, this was true for *E. azorica* (Fig. 2).

Table 11
Comparison of soil conductivity (ppm) and pH, phosphorus, potassium, nitrate and ammonia concentrations (kg/ha) in soil samples collected in different seasons and in areas with different degrees of infestation by *Clethra arborea* at Tronqueira (São Miguel Island, Azores). Different letters indicate significant differences (Nemenyi test for soil conductivity and nitrate concentration; Tukey HSD test for potassium concentration; α= 0.05). Only for those variables showing significant differences according to the Kruskal-Wallis test (Table 10).

Variable	Factor		
	Season		
	Winter	Spring	Summer
Soil conductivity	31.33 ± 3.56 a	43.77 ± 4.83 b	28.19 ± 1.54 a
	Area		
	HIGH	MEDIUM	LOW
Potassium	134.69 ± 11.82 a	177.65 ± 13.92 b	176.29 ± 26.12 b
Nitrate	5.80 ± 0.29 a	3.35 ± 0.57 b	5.50 ± 0.93 a

Table 12
Leaf litter (dry weight in g/m^2) accumulated in three areas with different degrees of infestation (High, Medium, Low) by *C. arborea* at Tronqueira (São Miguel Island, Azores). Different letters indicate significant differences (Tukey HSD test, α= 0.05). (Mean ± SE).

Season	Area		
	HIGH	MEDIUM	LOW
Winter	92.03 ± 16.63	98.49 ± 16.76	69.73 ± 14.26
Spring	97.95 ± 9.42	105.14 ± 14.48	55.44 ± 10.26
Summer	85.71 ± 20.87	55.50 ± 17.56	53.13 ± 11.40

Basal diameter of the trunk showed some variation between areas, for the same species (Fig. 3), but without significant differences (Table 13). While no significant differences were found between areas for canopy lower limit (Fig. 4, Table 13), significant differences were found for canopy upper limit (Table 13 and 14). Canopy diameter was significantly different between areas (Table 13), with a tendency for larger canopy at HIGH (Table 14).

At HIGH and MEDIUM, the greatest biovolume was provided by *C. arborea* (50%), while in LOW it was provided by *E. azorica* (50%) (Fig. 5). The percentage of *I. perado* ssp.

azorica biovolume was also highest at LOW. As expected, the mean biovolume of *C. arborea* decreased from HIGH to LOW (Fig. 6). Mean biovolume significantly increased from LOW to HIGH (Table 13 and 14). As expected, *C. arborea* projected biovolume per hectare was highest at HIGH (Fig. 7).

Table 13
Comparison of the vegetation structure in three areas with different degrees of infestation by *Clethra arborea* at Tronqueira (São Miguel Island, Azores). Kruskal-Wallis test ($\chi 2$, test statistic; p, probability; N, number of soil samples); one factor ANOVA (F, test statistic).

Variable	Area		
	$\chi 2$	p	n
Canopy upper limit	14.50	0.0007	180
	F	p	n
Biovolume	4.02	0.0196	180
Basal diameter	1.67	0.1917	180
Canopy diameter	7.40	0.0008	180
Canopy lower limit	1.14	0.3222	180

Table 14
Vegetation structure in three areas with different degrees of infestation (High, Medium, Low) by *Clethra arborea* in Tronqueira (São Miguel Island, Azores). Different letters indicate significant differences (HSD Tukey test; α=0.05). Only for those variables with significant differences given by ANOVA (Table 13). (Mean ± SE).

Variable Area	Mean SE
Biovolume (m^3)	
HIGH	20.09 ± 7.42 a
MEDIUM	7.28 ± 2.58 b
LOW	2.65 ± 0.56 c
Canopy diameter (m)	
HIGH	2.32 ± 0.32 a
MEDIUM	1.65 ± 0.24 ab
LOW	1.24 ± 0.17 b
Canopy upper limit (m)	
HIGH	2.32 ± 0.22 a
MEDIUM	2.57 ± 0.23 b
LOW	2.37 ± 0.17 a

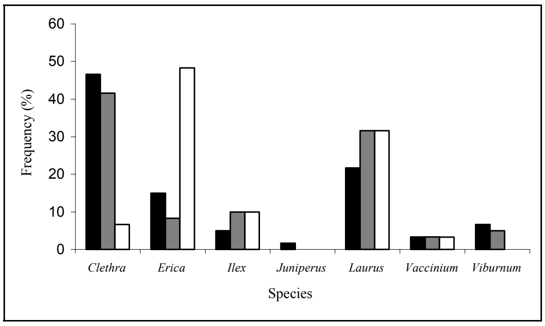

Fig 1. Frequency of tree species found in three areas with different degrees of infestation by *C. arborea* at Tronqueira (São Miguel Island, Azores): heavily invaded area (black); partially invaded area (gray); lightly invaded area (white). By order in the chart: *Clethra arborea*, *Erica azorica*, *Ilex perado* ssp. *azorica*, *Juniperus brevifolia*, *Laurus azorica*, *Vaccinium cylindraceum* and *Viburnum tinus* spp. *subcordatum*.

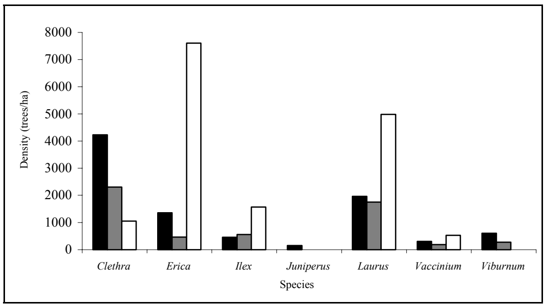

Fig. 2. Tree density (number of trees/ha) in three areas with different degrees of infestation by *Clethra arborea* at Tronqueira (São Miguel Island, Azores): heavily invaded area (black); partially invaded area (gray); lightly invaded area (white). (For species names see Fig. 1)

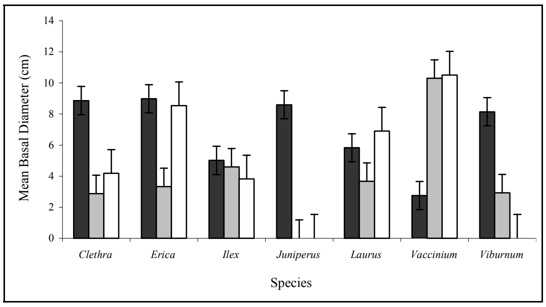

Fig. 3. Mean basal diameter of the species found in three different areas with different levels of infestation by *Clethra arborea* at Tronqueira (São Miguel Island, Azores): heavily invaded area (black); partially invaded area (gray); lightly invaded area (white). Error bar

corresponds to standard error. (For species names see Fig. 1).

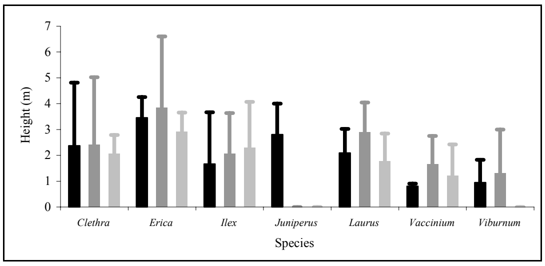

Fig. 4. Average lower and upper canopy limits (m) for each species found in three areas with different degrees of infestation by *C. arborea* at Tronqueira (São Miguel Island, Azores): heavily invaded area (black); partially invaded area (dark gray); lightly invaded area (light gray). Wider bar corresponds to trunk height. Error bars correspond to tree height. (For species names see Fig. 1).

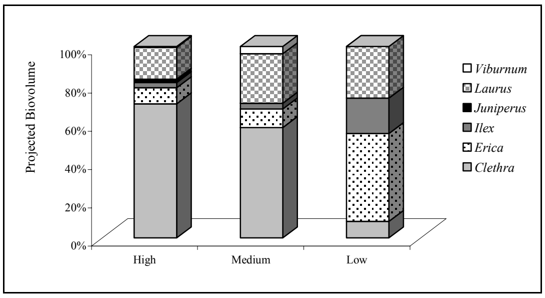

Fig. 5. Percentage of projected biovolume for each species in three areas with different degrees of infestation by *Clethra arborea*: High (heavily invaded); Medium (partially invaded); Low (lightly invaded). (For species names see Fig. 1).

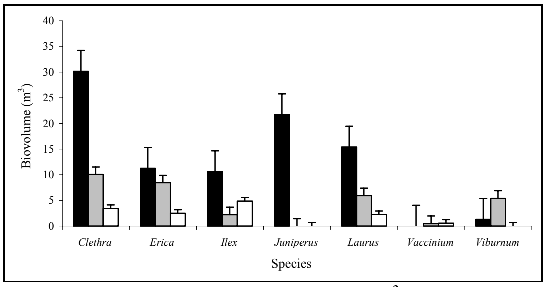

Fig. 6. Mean projected biovolume (m^3) per tree, for each species found in three areas with different degrees of infestation by *Clethra arborea*: heavily invaded area (black); partially invaded area (gray); lightly invaded area (white). Error bars correspond to standard error. (For species names see Fig. 1).

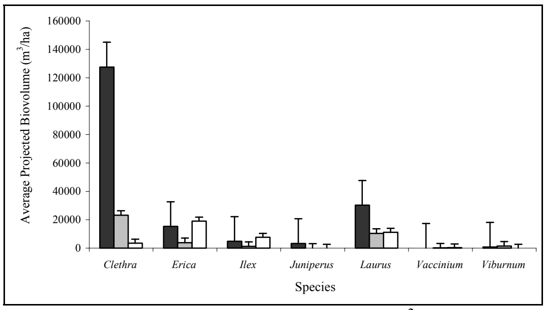

Fig. 7. Average projected biovolume (m^3/ha) for each species in three areas with different degrees of infestation by *Clethra arborea*: heavily invaded area (black); partially invaded area (gray); lightly invaded area (white). Error bars correspond to standard error. (For species names see Fig. 1).

DISCUSSION

The values for soil conductivity, pH and nutrient concentrations are consistent with the previous classification of the sampled soil as a Saturated Andosoil (MADRUGA 1996). While the considerable amount of ammonia found in the soil is probably associated with *C. arborea* via increased leaf litter production and its decomposition (DIAS 1996), the differences found in other soil properties for the three areas are not. Variation in soil parameters is probably due to the annual cycle of lixiviation and to the natural heterogeneity of soil properties (DIAS 1996). Thus, a direct impact of a plant invasion on soil properties was not confirmed in this work. However, an increase in leaf litter accumulation was clearly associated with the invasion by *C. arborea*. When comparing microhabitats associated to *C. arborea*, *L. azorica* and *I. perado* ssp. *azorica*, and areas with different degrees of infestation, it was clear that *C. arborea* produced larger amounts of leaf litter than native species. This is in agreement with previous observations of seasonal leaf litter production by *C. arborea*, which showed a considerable increase during autumn and winter (SILVA 2001). This might also be related to the high projected biovolume of *C. arborea*, in contrast with the much smaller biovolume of the native species. All of the tree species in the study are evergreen but *C. arborea* has large leaves, which are less lethery than others. Also, in São Miguel it was found to be semi-evergreen, with highest values of leaf fall in Autumn and Winter (SILVA 2001).

The number of seedlings is negatively associated with leaf litter production (CRAWLEY 1997). In this study, a tendency was found for a reduction of the number of all seedlings in *C. arborea* microhabitats. Clear reductions were found regarding the percentage of seedlings belonging to native taxa. In *C. arborea* microhabitats a high percentage of seedlings belonged to this species compared to numbers of native species.

Among the areas analysed, that showing a lower level of infestation by *C. arborea* corresponded to the alliance *Juniperion-brevifolii* as proposed by SJÖGREN (1973), and in particular to the association *Erico-Myrsinetum* On the other hand, the areas with higher levels of infestation are very similar to the *Clethro-Laurion* alliance from Madeira. In that alliance, *C. arborea* is expected to establish with *L. azorica*, after a stage dominated by shrubs (SJÖGREN 1972), namely *Erica scoparia* L. (Ericaceae) and *Vaccinium padifolium* Lk. (Ericaceae). Interestingly, in Madeira *C. arborea* is not a dominant tree in the Laurel Forest (NEVES *et al.* 1996), where it is surpassed by *L. azorica*, *Myrica faya* Aiton (Myricaceae) and *Octoea foetens* Baill (Aiton) (Lauraceae). In São Miguel, likewise, invaded vegetation is, for the most, in a shrub habit so that *C. arborea* enters the ecological succession in a stage where it later becomes the dominant tree.

C. arborea is a species with the ability to increase both density and biovolume/ha, and by this way forming monospecific stands, completely overgrowing native vegetation. The percentage of total projected biovolume in the invaded areas is much higher for *C. arborea* when compared to the native taxa. Native species showed a reduced vertical stratification of their canopy, leading to a reduced contribution to total projected biovolume. The projected biovolume for this type of vegetation was estimated at 48000 m^3/ha (DIAS 1996). In this work, this value was largely exceeded in the area with the highest infestation level (HIGH), where a value of 120000 m^3/ha was found. Thus, *C. arborea* has the ability to maintain both high densities and high biovolumes.

This is a very important fact regarding the conservation of the native vegetation remains in São Miguel and also *P. murina* habitat, since *C. arborea* is clearly affecting vegetation structure of the native communities. Further, *I. perado* ssp. *azorica*, an important food resource during *P. murina* breeding season (RAMOS 1993), showed a considerable reduction in biovolume percentage in the two more heavily invaded areas. We thus conclude that native vegetation and *P. murina* habitat have been negatively affected by the invasion of *C. arborea* at Tronqueira Special Protection Area.

ACKNOWLEDGEMENTS

Special thanks are due to the Entomology and Biological Control Section (Biology Department, University of the Azores).

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Accepted 3 December 2003.