



# The geographic distribution of pubescence in the sea daisy, *Borrichia aborescens*, on Bahamian Islands

LLOYD W. MORRISON

Section of Evolution and Ecology, Division of Biological Sciences, and Center for Population Biology, University of California, Davis, CA 95616, U.S.A.

## ABSTRACT

*Borrichia aborescens* (L.) DC. is a salt-tolerant perennial herb that is common on small islands in the central Bahamas. Two morphotypes are present: one with densely pubescent leaves and one with glabrous leaves. I conducted surveys in three archipelagos to document the geographical distribution of pubescence in this species and to infer the underlying mechanisms. *B. aborescens* was also grown from seed in a greenhouse. The pubescent form of *B. aborescens* was relatively more abundant on small islands than on nearby large 'mainland' islands. In two of the three archipelagos, pubescence increased with distance on small islands. The pubescent form was relatively more abundant on small islands

exposed to the open ocean compared to small islands that were protected by mainland islands or reefs on all sides. On a large mainland island, the pubescent form decreased in relative abundance inland from the coast. *B. aborescens* cultivated in a greenhouse revealed the effect of a genetic factor on the expression of pubescence. The observed patterns of variation are consistent with a physiological explanation for the adaptive benefit of pubescence. Trichomes may prevent physical blockage of the stomata by accumulation of salt in areas near breaking waves and salt spray.

**Key words** Archipelago, Bahamas, glabrous, island biogeography, leaf hairs, salt spray, stomata, trichomes.

## INTRODUCTION

The adaptive value of different morphological forms represents one of the most basic questions in evolutionary botany (Levin, 1973). The presence of trichomes, or pubescence, is an important character in this regard because of its near ubiquity in terrestrial plants, especially in angiosperms (Johnson, 1975). If selection pressures have been important in shaping the expression of pubescence, there should exist geographical patterns of its occurrence that are correlated with the causative environmental factors (Johnson, 1975).

Pubescence may function as an adaptation to biotic or ecophysiological factors (Johnson, 1975; Gutschick, 1999). Trichomes could be a defensive mechanism against predators, pathogens and parasites, as demonstrated or suggested by numerous studies (reviewed by Levin, 1973; Juniper & Southwood, 1986; Smith, 1989; Myers & Bazely, 1991; Fritz & Simms, 1992). Alternatively, pubescence could play a role in physiological functions, such as mediating water balance

or temperature (Johnson, 1975; Ehleringer *et al.*, 1976; Ehleringer & Mooney, 1978). In some cases trichomes may perform a dual role, having both defensive and physiological functions (Woodman & Fernandes, 1991).

*B. aborescens* (L.) DC. (Compositae) is a salt-tolerant perennial herb found in the Caribbean region that occurs as two forms: one with dense pubescence that gives the leaves a silver appearance and one with glabrous leaves that appear green. Some individuals have both pubescent and glabrous leaves (Semple, 1978; Correll & Correll, 1982). Both forms of *B. aborescens* are very common on small rocky islands in the central Bahamas. I conducted surveys to document the geographical distribution of pubescence in this species. *B. aborescens* was also grown from seeds in a greenhouse, to provide an initial appraisal of the relative contribution of the genetic and environmental factors that could affect the expression of pubescence.

The following questions were addressed: (1) what patterns of geographical variation of pubescence in *B. aborescens* exist within and among islands? (2) which variable(s) may predict the predominant form found in a particular area or on a particular island? and (3) how might pubescence be adaptive in this species?

Present address: Center for Medical, Agricultural and Veterinary Entomology, USDA-ARS, PO Box 14565, Gainesville, FL 32604 USA. E-mail: lmorrison@gainesville.usda.ufl.edu

## METHODS

### Island surveys

Surveys for *B. aborescens* were conducted in three archipelagos of small islands in the central Bahamas: (1) 107 islands in the Exuma Cays between O'Briens Cay to the north and Bitter Guana Cay to the south, (2) 25 islands to the south-west and 11 islands to the north-east of Georgetown, Great Exuma and (3) 48 islands off the north-east coast of Andros, between Nicholl's Town to the north and Staniard Creek to the south. All islands surveyed had vegetated areas < 6000 m<sup>2</sup>. Surveys were conducted in the Exuma Cays in May (1998); at Great Exuma in October 1998 and at Andros in April 1999.

The small islands in the Exuma Cays and south-west of Great Exuma are protected from the deep water Exuma Sound to the north-east by larger, mainland islands, but exposed to the shallow Great Bahama Bank to the south-west. Small islands on the north-east side of Great Exuma are protected by Stocking Island on one side and Great Exuma on the other. The small islands near Andros are located between the mainland island of Andros to the west and a barrier reef to the east (~8 km offshore), which provides protection from the deep water tongue of the ocean. Maps of the study regions are presented in Morrison (1997) (Exumas Cays and Andros) and Spiller *et al.* (1998) (Great Exuma).

Three 'mainland' island areas were also surveyed for *B. aborescens*: (1) the interior of Staniel Cay, a relatively large (~2.6 km<sup>2</sup>) island in the Exuma Cays; (2) along a lagoon on Staniel Cay from the ocean to the interior; and (3) an inland region of north-eastern Andros (the largest island in the Bahamas). 'Mainland' islands were several orders of magnitude larger than the small islands.

Surveys of the small islands were conducted by walking over each island in its entirety and visually estimating the proportion of *B. aborescens* leaves that were of the silver and green forms. Sizes of *B. aborescens* plants varied greatly, and estimates were based on plant biomass, rather than numbers, of individual plants. On the mainland islands, transects 100 m long by 10 m wide were surveyed in the same manner. Almost all individuals of *B. aborescens* were either entirely silver or entirely green. Rarely plants with both silver and green leaves were observed; in such cases, the older leaves were green and the younger leaves silver.

This method was inherently subjective. One form or the other was so predominant, however, that it accounted for ≥ 95% (estimated) of the total foliage in most cases (69% of the mainland island transects and 70% of the small islands). Often only one form was present (26% of the mainland island transects and 49% of the small islands). Because the data are so robust (see Results), it is unlikely that subjectivity associated with the sampling biased the significance of the results. Additionally, all transects and small islands were sampled by the same investigator. Because of the number and size of the

small islands and transects sampled, and the structural vegetation complexity, no methods of quantifying variation in leaf morphology would have been without sampling error, and more objective methods would have been more time-consuming than necessary.

A simple linear regression was employed to describe the relationship between frequency of pubescence and distance inland along the lagoon on Staniel Cay. Stepwise multiple regressions were performed on the data for the three archipelagos of small islands. The dependent variable was proportion of the pubescent form of *B. aborescens* (arc-sine square-root transformed). Three independent variables were tested: vegetated area (log transformed), distance to the nearest mainland island (log transformed), and island elevation. A forward stepwise procedure was used, which selected predictor variables sequentially in order of their relative reduction of sums of squares, if their partial *F* exceeded the *F*-to-enter level. The minimum *F* acceptable to enter was set at 4, corresponding to a ~0.05 level of significance for any single test (Neter *et al.*, 1985).

### Greenhouse experiment

Seeds were collected at random from 10 pubescent and 10 glabrous *B. aborescens* plants in the interior of Staniel Cay, Exumas in May 1998. Seeds from different plants were randomly mixed within each category of parental type (pubescent or glabrous), and planted in a common greenhouse environment in July 1998. In September 1998, 30 seedlings from each parental type were selected and transplanted in individual pots. The first leaves of the pubescent and glabrous forms are both glabrous (Semple, 1978), so at the time of transplanting no pubescence was apparent. The plants were maintained under a 12 : 12 light : dark cycle and watered three times per week. The experiment was terminated after 10 months, and numbers of pubescent and glabrous plants were recorded. A chi-square test of homogeneity (Daniel, 1990) was used to test whether the two parental forms produced different frequencies of pubescent offspring.

## RESULTS

### Island surveys

*B. aborescens* occurred on 66.4, 97.2 and 35.4% of the vegetated islands surveyed in the Exuma Cays, Great Exuma and Andros regions, respectively (Table 1). A number of islands near Andros were low-lying and contained only intertidal mangrove species (red mangrove, *Rhizophora mangle* L.; white mangrove, *Laguncularia racemosa* [L.] Gaertn. f.; and black mangrove, *Avicennia germinans* [L.] L.), and were probably not able to support *B. aborescens*. If these mangrove-only

**Table 1** Distribution of the glabrous and pubescent forms of *Borrhichia aborescens* (L.) DC. in three archipelagos of Bahamian islands

Archipelago	Number of islands surveyed	% of islands with both forms	% of islands with pubescent leaves only	% of islands with glabrous leaves only	% of islands with no <i>B. aborescens</i>
Exuma Cays	107	38.4	27.1	0.9	33.6
Great Exuma	36	33.3	61.1	2.8	2.8
Andros	48	25.0	2.1	8.3	64.6
Andros (excluding mangrove-only islands)	28	42.9	3.6	14.3	39.2

**Table 2** The proportion (mean  $\pm$  SD) of the pubescent form of *Borrhichia aborescens* (L.) DC. on small islands in three archipelagos and on three mainland island transects. 'n' is the number of islands or transects. *P*-values indicate significance of two-tailed one sample *t*-tests that compared the observed proportion to a proportion of 0.5, to determine whether the pubescent or glabrous form predominated in an area

Location	Proportion of pubescent form	<i>n</i>	<i>P</i>
Archipelago			
Exuma Cays	0.87 $\pm$ 0.21	66	0.0001*
Great Exuma	0.93 $\pm$ 0.21	35	0.0001*
Andros	0.35 $\pm$ 0.35	17	0.0946
Mainland transects			
Staniel Cay, Exuma Cays (inland)	0.04 $\pm$ 0.04	10	0.0001*
Staniel Cay, Exuma Cays (lagoon)	0.19 $\pm$ 0.17	10	0.0012*
Andros (inland)	0.04 $\pm$ 0.06	15	0.0001*

\* Significant at  $\alpha = 0.05$  by the sequential Bonferroni method (Rice, 1989).

islands are excluded, *B. aborescens* occurred on 60.8% of the islands near Andros. In all archipelagos, both forms of *B. aborescens* were found on at least one-third of the islands (excluding mangrove-only islands near Andros). A relatively large proportion of small islands in the Exuma Cays and at Great Exuma contained only the pubescent form, although this was not true for islands near Andros (Table 1).

Considering the relative proportion of pubescence on the small islands, pubescent leaves comprised 87, 93 and 35% of the *B. aborescens* foliage on small islands in the Exuma Cays, Great Exuma and Andros regions, respectively (Table 2). Significantly more foliage was pubescent than glabrous on the small islands in the Exuma Cays and Great Exuma, but not at Andros (two-tailed one-sample *t*-tests). The small islands in all three archipelagos were physically similar, composed of hard limestone and containing very little soil. The small islands near Andros were not as high as the islands

in the Exuma Cays or Great Exuma, however [Andros,  $0.46 \pm 0.35$  m; Exuma Cays,  $1.93 \pm 0.96$  m; Great Exuma,  $1.73 \pm 0.88$  m (mean  $\pm$  SD)], but otherwise were similar in appearance.

In all three mainland island areas surveyed, the glabrous form of *B. aborescens* predominated (Table 2). In the inland areas of both Staniel Cay and Andros 96% of the foliage was glabrous. Along the lagoon of Staniel Cay, 81% of the foliage was glabrous. In all three transects significantly more foliage was of the glabrous form (two-tailed one-sample *t*-tests).

Significantly more foliage was pubescent on the small islands compared to the mainland for both the Exuma Cays and Andros (Table 2) [two-tailed *t*-tests,  $P = 0.0001$  for the Exuma Cays (combining the lagoon and inland transects for the mainland sample);  $P = 0.0004$  for Andros].

On Staniel Cay, Exumas, a greater proportion of pubescence was found along the lagoon than in the interior of the island (Table 2) (two-tailed *t*-test,  $P = 0.035$ ). Transects surveyed along the lagoon revealed a significant decrease in the proportion of the pubescent form as distance from the ocean increased ( $Y = 38.36 - 0.042X$ ,  $r^2 = 0.44$ ,  $F = 6.21$ ,  $P = 0.037$ ).

In the archipelagos at Andros and Great Exuma, distance was the only independent variable selected as significant by the stepwise procedure. The proportion of pubescence increased with distance for both archipelagos (Table 3). No independent variables were selected as significant predictors for the Exuma Cays.

At Great Exuma, a significantly greater proportion of pubescence in *B. aborescens* was found on small islands exposed to the open ocean (SW side) compared to small islands protected on both sides (NE side) [ $99.2 \pm 1.5$  vs.  $77.7 \pm 33.4$  (mean  $\pm$  SD), exposed and protected islands, respectively;  $P = 0.005$ , two-tailed *t*-test]. Exposed islands were more distant from the mainland of Great Exuma than protected islands, however, by an order of magnitude [ $3854 \pm 3307$  vs.  $396 \pm 388$  m (mean  $\pm$  SD), exposed and protected islands, respectively;  $P = 0.0001$ , two-tailed *t*-test following a log transformation]. If the proportion of pubescence as a function of distance is examined separately for protected and exposed islands, neither regression is significant

**Table 3** Variables selected by the forward stepwise multiple linear regression analyses for the three different archipelagos. 'Pub' = proportion of pubescence, 'Dist' = distance to the nearest mainland island

Archipelago	Best model	$r^2$	$F$
Andros	Pub = $-50.77 + 31.12$ Dist	0.25	5.08
Exuma Cays	No variables selected as significant		
Great Exuma	Pub = $36.23 + 14.40$ Dist	0.28	11.49

**Table 4** Results of greenhouse experiments. 'n' is the number of plants surviving until the end of the experiment

Parental form	Proportion of offspring			n
	Glabrous	Pubescent	Intermediate	
Pubescent parent	66.7	30.0	3.3	30
Glabrous parent	96.7	3.3	0.0	30

( $F = 1.75$ ,  $P = 0.22$  for protected islands,  $F = 0.24$ ,  $P = 0.63$  for exposed islands).

Overall, small islands that were protected on all sides by mainland islands or reefs had a lower proportion of pubescence than small islands exposed on one side to the open ocean [i.e. Andros (35%) and small islands NE of Great Exuma (78%) vs. the Exuma Cays (87%) and small islands SW of Great Exuma (99%)].

### Greenhouse experiment

*B. aborescens* was easily cultivated in a greenhouse, and mortality of the plants selected for the experiment was zero. The majority of offspring from both pubescent and glabrous parents was of the glabrous form. Glabrous parents produced significantly more glabrous offspring, however ( $\chi^2 = 9.0$ ,  $P = 0.01$ ; Table 4). A few intermediate offspring (with both glabrous and pubescent leaves or leaves with partial pubescence) were observed from pubescent parents, but none from glabrous parents.

## DISCUSSION

### Distribution of the pubescent and glabrous forms

*B. aborescens* occurs in southern Florida, the West Indies, Bermuda and the Atlantic coast of northern Central America (Semple, 1978; Correll & Correll, 1982). At one time the two morphotypes were considered separate species, *B. glabrata* and *B. argentea*, referring to the glabrous and pubescent forms, respectively. Some plants throughout this range have both glabrous and pubescent leaves, however,

indicating the existence of a single, variable species (Semple, 1978).

My surveys revealed that, in the central Bahamas, the pubescent form of *B. aborescens* was relatively more common: (1) on smaller islands compared to nearby large mainland islands, in all three archipelagos; (2) near the coast compared to the interior of a large mainland island; (3) on more distant small islands in two of three archipelagos; (4) and on small islands exposed to the open ocean compared to islands sheltered on all sides by larger islands or reefs, in two possible comparisons.

### Greenhouse experiment

The greenhouse experiment indicated the presence of a genetic factor acting on pubescence, as significantly fewer pubescent offspring arose from glabrous parents. It is likely that the glabrous form predominated in the greenhouse experiments overall because seeds were collected from plants in the interior of Staniel Cay, where the glabrous form was abundant.

Because juvenile leaves of seedlings are always glabrous (Semple, 1978) and the timing of the onset of pubescence is unknown, it is possible that some of the glabrous individuals could have eventually produced pubescent leaves. Although the greenhouse experiment was run for 10 months, most *B. aborescens* plants on the islands surveyed were many years old (Morrison, 1997).

Flowers in *Borrchia* are clustered together in dense heads, which are composed of both pistillate ray florets and perfect disc florets. Although the degree of self-compatibility in *B. aborescens* has not been evaluated, a study of the neighbourhood genetic structure of the congener *B. frutescens* revealed evidence for complete outbreeding (Antlfinger, 1982).

In the only other account of cultivation of *B. aborescens* in a greenhouse, a single plant was observed to cycle between leaf forms over seasons, suggesting a possible inducement of pubescence by some environmental factor (Semple, 1978). Thus the overall expression of pubescence in nature may result from a complex interaction of genetics and environment.

### Benefits of pubescence

#### Defensive functions

Mechanical defence has been attributed to trichomes in many species (see reviews in Levin, 1973; Southwood, 1986; Myers & Bazely, 1991; Gutschick, 1999). In the central Bahamas the buttonwood, *Conocarpus erectus* L., is very common and exhibits similar morphological variation in leaf pubescence (Semple, 1970). Schoener (1987, 1988) determined that buttonwood trees with pubescent leaves had less herbivore damage than trees with glabrous leaves, and found a higher percentage of pubescence in buttonwood on large islands and

near islands. Higher frequencies of pubescent leaves on buttonwood were positively correlated with herbivore abundance, which increases with island size and decreases with distance. Thus Schoener's (1987, 1988) results suggest that pubescence in buttonwood is adaptive against herbivory.

This is contrary to the pattern observed in *B. aborescens*, in which pubescence was relatively more common on distant islands, and on small islands compared to large, mainland islands. Qualitatively, herbivory damage in *B. aborescens* in general appears to be much less than that documented for buttonwood (Schoener, 1987) in the central Bahamas (L.W. Morrison, personal observations). It is possible that *B. aborescens* is chemically defended against herbivores, or that it contains relatively little nutritional value.

### Ecophysiological functions

Pubescence has been positively associated with 'harsh' environments (Johnson, 1975). Most hypotheses relating to the physiologically adaptive value of pubescence centre around water economy, usually focusing on transpiration or radiant energy absorption (reviewed in Johnson, 1975). In general, pubescence is thought to affect physiological processes both directly and indirectly, through changes in light absorbance and modification of boundary layer characteristics, which in turn influence photosynthesis and transpiration, both of which are dependent upon temperature (Ehleringer & Mooney, 1978).

The ultimate functional significance of leaf structure is dependent upon the environment, however, and the relationship between functional significance and structure is not always intuitive (Press, 1999). For example, photosynthetic gas exchange is limited on wet leaf surfaces because carbon dioxide diffuses much more slowly through water than air. Recent studies have demonstrated that trichomes may reduce the amount of moisture in direct contact with the leaf epidermis and stomata, thus limiting the interference of surface moisture on gas exchange (Smith & McClean, 1989; Brewer & Smith, 1995, 1997).

By the same token, trichomes in *B. aborescens* may function to prevent physical blockage of the stomata, not by moisture *per se*, but rather by the accumulation of salt crystals from wave spray. Waves breaking on islands produce a salt spray that settles out with distance from the source. This spray would accumulate on the leaves of plants near the shore, and as the water evaporated a salt crust would be left behind. On glabrous leaves, the salt crust would be in direct contact with the leaf surface and stomata, whereas on pubescent leaves trichomes may limit direct contact of salt crystals with stomata.

This hypothesis fits the observed patterns well. The amount of salt spray settling on plants would be greater on smaller

islands (which have relatively more coastline and on which any given point is relatively closer to the coastline), distant islands (which are on average located in deeper water and are exposed to high wave energy), and along the coast compared to the interior of large islands.

*B. frutescens* (L.) DC. is a congener of *B. aborescens* that occurs along shores of the Gulf of Mexico and Atlantic coast of the south-eastern United States. *B. frutescens* is almost always characterized by pubescent leaves, although some plants may rarely produce glabrous leaves (Semple, 1978). A study of *B. frutescens* conducted in Georgia documented that numerous morphological characters revealed significant variation over very short distances (2–5 m) associated with a salinity gradient, although pubescence was not one of the characters evaluated (Antlfinger, 1981).

### Implications

Pubescence in *B. aborescens* varied dramatically both among and within islands. Little herbivore damage was observed on either the glabrous or pubescent forms, suggesting that pubescence in this species is more advantageous to physiological processes than defensive functions. The expression of pubescence appears to be controlled to some extent by genetic factors, although environmental inducements cannot be ruled out. Preventing physical blockage of stomatal pores by salt crystals may be the most important benefit conferred to *B. aborescens* by leaf trichomes in this archipelago. In all comparisons, islands or regions of islands with higher frequencies of pubescence represented areas with more salt spray.

The patterns documented here may not be unique to this taxon. For example, the genus of rock-daisies, *Perityle* (Asteraceae), occurring on islands in the Gulf of California, reveal varying amounts of leaf pubescence (Cody *et al.*, 1983). Although variation in leaf morphology of this group has not been quantitatively examined, analogous patterns may exist.

This study is the first, to my knowledge, to propose the hypothesis that trichomes may function to prevent physical blockage of stomata by accumulated salt crystals in coastal environments. Such a benefit would not necessarily be restricted to this species, and any plant species or populations found near areas of salt spray may benefit from pubescent leaves.

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## BIOSKETCH

**Lloyd Morrison** has studied Bahamian ants and plants since 1989. His research interests include island biogeography, metapopulation dynamics, invasion ecology and resistance and resilience of insular communities in relation to disturbance.