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ORNITHOCOPROPHILOUS PLANTS OF MOUNT DESERT ROCK, A REMOTE BIRD-NESTING ISLAND IN THE GULF OF MAINE, U.S.A.

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ABSTRACT. Plants growing on seabird-nesting islands are uniquely adapted to deal with guano-derived soils high in N and P. Such ornithocoprophilous plants found in isolated, oceanic settings provide useful models for ecological and evolutionary investigations. The current study explored the plants found on Mount Desert Rock (MDR), a small seabird-nesting, oceanic island 44 km south of Mount Desert Island (MDI), Hancock County, Maine, U.S.A. Twenty-seven species of vascular plants from ten families were recorded. Analyses of guano-derived soils from the rhizosphere of the three most abundant species from bird-nesting sites of MDR showed significantly higher ($P < 0.05$) NO_3^-, available P, extractable Cd, Cu, Pb, and Zn, and significantly lower Mn compared to soils from the rhizosphere of conspecifics on non-bird nesting coastal bluffs from nearby MDI. Bio-available Pb was several-fold higher in guano soils than for background levels for Maine. Leaf tissue elemental analyses from conspecifics on and off guano soils showed significant differences with respect to N, Ca, K, Mg, Fe, Mn, Zn, and Pb, although trends were not always consistent. Two-way ANOVA indicated a significant interaction between species and substrate for Ca, Mg, Zn, and Pb tissue accumulation, showing that for these four elements there is substantial differentiation among species found on and off of guano soil. A compilation of species lists from other important seabird-nesting islands in the region suggested an ornithocoprophilous flora for northeastern North America consisting of 168 species from 39 families, with Asteraceae (29 taxa; 17.3%), Poaceae (25 taxa; 14.9%), Polygonaceae (10 taxa; 5.95%), Caryophyllaceae (9 taxa; 5.4%), and Rosaceae (9 taxa; 5.4%) as the most species-rich families. The taxa were predominantly hermaphroditic (69%) and perennial (66%) species, native (60%) to eastern North America.

Key Words: coastal ecology, insular ecology, ecotypic differentiation, geobotany, heavy metals, nitrophilous plants, ornithocoprophilous plants, phytogeography

The impacts of birds on the plants of islands are of major interest to botanists (Sekercioglu 2006); they are considered important not only for the distribution of propagules but also for the maintenance of plant communities (Cruden 1966; Gillham 1970; Howe and Smallwood 1982; Mulder and Keall 2001; Nathan and Muller-Landau 2000; Ornduff 1965). Birds of oceanic islands are of particular appeal to botanists as they often determine which plant species are dispersed and become established in such remote and often harsh settings (Magnusson and Magnusson 2000; Morton and Hogg 1989). Thus, in the last several decades, oceanic islands with nesting and roosting seabird colonies have attracted attention as model habitats for the study of plants uniquely adapted to long-distance dispersal and survival under edaphic conditions that are often physically and chemically extreme (Gillham 1953, 1956a, 1956b, 1961; Ornduff 1965; Sobey and Kenworthy 1979; Vasey 1985).

Birds affect island plants primarily via deposition of nutrients in urine and feces (Sobey and Kenworthy 1979; Wainright et al. 1998), feathers (Williams and Berruti 1978), egg shells (Siegfried et al. 1978), and carcasses (Williams et al. 1978)—often contributing to enhanced productivity of island ecosystems (Ellis 2005; Polis and Hurd 1996; Sánchez-Piñero and Polis 2000). In an era in which atmospheric N deposition is an increasing global concern (Adams 2003; Phoenix et al. 2006), the response of plants to excessive N deposition from seabirds is of considerable ecological interest (Ellis 2005; Hobara et al. 2005; Mizutani and Wada 1988; Sánchez-Piñero and Polis 2000). Seabird guano and other organic wastes are extremely high in PO_4^{3-}, NO_3^-, and NH_4^+ leading to poor growth and high rates of mortality in some species while enhancing growth in other species (Burger et al. 1978; Polis et al. 1997), often at the expense of many co-occurring species (Gillham 1961; Hogg and Morton 1983; Norton et al. 1997; Sobey and Kenworthy 1979). Seabirds directly have increased soil N and P concentrations up to six-fold in islands in the Gulf of California (Anderson and Polis 1999); deposition rates of 1000 kg N ha^{-1} yr^{-1} have been reported for Black Noddy (*Anous minutus*; Laridae) colonies on Heron Island, a subtropical coral cay of the Great Barrier Reef in Australia (Allaway and Ashford 1984). These rates far outweigh deposition rates associated with agricultural fertilizer application in the northern hemisphere (Pearson and Stewart 1993). Relative to annual N input from rainwater, N deposition by seabirds may be

100 times as high or more while P deposition may be 400 times greater (Mulder and Keall 2001).

Nitrogen found in guano is largely in the form of uric acid, with minor amounts as NH_4^+, amino acids, and protein (Lindeboom 1984; Schmidt et al. 2004). The rapid mineralization of uric acid to NH_4^+, however, converts guano-N to a form readily available for plant uptake (Wainright et al. 1998). High levels of NH_4^+ can adversely affect plants by inhibiting nitrate uptake (Boxman and Roelofs 1988), reducing uptake of essential cations (van Dijk et al. 1989), increasing tissue anion content (Errebhi and Wilcox 1990), and acidifying soils (Pearson and Stewart 1993). Toxic heavy metals and radionuclides also have been found at high concentrations in soils associated with seabirds (Dowdall et al. 2005; García et al. 2002; Hawke and Powell 1995; Liu et al. 2006; Pérez 1998). Soil pH is often low (3.3–6.4; Vasey 1990) in seabird colonies; however, this can vary depending on soil type and exposure to salt spray (Ellis 2005). In addition to changes in soil chemistry, seabirds generate considerable physical disturbance via courtship and nesting activities (Gillham 1956a; Sobey and Kenworthy 1979). Burrowing as well as activities such as trampling and uprooting can damage leaves and other plant parts, causing a detrimental impact on plant growth in seabird colonies.

The plant ecology of seabird colonies has been investigated to varying degrees worldwide (Ellis 2005). However, despite thousands of islands on the rocky coast of northeastern North America—many with nesting seabirds—there are only a handful of published studies that have examined aspects of plant ecology on maritime islands in the region (Ellis et al. 2006; Hodgdon and Pike 1969; Nichols and Nichols 2008; Smith and Schofield 1959). The current study explored the guano-associated flora of Mount Desert Rock, a remote, gull-nesting island off of the coast of Maine, U.S.A. The primary objectives of the study were to generate a checklist of plants on the island, to examine soil-tissue relations of nutrients and select heavy metals for a sample of species, and to compare with those of conspecifics collected from ecologically similar, yet non-bird nesting, coastal bluffs of nearby Mount Desert Island. We also compared previous checklists and herbarium specimens for six major seabird nesting islands in northeastern North America for which we were able to locate floristic data, including Mount Desert Rock, to determine if there is a unique plant community associated with seabird colonies in the region. Using this list, we determined plant habit, distributional range, and sexual system for the recorded species to elucidate any significant trends.

SITE DESCRIPTIONS

Mount Desert Rock (MDR; 43°58′12″N, 68°07′48″W) is a remote, treeless island in the Gulf of Maine, approximately 2 ha at low tide (Figure 1). The island, composed of granite, is approximately 9.1 m above sea level at its highest point at low tide. Since the early 19th century, the island has housed a lighthouse and several buildings to accommodate the light-keeper families. The island was occupied by the United States Coastguard from the 1950s to the late 1970s. The island was acquired by College of the Atlantic (COA) in 1996 and is currently home of the Edward McC. Blair Marine Research Station. The mean annual temperature for the island (1984–2001) is 6.9°C (range: −21.4 to 23.3°C; Allied Whale, COA, pers. comm.). There are no data for mean annual precipitation for MDR.

The island is a nesting site for approximately 300 birds each of Herring Gulls (*Larus argentatus*; Laridae) and Great Black-backed Gulls (*Larus marinus*; Laridae; Lillian Weitzman, COA, pers. comm.). Both gull species are abundant along the coast of Maine and are often found nesting sympatrically on offshore islands throughout northeastern North America (Rome and Ellis 2004). A large number of Harbor Seals (*Phoca vitulina*; Phocidae) and Gray Seals (*Halichoerus grypus*; Phocidae) also make MDR their home.

There is little soil development on the island, with most plants found adjacent to the buildings and lighthouse. The soil is coarse sand and gravel with incorporated organic matter. Bird droppings occur throughout the island, some areas more intensely covered than others. Plants are often found in rock crevices, in the shade of buildings, and in areas that retain moisture due to greater soil depth (up to 10 cm) and/or accumulation of organic debris. The COA Herbarium (HCOA), Bar Harbor, Maine, houses 25 vascular plant species collected from the island from 1973–1989. Bryophytes are surprisingly absent from the island while the lichen species *Xanthoria parietina* (L.) Th. Fr. (Teloschistaceae), is abundant on rock surfaces and wooden debris.

Mt. Desert Island (MDI; 44°34′8″N, 68°34′4″W; Figure 1), located 44 km north of MDR, is a large (ca. 28,100 ha) coastal island in Hancock County, Maine. A major tourist destination in

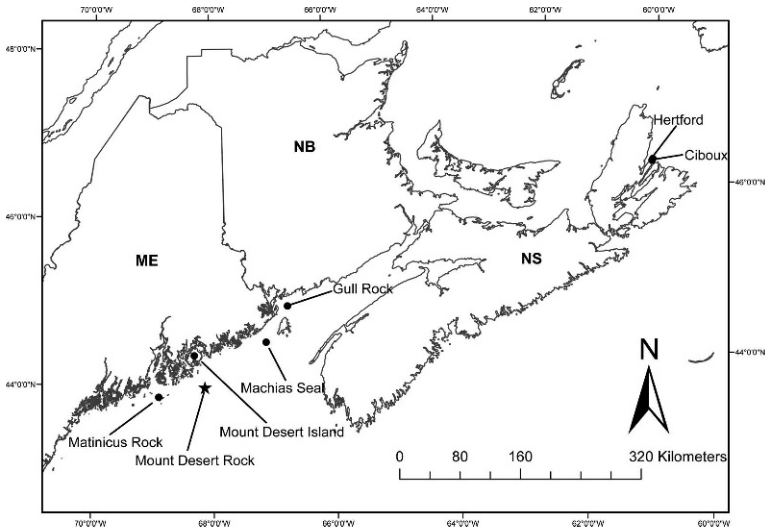

Figure 1. Location of Mount Desert Rock off the coast of northeastern North America, and five other gull-nesting islands used for floristic comparisons in this study. The location of Mount Desert Island is also indicated. Credit: Apoorv Gehlot.

the Northeast, MDI is home to Acadia National Park (ANP), with numerous rocky beaches, ocean cliffs, and coastal bluffs. The flora of ANP was recently reviewed by Greene et al. (2005). The island is approximately 470 m above sea level at its highest point at low tide and is exposed to the open waters of the Atlantic Ocean on the southeast. The bedrock is dominated by granite (Gilman et al. 1988); soil development varies throughout the island but is limited on coastal bluffs where comparisons for this study were made. The mean annual temperature is 7.5°C (range: −4.5°C to 20.1°C). Mt. Desert Island receives a mean annual rainfall of 138.30 cm and a mean annual snowfall of 181.86 cm. Averages for MDI were generated from data collected from 1985–2005 from National Oceanic and Atmospheric Administration weather station 170100/ 99999 located in ANP.

Soil and tissue sampling were carried out on both MDR and MDI from sites with similar ecological attributes with presence of seabirds as the only obvious variable. All sites sampled had similar aspect, elevation, exposure, proximity to water, and approximate soil depth. Soils on MDR were mostly organic due to abundant ornithogenic products while those collected from MDI were mostly mineral.

MATERIALS AND METHODS

Plant inventory. We visited MDR in August, 2007, and collected all vascular plant species found growing on the island. Plants were identified using Magee and Ahles (2007), Haines and Vining (1998), and Fernald (1991). All specimens were deposited at HCOA (N. Pope and N. Rajakaruna sample ID G001–G033). Nomenclature follows Integrated Taxonomic Information System [website (http://www.itis.gov); last accessed March 2008]. We also examined the collection at HCOA to record specimens collected from MDR during field excursions in 1973, 1978, and 1989.

Soil analysis. On MDR, approximately 200g of soil was dug using a plastic hand trowel from the rhizosphere of three individuals each of *Ligusticum scoticum* var. *hultenii* (Apiaceae), *Plantago major* (Plantaginaceae), and *Sonchus arvensis* subsp. *arvensis* (Asteraceae) growing on or adjacent to nesting sites. Sampling sites were selected based on the occurrence of plants of similar size and phenological states. Each sampling location was separated by at least 4 m; sampling depth was within 10 cm from the soil surface. Using the same criteria, soil samples were also collected from the rhizosphere of three individuals each, of the same three taxa, from coastal bluffs on MDI lacking seabird nesting sites but otherwise similar in aspect, exposure, soil depth, and elevation to sites on MDR. Samples were air-dried in the laboratory after which they were rid of stones, large gravel, bones, feathers, and other ornithogenic products; then the <2 mm fraction was obtained using a stainless steel sieve.

Analyses were conducted on the <2 mm fraction. Values for pH were obtained using the 1:2 soil-to-solution method with distilled water (Kalra and Maynard 1991). Exchangeable acidity was measured by titration using an extraction in 1M KCl (Burt 2004). Electrical conductivity (EC) was measured using a saturated paste extraction with distilled water (Gavlak et al. 2003). Nitrogen (NO_3^- and NH_4^+) was determined by extraction in a 1M KCl solution and measured by an ion analyzer (Burt 2004). Plant-available P was determined by extraction with a modified Morgan extract (0.62 N NH_4OH + 1.25 N CH_3COOH at pH 4.8; Wolf and Beegle 1995) and measured using inductively coupled plasma optical emission spectrometry (ICP-OES). Soils were analyzed for Al, Cd, Cr, Cu, Fe, Mn, Mo, Ni, Pb, and Zn by extraction with 0.005M diethylene triamine pentaacetic acid (DTPA) buffered with triethanolamine to pH 7.3 (Lindsay and Norvell 1978) for 2 hr. and subsequent detection by ICP-OES using matrix-matched calibration standards. Soils were analyzed for exchangeable cations (Ca, K, Mg, and Na) by extraction with 1M neutral ammonium acetate (Kalra and Maynard 1991) and concentrations determined by ICP-OES analysis. Cation exchange capacity (CEC) was calculated by summation of milliequivalent levels of exchangeable cations and acidity. Metal and nutrient analyses were conducted by the Analytical Laboratory at the University of Maine at Orono (UMO).

Tissue analysis. Five to ten leaves were collected from each of three widely-separated (ca. 4–5 m) individuals of eight species each on MDR: *Ligusticum scoticum* var. *hultenii*, *Plantago maritima* var. *juncoides*, *P. major*, *Rosa rugosa* (Rosaceae), *Rumex pallidus* (Polygonaceae), *Sonchus arvensis* subsp. *arvensis*, *Spergularia salina* (Caryophyllaceae), and *Stellaria media* (Caryophyllaceae). On MDI, tissues from five of these species (*L. scoticum* var. *hultenii*, *P. major*, *P. maritima* var. *juncoides*, *Rosa rugosa*, and *Sonchus arvensis* subsp. *arvensis*) were also collected from three widely-separated (ca. 4–5 m) individuals each from coastal bluffs lacking bird-nesting sites. For *L. scoticum* var. *hultenii*, *P. major*, and *Sonchus arvensis* subsp. *arvensis*, leaves were collected from the same plants used for the collection of soil samples to allow specific soil-tissue elemental relations to be evaluated for the species growing on and off guano-derived soils. Leaves were collected from the topmost portion of each plant and were washed with distilled water in the field until they were rid of visible dust and other debris. Leaves were air-dried for one day, then dried for 24 hr. at 70°C in a forced draft oven. The dried leaves of each individual plant were ground separately using a coffee grinder and/or a mortar and pestle with liquid N. Total tissue elemental concentrations for all elements but N were determined by dry ashing at 450°C for five hours, digesting in 50% HCl, and using ICP-OES. Total tissue N was estimated by direct combustion analysis at 1150°C in pure oxygen with subsequent detection by thermal conductivity in the combustion gases. All analyses were conducted at the University of Maine Analytical Laboratory.

Ornithocoprophilous flora. Using previous species lists from five important seabird nesting islands in northeastern North America, including Matinicus Rock, Machias Seal, Gull Rock, Hertford Island, and Ciboux Island (Hodgdon and Pike 1969; Mittelhauser 2007; Smith and Schofield 1959), as well as voucher specimens for MDR housed at HCOA, we compiled a list of ornithocoprophilous plants for the region's key seabird nesting islands. We examined the list for trends associated with growth habit, distribution, and sexual system. Growth habit and range were determined using Haines and Vining (1998). Robert Bertin (College of the Holy Cross, unpubl. data) generously provided data on sexual systems. Additional online sources (Appendix) were used as needed to determine the sexual system of the species listed.

Statistical analysis. All statistical analyses were conducted on log-transformed data. Natural log transformations satisfied the assumptions for parametric tests. Paired t-Tests (Table 1), one-way ANOVA (Tables 2, 3), and two-way ANOVA (Table 4) were conducted using SYSTAT 12 for Windows (SYSTAT Software Inc., San José, CA).

RESULTS

In 2007, we found 22 species of vascular plants on MDR (Appendix). Five taxa previously collected from the island and deposited at HCOA were not found during the 2007 survey: *Cakile edentula*, *Capsella bursa-pastoris* (Brassicaceae); *Puccinellia tenella* subsp. *alascana* (Poaceae); *Senecio vulgaris* (Asteraceae); and *Spergularia canadensis* (Caryophyllaceae). Two previously uncollected taxa were found: *Matricaria recutita* and *Symphyotrichum novi-belgii* (Asteraceae). A total of 27 vascular plant species from 10 families are now recorded for MDR (Appendix). Asteraceae (8 taxa; 29.6%), Poaceae (5 taxa; 18.5%), and Caryophyllaceae (4 taxa; 14.8%) represent the most species-rich families. Of the taxa encountered, 48% were strict herbaceous perennials while 44% were obligate annuals. The remaining taxa were either woody shrubs or those with a perennial/annual habit. Fifty-six percent of the flora were alien (non-native) while 44% were considered native to eastern North America. Fifty-nine percent of the taxa encountered were hermaphroditic.

Including the current study, 168 species of vascular plant taxa have been reported from six major bird-nesting islands off the coast

Table 1. Results from soil analyses for samples collected from seabird nesting sites on Mount Desert Rock (Guano; n = 9) and coastal bluffs on Mount Desert Island (Non-guano; n = 9). Electrical conductivity (EC) was measured in mmhos cm^{-1}. Effective cation exchange capacity (ECEC) was measured in meq 100 g^{-1}. Exchangeable acidity (Acidity) was measured by titration using an extraction in 1M KCl. All elemental concentrations are in μg g^{-1} dry soil (ppm). Values listed are means ± SE (range). *P* values are based on a paired t-Test. Significant *P* values are listed in bold font.

Soil Variable	Guano	Non-guano	*P* Value
pH	6.90 ± 0.34 (5.2–7.9)	6.87 ± 0.21 (5.9–8.0)	0.98
EC	1.82 ± 0.34 (0.40–3.88)	5.26 ± 1.77 (0.30–16.80)	0.33
ECEC	9.77 ± 1.39 (4.1–14.9)	12.79 ± 2.24 (1.6–19.6)	0.83
Acidity	0.12 ± 0.01 (<0.10–0.20)	<0.10 ± 0.00 (0.10)	0.16
NO_3^-	111.30 ± 44.26 (9.5–450)	27.33 ± 10.02 (0.7–83.2)	**0.04**
NH_4^+	9.81 ± 5.23 (0.8–46.9)	3.60 ± 1.84 (0.1–18)	0.35
Avail. P	49.89 ± 5.46 (34–87)	4.18 ± 1.06 (1.6–11.7)	**0.00**
Ca	1153.27 ± 151.61 (468–1751)	809.18 ± 184.98 (176–1691)	0.12
K	89.01 ± 10.78 (33–135)	212.27 ± 48.63 (23–424)	0.16
Mg	330.11 ± 57.32 (125–570)	479.64 ± 100.95 (29–934)	0.82
Na	233.29 ± 64.44 (44–640)	977.29 ± 263.41 (28–2305)	0.1
Al	9.24 ± 3.66 (1.1–34)	62.6 ± 23.29 (5.1–184)	0.1
Cd	0.28 ± 0.10 (0.07–1.04)	0.09 ± 0.02 (<0.02–0.15)	**0.01**
Cr	0.08 ± 0.01 (0.05–0.15)	0.14 ± 0.03 (<0.02–0.28)	0.81
Cu	19.09 ± 6.52 (3.4–63)	10.57 ± 9.55 (0.31–87)	**0.008**
Fe	58.16 ± 17.13 (4.6–147)	97.06 ± 27.18 (10–263)	0.46
Mn	4.84 ± 1.21 (0.7–9.2)	11.33 ± 2.95 (2.9–27)	**0.03**
Mo	0.12 ± 0.02 (0.07–0.22)	0.13 ± 0.02 (<0.05–0.19)	0.30
Ni	0.39 ± 0.06 (0.12–0.74)	0.32 ± 0.07 (<0.04–0.70)	0.18
Pb	295.30 ± 81.75 (32–862)	16.01 ± 7.19 (0.5–71)	**0.000**
Zn	199.01 ± 63.27 (33–657)	7.09 ± 2.93 (0.4–27)	**0.000**

of Maine and adjacent Canada (Matinicus Rock, 83 taxa; Machias Seal, 76 taxa; Gull Rock, 34 taxa; Hertford Island, 49 taxa; Ciboux Island, 81 taxa; Mount Desert Rock, 27 taxa; Hodgdon and Pike 1969; Mittelhauser 2007; Smith and Schofield 1959; Appendix; Figure 1). Table 5 lists the geographical features of the islands examined, as well as the total number of guano-associated species recorded for each island. The species recorded belong to 39 plant families; the dominant plant families represented were Asteraceae (29 taxa; 17.3%), Poaceae (25 taxa; 14.9%), Polygonaceae (10 taxa; 5.95%), Caryophyllaceae (9 taxa; 5.4%), and Rosaceae (9 taxa; 5.4%). Surprisingly, only two taxa (*Ligusticum scoticum* var. *hultenii* and *Festuca rubra* subsp. *rubra*; Poaceae) were shared by all six islands while 47% of taxa occurred on only one island. Sixty-six

Table 2. Tissue elemental concentrations for 38 plant tissue samples belonging to 8 plant species collected from guano-derived soils on Mount Desert Rock (Guano; n = 23 samples from 8 plant species) and 5 of the same plant species from coastal bluffs on Mount Desert Island (Non-guano; n = 15 samples from 5 plant species). Concentrations are reported as percent (%) for N, Ca, K, Mg, and P and μg g^{-1} dry tissue (ppm) for all other elements. Values listed are means ± SE (range). *P* values are based on a one-way ANOVA. Significant *P* values are listed in bold font.

Element	Guano	Non-guano	*P* Value
N	2.92 ± 0.26 (1.91–4.58)	2.18 ± 0.17 (1.10–3.27)	**0.00**
Ca	0.89 ± 0.12 (0.16–2.54)	1.4 ± 0.16 (0.86–2.83)	**0.008**
K	1.34 ± 0.10 (0.50–2.12)	1.95 ± 0.16 (0.97–3.28)	**0.004**
Mg	0.69 ± 0.09 (0.19–1.91)	0.64 ± 0.09 (0.28–1.46)	0.87
P	0.36 ± 0.03 (0.16–0.76)	0.23 ± 0.02 (0.12–0.37)	**0.003**
Al	138.10 ± 51.89 (14.9–1010)	106.1 ± 34.53 (39.1–543)	0.45
B	28.53 ± 1.57 (19.1–47.6)	45.23 ± 8.46 (25–85.7)	**0.01**
Cu	10.18 ± 1.09 (5.01–23.3)	8.97 ± 0.95 (3.81–19.30)	0.51
Fe	70.97 ± 9.04 (29.8–204)	131.15 ± 46.7 (42.4–727)	0.1
Mn	53.17 ± 12.02 (7.14–244)	64.95 ± 10.48 (9.29–143)	0.14
Zn	178.15 ± 52.35 (1–869)	42.86 ± 10.19 (8.6–149)	**0.048**
Pb	14.20 ± 3.64 (1.50–51.50)	1.85 ± 0.46 (1.50–8.30)	**0.004**

percent of the species were herbaceous perennials while 21% were annuals. The remaining species were shrubs, trees, and those with mixed habits. Sixty percent of the species were native while 40% were aliens. Sixty-nine percent were hermaphroditic. The trends observed with respect to floristics, plant habit, and sexual system for species from MDR were mirrored by the other five islands.

Results from the soil analyses of samples collected from guano-derived soils (n = 9) and non-guano coastal bluff soils (n = 9) are listed in Table 1. The guano-derived soils on MDR had significantly ($P < 0.05$) higher concentrations of NO_3^-, available P, and the heavy metals Cd, Cu, Pb, and Zn, and significantly lower Mn than soils collected from coastal bluffs on MDI where there was no seabird nesting activity.

Results from the tissue analyses are listed in Table 2. Based on a total of 38 tissue samples from 8 species (guano, n = 23; non-guano, n = 15) the results show that, at the community level, tissues from plants associated with guano deposits on MDR have significantly ($P < 0.05$) higher total N, P, Pb, and Zn, and significantly lower Ca, K, and B than tissues collected from coastal bluffs of MDI.

Table 3 compares tissue elemental concentrations for five species (*Ligusticum scoticum* var. *hultenii*, *Plantago major*, *P. maritima* var.

Table 3. Mean tissue elemental concentrations (± SE) for five species collected from guano (G; Mount Desert Rock) and non-guano (Ng; Mount Desert Island) sites. Concentrations are reported as percent (%) for N, Ca, K, Mg, and P and μg g^{-1} dry tissue (ppm) for all other elements. P values based on a one-way ANOVA conducted on 3 specimens per species per substrate. Significant means ($P < 0.05$) are in bold.

	N		Ca		K		Mg		P		Al		B		Cu		Fe		Mn		Zn		Pb	
Species	G	Ng	G	Ng	G	Ng	G	N	G	Ng	G	Ng	G	Ng	G	Ng	G	Ng	G	Ng	G	Ng	G	Ng
Ligusticum scoticum	3.19 ± 0.08	2.85 ± 0.25	0.87 ± 0.03	1.05 ± 0.10	1.66 ± 0.16	2.23 ± 0.20	**0.24** ± 0.02	**0.44** ± 0.02	0.35 ± 0.01	0.31 ± 0.04	45.8 ± 29.5	110 ± 9.02	21.5 ± 0.88	27.9 ± 2.53	8.15 ± 1.03	9.92 ± 0.88	**54.2** ± 1.26	**79.6** ± 7.70	**21.9** ± 5.51	**73.2** ± 11.8	40.7 ± 4.87	28.2 ± 3.36	5.97 ± 4.47	1.5 ± 0
Plantago major	**4.31** ± 0.12	**2.11** ± 0.39	1.79 ± 0.45	2.13 ± 0.36	1.64 ± 0.31	2.62 ± 0.34	0.88 ± 0.12	1.07 ± 0.24	0.43 ± 0.10	0.23 ± 0.01	22.2 ± 2.76	120 ± 66.3	32.8 ± 1.82	33.1 ± 4.52	11.6 ± 1.31	7.78 ± 0.85	58.1 ± 3.15	172 ± 89.8	41.7 ± 22.1	78.6 ± 37.7	**124** ± 22.2	**45.3** ± 9.83	21.6 ± 11.5	1.5 ± 0
Plantago maritima	2.22 ± 0.3	1.43 ± 0.17	**1.04** ± 0.09	**0.68** ± 0.05	1.50 ± 0.31	1.44 ± 0.31	0.50 ± 0.03	0.66 ± 0.11	0.18 ± 0.01	0.16 ± 0.03	85.7 ± 38.3	224 ± 159	23.0 ± 0.52	26.1 ± 2.56	7.84 ± 1.08	10.5 ± 0.36	50.0 ± 7.17	277 ± 224	28.3 ± 5.80	28.0 ± 8.16	**106** ± 31.4	**13.3** ± 2.58	**36.0** ± 6.52	**1.0** ± 0
Rosa rugosa	2.72 ± 0.03	1.94 ± 0.33	**0.81** ± 0.05	**1.28** ± 0.03	1.23 ± 0.17	1.23 ± 0.04	0.23 ± 0.03	0.26 ± 0.06	0.29 ± 0.04	0.16 ± 0.03	15.9 ± 1	35.3 ± 6.32	36.7 ± 8.75	91.3 ± 30.6	8.05 ± 2.35	4.63 ± 0.43	35.7 ± 5.90	60.2 ± 9.66	58.6 ± 35.9	69 ± 13.7	64.4 ± 31.4	20.4 ± 7.02	2.27 ± 0.77	3.77 ± 2.27
Sonchus arvensis	3.85 ± 0.53	2.55 ± 0.19	1.5 ± 0.12	1.85 ± 0.15	**1.06** ± 0.29	**2.21** ± 0.04	**1.59** ± 0.16	**0.80** ± 0.04	0.28 ± 0.02	0.3 ± 0.04	**21.9** ± 3.86	**39.6** ± 5.25	39.1 ± 4.47	47.7 ± 7.67	15.4 ± 4.04	11.9 ± 3.70	65.1 ± 7.51	65.6 ± 3.95	173 ± 35.6	75.8 ± 34.1	**594** ± 137	**106** ± 24.8	2.22 ± 0.72	1.5 ± 0

Table 4. Results of the two-way ANOVA model using log-transformed data for tissue elemental analyses of five species found on and off of guano soil on Mount Desert Rock and Mount Desert Island, respectively. Significant source variables ($P < 0.05$) with respect to each tissue element are indicated in bold.

Source	N	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Zn	Pb
Substrate												
Sum of squares	1.216	0.117	0.719	0.051	0.646	6.409	0.525	0.131	2.047	0.391	11.278	12.133
Degrees of freedom	1	1	1	1	1	1	1	1	1	1	1	1
P value	**0.000**	0.12	**0.01**	0.38	**0.003**	**0.002**	**0.016**	0.22	**0.03**	0.43	**0.000**	**0.000**
Species												
Sum of squares	1.429	3.017	1.010	9.861	1.934	7.036	2.585	1.511	1.332	6.350	17.346	6.162
Degrees of freedom	4	4	4	4	4	4	4	4	4	4	4	4
P value	**0.000**	**0.000**	**0.05**	**0.000**	**0.000**	**0.021**	**0.000**	**0.008**	0.46	0.07	**0.000**	0.07
Substrate × Species												
Sum of squares	0.301	0.621	0.754	1.331	0.500	0.852	0.514	0.785	0.822	4.137	2.455	13.259
Degrees of freedom	4	4	4	4	4	4	4	4	4	4	4	4
P value	0.17	**0.03**	0.113	**0.005**	0.107	0.772	0.19	0.081	0.68	0.19	**0.04**	**0.003**

Table 5. Geographical features for the seven islands examined for the study. Total recorded plant species associated with bird nesting sites for all islands, excluding Mount Desert Island, is also listed.

Name of Island	Area (ha)	Distance to Mainland (km)	Total Guano-Associated Species	Latitude	Longitude
Mount Desert Island	28100	0.6	–	44°13′–44°27′N	68°10′–68°26′W
Machias Seal	8.5	16	76	44°30′10″N	67°06′10″W
Matinicus Rock	10	25.1	83	43°51′42″N	68°53′38″W
Mount Desert Rock	8	32	27	43°58′12″N	68°7′48″W
Gull Rock	4	12	34	44°55′47″N	66°43′36″W
Ciboux	19.2	4	81	46°23′00″N	60°22′00″W
Hertford	13.2	4	49	46°22′1″N	60°22′58″W

juncoides, *Rosa rugosa*, and *Sonchus arvensis* subsp. *arvensis*) found on and off guano-derived soils. Significant differences were observed for tissue concentrations of N, Ca, K, Mg, Fe, Mn, Zn, and Pb; however, the trends were not always consistent for these elements across all species tested. Zinc and Pb were always found at higher concentrations in plants from MDR. Significant differences for Zn were observed for *S. arvensis* subsp. *arvensis*, *P. major*, and *P. maritima* var. *juncoides*. For Pb, significant differences were found only for *P. maritima* var. *juncoides*. While all species showed some significant differences with respect to tissue accumulation of certain elements, *S. arvensis* subsp. *arvensis*, *L. scoticum* var. *hultenii*, and *P. maritima* var. *juncoides* showed many differences with respect to key elements.

We used a two-way ANOVA model to examine the relationships between species and substrate (independent variables) on element accumulation (dependent variable) patterns in tissue samples (Table 4). The species variable was significant for N, Ca, K, Mg, P, Al, B, Cu, and Zn, suggesting that the species were physiologically distinct with respect to these elemental accumulation patterns. The substrate variable was significant for N, K, P, Al, B, Fe, Zn, and Pb, suggesting that the edaphic habitat differences (guano and non-guano) were responsible for the accumulation differences. A significant interaction between these two source variables was observed only for Ca, Mg, Zn, and Pb, suggesting that for these four elements there was significant genetic variation among species with respect to substrate (guano and non-guano).

DISCUSSION

Islands of northeastern North America are ideal habitats for studying factors contributing to the generation and maintenance of plant diversity in remote localities, including the impact of nesting seabirds on plant community assembly (Ellis 2005). Birds are well known as effective transporters of seeds to distant islands (Burger 2005). Although there is an increasing awareness of this avian ecological function (Sekercioglu 2006), the current study is one of few (Ellis et al. 2006; Hodgdon and Pike 1969; Smith and Schofield 1959) examining this potentially unique seabird-plant relationship in northeastern North America's oceanic islands. A recent study by McMaster (2005) of 22 islands off the coast of eastern North America, including four islands examined in this study (Machias Seal, Matinicus Rock, Gull Rock, and MDI), suggested that plant species richness is positively correlated with island area and negatively correlated with latitude and distance from the nearest land mass. McMaster suggested that ground-nesting pelagic birds may contribute to patterns of plant diversity, especially in accounting for the high percentage of non-native species on some islands. Guano-enriched substrates contribute to edaphic diversity of remote islands and may result in distinct species assemblages. Species richness on islands is not only controlled by island position, size, and distance from source populations (McMaster 2005), but also by habitat heterogeneity on the island itself (Hannus and von Numers 2008).

Interestingly, only two taxa listed for the six islands examined were shared by all islands (*Ligusticum scoticum* var. *hultenii* and *Festuca rubra* subsp. *rubra*); however, at the family level almost half of the plants listed belonged to only five families: Asteraceae, Poaceae, Polygonaceae, Caryophyllaceae, and Rosaceae. Many species found on the islands were native to the region (60%) and had a perennial habit (66%), contradicting the previously documented trend of seabird-nesting island floras being dominated by ruderal, annual, and alien species (Ellis 2005; Hogg et al. 1989; McMaster 2005; Vidal et al. 1998, 2000). Our findings suggest that remote, harsh habitats may favor the persistence of rare, perennial, native species (Dean et al. 1994; Norton et al. 1997; Vasey 1985).

Persistence of well-adapted genotypes, as found in perennial, native species, may be advantageous in such settings compared to the dependence of annual, alien species on frequent dispersal and colonization.

Five taxa previously collected from MDR (*Cakile edentula*, *Capsella bursa-pastoris*, *Puccinellia tenella* subsp. *alascana*, *Senecio vulgaris*, and *Spergularia canadensis*) were not found during our 2007 survey, despite extensive searches. Similarly, two new taxa were collected from the island (*Matricaria recutita* and *Symphyotrichum novi-belgii*). Although minimal, there has clearly been some turnover of species since the last survey in 1989 (from voucher specimens at HCOA). It is unclear whether seabirds, more frequent visits to the island by researchers, other ecological factors, or some combination of the above are responsible for the new arrivals and the loss of previously collected taxa.

The many taxa we have listed for the offshore islands belong to plant families known to have fruit morphologies that suit dispersal via birds and wind. In a study on a seabird-island endemic, *Lasthenia maritima* (Asteraceae), from the Californian Floristic Province, Vasey (1985) noted that the range for the species strongly corresponds to the flight pattern of the Western Gull (*Larus occidentalis*; Laridae), and that cypselae (achene-like fruit) have often been found embedded in the feathers of dead birds. Of the 168 taxa recorded for bird-nesting islands in the region, 29 (17.3%) belong to Asteraceae, the most-widely represented family among the region's ornithocoprophilous flora (Appendix). Cypselae of Asteraceae, often with barbs, hooks, or viscid outgrowths, are effective at adhering to animals (Sorensen 1986).

Stellaria media (Caryophyllaceae) was one of 13 taxa to be found on five of the six islands examined (Table 5). This weedy taxon is ideally suited for dispersal by seabirds (Gillham 1963; Sobey 1981; Vidal et al. 2003). Seed output per plant can range from 600 to 15,000 (Lutman 2000) while vegetative reproduction can also occur via stem fragments (Sobey 1981). The seeds have been shown to be transported by various animals, including seabirds (Gillham 1956b; Sobey 1981; Sobey and Kentworthy 1979) and have been shown to remain viable even after immersion in seawater (Sobey 1981). Seeds are also known to remain viable in the soil for 40–60 years (Evans 1962; Salisbury 1961), suggesting the seed bank could be a long-term source for establishment. Another feature that likely aids in its post-arrival establishment is the ability to produce viable seed through self-fertilization.

Ligusticum scoticum, one of the most abundant species on MDR, is a perennial, insect-pollinated hermaphrodite found on cliffs and rocky shores of temperate latitudes (Palin 1988). It is rarely found directly on bird-nesting sites (Goldsmith 1975), as it is unable to tolerate the physical disturbance associated with breeding and nesting activities of gulls (Palin 1988). At MDR, however, it is abundant on gull nesting sites and appears to be unaffected by physical disturbance there. It is one of two species collected from all other bird-nesting islands examined in the study (the other being *Festuca rubra* subsp. *rubra*; Appendix). A single individual of *L. scoticum* is able to produce up to 2000 seeds (Palin 1988), which are able to float in seawater for 2–3 months and retain their viability even after one year of immersion in seawater (Okusanya 1979). Individual seeds or whole or partial umbels can be dispersed by both wind and sea and can also become trapped in feathers or in mud stuck to the feet of seabirds (Palin 1988). Given the prevalence of *F. rubra* subsp. *rubra* and *L. scoticum* on all seabird nesting islands, they are worthy candidates for further investigations of ecotypic differentiation with respect to guano habitats.

These examples illustrate several features that may aid in effective dispersal to seabird nesting islands. Key among these features are: production of a large number of small seeds, seeds with traits suited for adhesion to birds, and seeds with the ability to tolerate immersion in seawater (Mueller-Dombois 1992). Many of the species listed in the Appendix demonstrate these traits (Baskin and Baskin 2001; Uva et al. 1997), making them well-equipped to reach such off-shore islands.

The Brassicaceae, Poaceae, and Polygonaceae are families widely represented on bird nesting sites; species of these families retain high levels of NO_3^- in the leaf tissue and have high levels of leaf nitrate reductase activity (Odasz 1994). Ability to deal with high levels of N is an important adaptation in N-rich guano habitats. For example, *Lasthenia maritima* has high levels of nitrates in its foliage compared to its presumed ancestor *L. minor*, a guano-intolerant, coastal bluff species (Ornduff 1965), although the levels determined could simply reflect concentration differences in soils where these taxa are found. Vasey (1985), however, suggested that *L. maritima* may have overcome a key factor limiting plant growth on guano—water stress resulting from high osmotic potential in the soil—by accumulating nitrates and other organic compounds in the leaf vacuoles. Overall, the total leaf N content in all five species we tested was higher on guano soils compared to non-guano soils, with *P. major* showing significantly higher total leaf N in guano compared to non-guano soils (4.3% vs. 2.1%; $P = 0.006$). This taxon might be of interest for further study with respect to its nitrogen uptake in populations found on and off of guano soils.

High levels of heavy metals and radionuclides have been previously reported from guano soils (Dowdall et al. 2005; García et al. 2002; Hawke and Powell 1995; Liu et al. 2006; Pérez 1998); however, the Pb concentrations found in the guano-associated soils of MDR greatly exceeded those of other studies (Table 1). Normal background levels of total Pb in soils from Maine range from 10–50 ppm (Bruce Hoskins, Univ. Maine, Orono Analytical Lab, pers. comm.) while worldwide the upper limit has been reported as 70 ppm (Kabata-Pendias 2001). The amounts of Pb extracted from chelators such as DTPA, as in the case of our study, are generally less than the total content and give a better index of bioavailability (Cui et al. 2004). Because the range we report for MDR (32–862 ppm; mean 295.30 ppm $\pm$ 81.75) represents bioavailable Pb, our values are many-fold higher than normal background values reported as total Pb (B. Hoskins, pers. comm.) as well as bioavailable values reported from our sites on MDI (0.5–71 ppm; mean 16.01 $\pm$ 7.19). This high level of extractable Pb in guano-associated soils of MDR is of concern as Pb is highly toxic to many organisms (Goyer 1993; Påhlsson 1989; Seregin and Ivanov 2001). Furthermore, the high levels found in plant tissues in this study indicate a strong possibility for transfer to higher trophic levels (Torres and Johnson 2001).

We also found significantly higher concentrations of Zn in guano-associated soils on MDR (33–657 ppm; mean 199.01 $\pm$ 63.27) compared to non-guano soils on MDI (0.4–27 ppm; mean 7.09 $\pm$ 2.93). Our values also exceeded the upper limit (64 ppm) reported for this metal from surface soils globally (Kabata-Pendias 2001). Other metals on MDR, including Cr, Cd, and Cu were found within the range observed in other studies (Liu et al. 2006; Pérez 1998). Metal concentrations in the feces of seabirds are affected by factors such as diet, feeding behavior, and physiology (Headley 1996; Pérez 1998). The transfer of metals from oceanic and terrestrial feeding grounds to the nesting sites of seabirds is of ecological concern, however the exact source is often unclear.

While excessive elemental concentrations in soils, especially of metals such as Pb and Zn are of ecological concern, leaf tissue concentrations are a better indicator of the overall impact of heavy metals in the environment (Sarkar 2002). Our findings clearly indicate the transfer of metals from soil to plants and suggest the possibility for subsequent transfer to higher trophic levels. Zinc and Pb in some of the taxa collected from guano soils on MDR exceeded the concentrations considered normal in plants (<100, <10 ppm, respectively; Kabata-Pendias 2001). Mean leaf Zn concentration in *Sonchus arvensis* subsp. *arvensis* was significantly greater on guano (594 ppm) than on non-guano (106 ppm) soils (Table 3), with the level found on guano exceeding the upper range considered toxic for plants (100–500 ppm; Kabata-Pendias 2001); a similar trend was observed for Zn in *Plantago maritima* var. *juncoides* (guano: 106 ppm; non-guano: 13.3 ppm). *Stellaria media* also accumulated high levels of Zn (497 ± 187 ppm), although we could not compare values for plants found on non-guano soils. Similarly, mean leaf Pb concentrations for *P. major* (21.6 ppm) and *P. maritima* var. *juncoides* (36 ppm) on MDR were significantly higher than values obtained for these two species when collected from non-guano soils on MDI (1.5 and 1 ppm, respectively). Both of these species, as well as *Stellaria media* (39 ppm), showed tissue Pb levels exceeding the normal range for plants (0.1–10 ppm; Kabata-Pendias 2001; Temminghoff and Novozamsky 1992).

Our findings point to the important role edaphic conditions may play in the species distribution and abundance on the region's islands, in addition to those factors examined by McMaster (2005). Of special concern are the higher levels of macronutrients N and P and toxic heavy metals, especially Zn and Pb, in the seabird nesting habitats compared to sites with no seabird activity. Nutrient enrichment (Clark and Tilman 2008) as well as heavy metal toxicities (Salemaa et al. 2001) can play a significant role in shaping plant community composition and structure. Further, the study indicates the need for common garden and genetic studies of several taxa with respect to their adaptation to guano soils. In this regard, macronutrients N, P, Ca, and Mg may be of importance. Common garden studies of taxa that are physiologically distinct with respect to their elemental uptake may reveal evidence for ecotypic differentiation, both in terms of traits that are important for guano tolerance as well as traits that confer reproductive isolation. Heavy metals, especially Pb and Zn, are also of special concern given their accumulation in plant tissues of several taxa, providing avenues to explore plant metal-uptake and the nature of metal transfer from mainland and oceanic habitats to seabird colonies on remote islands.

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APPENDIX

VASCULAR PLANTS RECORDED

Vascular plants recorded for bird-nesting oceanic islands along northeastern North America. Sources include published floras for Ciboux Island (CI; Smith and Schofield 1959), Hertford Island (HI; Smith and Schofield 1959), Matinicus Rock (MR; Hodgdon and Pike 1969; Mittelhauser 2007), Machias Seal Island (MS; Hodgdon and Pike 1969), and Gull Rock (GR; Hodgdon and Pike 1969), as well as species collected from Mount Desert Rock (MDR). The five taxa with

(*) represent species collected during previous field excursions (1973, 1978, 1989) to MDR and not found during the current visit (2007). All MDR specimens are deposited at HCOA. All taxa and authorities updated according to Integrated Taxonomic Information System [website (http://www.itis.gov/); accessed 22 March 2008], International Plant Names Index [website (http://www.ipni.org/index.html); accessed 24 March 2008], and USDA, NRCS 2008. Plant habit (A = annual, B = biennial, P = perennial, S = shrub, T = tree) and range (N = native to eastern North America, A = alien/naturalized) are from Haines and Vining (1998) and USDA, NRCS 2008. Sexual system information was obtained from a dataset from Robert Bertin (College of the Holy Cross, unpubl. data), websites [(http://www.herbarium.usu.edu/grassmanual/), accessed 05 April 2008; (http://www.bcflora.org/), accessed 05 April 2008; (http://www.pfaf.org/), accessed 02 April 2008], and USDA, NRCS 2008. H = hermaphroditic, M = monoecious, D = dioecious, AM = andromonoecious, GD = gynodioecious, GM = gynomonoecious, V = varies, HS = homosporous.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
APIACEAE				
Angelica lucida L.	P	N	H	MS, MR, GR, CI
Carum carvi L.	B	A	AM	MS, CI
Heracleum maximum Bartr.	P	N	AM	CI
Ligusticum scoticum L. var. *hultenii* (Fernald) Calder & Roy L. Taylor	P	N	H	MDR, MR, MS, CI, HI, GR
ASTERACEAE				
Achillea millefolium L.	P	A	GM	MR
A. millefolium var. *borealis* (Bong.) Farw.	P	A	GM	MS, GR
A. millefolium var. *occidentalis* DC.	P	A	GM	MS, MR, HI, CI
Ambrosia artemisiifolia L.	A	N	M	MR
Anaphalis margaritacea (L.) Benth. & Hook. f.	P	N	D	CI
Arctium minus Bernh.	B	A	H	HI
Bidens frondosa L.	A	N	H	MR
Cirsium arvense (L.) Scop.	P	A	GD	MS, MR, HI, CI
C. vulgare (Savi) Ten.	B	A	H	MR, HI
Doellingeria umbellata (Mill.) Nees var. *umbellata*	P	N	GM	MS, GR
Gnaphalium uliginosum L.	A	N	GM	MDR, MS
Hieracium aurantiacum L.	P	A	H	CI
H. floribundum Wimm. & Grab.	P	A	H	HI, CI
H. pilosella L.	P	A	H	HI, CI

Appendix. Continued.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
Leontodon autumnalis L.	P	A	H	MS, HI, CI
Matricaria discoidea DC.	A	A	GM	MDR, MR, MS, CI, GR
M. recutita L.	A	A	GM	MDR
Senecio jacobaea L.			GM	CI
**S. vulgaris* L.	A	A	H	MDR, CI, HI
Solidago rugosa Mill. var. *villosa* (Pursh) Fernald	P	N	GM	GR
S. sempervirens L.	P	N	GM	MR, CI
Sonchus arvensis L. subsp. *arvensis*	P	A	H	MDR, MR, CI
S. asper (L.) Hill	A	A	V	MDR, MS
S. oleraceus L.	A	A	H	MDR, MR
Symphyotrichum foliaceum (DC.) G.L. Nesom var. *foliaceum*	P	A	GM	MS, MR, GR
S. novi-belgii (L.) G.L. Nesom	P	N	GM	MDR, MR, CI, HI, GR
S. novi-belgii var. *villicaule* (A. Gray) J. Labrecque & L. Brouillet	P	N	GM	MS
Taraxacum laevigatum (Willd.) DC.	P	A	H	MS
T. officinale F.H. Wigg.	P	A	H	MS, MR, HI, CI
BALSAMINACEAE				
Impatiens capensis Meerb.	A	N	H	MS, MR, GR
BORAGINACEAE				
Mertensia maritima (L.) S.F. Gray	P	N	H	MR
BRASSICACEAE				
Brassica juncea (L.) Czern.	A	A	H	MR
**Cakile edentula* (Bigelow) Hook.	A	N	H	MDR, MR
**Capsella bursa-pastoris* (L.) Medik.	A	A	V	MDR, MR, MS, CI, HI
Cardamine parviflora L. var. *arenicola* (Britton) O.E. Schulz	A/B	N	H	HI, CI
Raphanus raphanistrum L.	A	A	H	MR, CI
CALLITRICHACEAE				
Callitriche heterophylla Pursh	A	N	M	MS
CAMPANULACEAE				
Campanula rotundifolia L.	P	N	H	HI, CI

Appendix. Continued.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
CAPRIFOLIACEAE				
Sambucus racemosa A. Gray var. *racemosa*	S	N	H	HI
CARYOPHYLLACEAE				
Cerastium arvense L.	P	N	GD	MR
C. fontanum Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet	P	A	H	MS, MR, GR, HI, CI
Moehringia lateriflora (L.) Fenzl	P	N	H	MS, HI, CI
Sagina procumbens L.	P	N	GD	MDR, MR, MS, CI, HI
**Spergularia canadensis* (Pers.) G. Don	A	N	V	MDR, MR
S. rubra (L.) J. Presl & C. Presl	A/P	A	V	CI
S. salina J. Presl & C. Presl	A	A	V	MDR, MR, MS, GR
Stellaria graminea L.	P	A	GD	MS, HI, CI
S. media (L.) Vill.	A	A	H	MDR, MR, MS, CI, GR
CHENOPODIACEAE				
Atriplex glabriuscula Edmondston	A	N	M	MS, MR
A. patula L.	A	A	M	MS, MR, GR
A. prostrata DC.	A	A	M	MR
Chenopodium album L.	A	A	H	MR
C. berlandieri Moq. var. *macrocalycium* (Aellen) Cronquist	A	N	H	MR
Suaeda calceoliformis (Hook.) Moq.	A	N	H	MR
S. maritima (L.) Dumort. subsp. *richii* (Fernald) Bassett & C.W. Crompton	A	A	H	MR
CONVALLARIACEAE				
Maianthemum stellatum Link	P	N	H	GR, CI
CONVOLVULACEAE				
Calystegia sepium (L.) R. Br. subsp. *sepium*	P	N	H	CI, MR
CRASSULACEAE				
Rhodiola rosea L.	P	N	D	MS, MR, GR
CUPRESSACEAE				
Juniperus communis L. var. *montana* Aiton	S	N	D	CI
Juniperus horizontalis Moench	S	N	D	CI

Appendix. Continued.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
CYPERACEAE				
Carex brunnescens (Pers.) Poir. subsp. *sphaerostachya* (Tuck.) Kalela	P	N	H	MS
C. canescens L. subsp. *canescens*	P	N	M	MS
C. crinita Lam. var. *crinita*	P	N	H, GM	GR
C. hormathodes Fernald	P	N	H	MS, MR
C. nigra (L.) Reichard	P	N	AM	CI
C. paleacea Wahlb.	P	N	H	MS, MR
C. scoparia Willd.	P	N	H	MS
C. silicea Olney	P	N	H	MS, HI, CI
Eleocharis uniglumis (Link) Schult.	P	N	H	MR
Schoenoplectus maritimus (L.) Lye	P	N	H	MR
S. tabernaemontani (C.C. Gmel.) Palla	P	N	H	MR
DRYOPTERIDACEAE				
Dryopteris carthusiana (Vill.) H.P. Fuchs	P	N	HS (M)	CI
D. filix-mas (L.) Schott	P	N	HS (M)	CI
ERICACEAE				
Empetrum nigrum L.	S	N	H	CI
Vaccinium angustifolium Aiton	S	N	H	CI
V. vitis-idaea L. subsp. *minus* (Lodd.) Hultén	S	N	H	HI, CI
FABACEAE				
Lathyrus japonicus Willd.	P	N	H	MR, GR
L. palustris L.	P	N	H	MS
Trifolium hybridum L.	P	A	H	MS, CI
T. pratense L.	P	A	H	MS
T. repens L.	P	A	H	MS, MR, GR, HI, CI
Vicia cracca L.	P	A	H	MS, CI
V. sativa L. subsp. *nigra* (L.) Ehrh.	A	A	H	MS
GROSSULARIACEAE				
Ribes lacustre (Pers.) Poir.	S	N	H	CI
IRIDACEAE				
Iris versicolor L.	P	N	H	MS, MR, GR
Sisyrinchium montanum Greene var. *crebrum* Fernald	P	N	H	CI, MS, MR
JUNCACEAE				
Juncus ambiguus Guss.	A	N	H	MS
J. bufonius L. var. *bufonius*	A	N	H	MDR, MR, CI, MS

Appendix. Continued.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
J. gerardii Loisel. var. *gerardii*	P	N	H	MDR, MR
J. greenei Oakes & Tuck.	P	N	H	MR
J. tenuis Willd.	P	N	H	HI
Luzula multiflora (Ehrh.) Lej.	P	A	H	CI
LAMIACEAE				
Lycopus uniflorus Michx.	P	N	H	MS
Mentha suaveolens Ehrh.	P	A	H	MDR
ONAGRACEAE				
Epilobium ciliatum Raf. subsp. *ciliatum*	P	N	H	MR
Oenothera biennis L.	B/P	N	H	CI
OSMUNDACEAE				
Osmunda cinnamomea L.	P	N	HS (M)	MS
PINACEAE				
Abies balsamea (L.) Mill.	T/S	N	M	HI
Picea glauca (Moench) Voss	T	N	M	HI, CI
PLANTAGINACEAE				
Plantago major L.	P/A	A	H	MDR, MR, CI, HI, MS
P. maritima L. var. *juncoides* (Lam.) A. Gray	P	N	GD	MDR, MR, MS, HI, CI
POACEAE				
Agrostis gigantea Roth	P	A	H	CI, HI, MS
A. stolonifera L.	P	A	H	MDR, MR, MS, GR
Alopecurus pratensis L.	P	A	H	CI
Anthoxanthum odoratum L.	P	A	AM	MS, HI
Calamagrostis canadensis (Michx.) P. Beauv.	P	N	H	MS, GR
Danthonia spicata (L.) Roem. & Schult.	P	N	H	HI, CI
Deschampsia flexuosa (L.) Trin.	P	N	H	GR, HI, CI
Dichanthelium boreale (Nash) Freckmann	P	N	H	CI
Elymus repens (L.) Gould	P	A	H	MDR, MR, MS, GR, CI
E. trachycaulus (Link) Gould subsp. *trachycaulus*	P	N	H	CI
E. virginicus L.	P	N	H	MR
Festuca rubra L. subsp. *rubra*	P	A	H	MDR, MR, CI, HI, GR, MS

Appendix. Continued.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
Hordeum jubatum L.	P	N	AM	MR
Leymus mollis (Trin.) Pilg. subsp. *mollis*	P	N	H	MDR, MR, MS, GR, CI
Phleum pratense L.	P	A	H	MS, MR, HI, CI
Poa alpina L.	P	A	H	CI
P. annua L.	A	A	H	MS, MR, GR, HI, CI
P. compressa L.	P	A	H	GR
P. palustris L.	P	N	H	MS, HI, CI
P. pratensis L.	P	A	H	MS, MR, HI, CI
P. trivialis L.	P	A	H	HI, CI
Puccinellia laurentiana Fernald & Weath.	P	N	H	GR
**P. tenella* (Lange) A.E. Porsild subsp. *alascana* (Scribn. & Merr.) Tzvelev	P	N	H	MDR, MR, MS, GR
Spartina alterniflora Loisel.	P	N	H	MR
S. pectinata Link	P	N	H	MR
POLYGONACEAE				
Polygonum aviculare L.	A	A	H	MS, MR, GR, HI
P. buxiforme Small	A	N	H	MR
P. cilinode Michx.	P	N	H	HI
P. convolvulus L. var. *convolvulus*	A	A	H	MR
P. persicaria L.	A/P	A	H	MR
Rumex acetosella L.	P	A	D	MS, MR, GR, HI, CI
R. crispus L.	P	A	H	MS, MR, CI
R. longifolius DC.	P	A	H	MR
R. orbiculatus A. Gray	P	N	H	MS, MR, HI
R. pallidus Bigelow	P	N	V	MDR, MR
PRIMULACEAE				
Glaux maritima L.	P	N	H	MS
RANUNCULACEAE				
Ranunculus acris L.	P	N	H	MS, MR, CI
R. cymbalaria Pursh	P	N	H	MR
R. repens L.	P	A	H	HI, CI, MS
Thalictrum pubescens Pursh	P	N	D	MS, GR
ROSACEAE				
Argentina anserina Rydb.	P	N	H	MS, MR

Appendix. Continued.

Family/Species	Habit	Range	Sexual System	Occurrence (Island)
A. egedii (Wormsk.) Rydb. subsp. *groenlandica* (Tratt.) A. Löve	P	N	H	MR, MS
Fragaria vesca L. subsp. *americana* (Porter) Staudt	P	N	H	CI
F. virginiana Mill.	P	N	H	HI, CI
Potentilla norvegica L.	A/P	N	H	MS, MR, GR, CI
Prunus virginiana L.	S/T	N	H	HI
Rosa rugosa Thunb.	S	A	H	MDR
Rubus idaeus L. subsp. *strigosus* (Michx.) Focke	B	A	H	GR, HI, CI
Sibbaldiopsis tridentata (Aiton) Rydb.	P	N	H	HI, CI
RUBIACEAE				
Galium aparine L.	A	N	H	MR
G. tinctorium L.	P	N	H	MS
SCROPHULARIACEAE				
Euphrasia nemorosa (Pers.) Wallr.	A	A	H	MS, HI, CI
E. randii B.L. Rob.	A	N	H	MS, MR, CI
Linaria vulgaris (L.) Mill.	P	A	H	CI
Rhinanthus minor L. subsp. *minor*	A	N	H	MS, CI
Veronica serpyllifolia L.	P	N	H	HI
SOLANACEAE				
Solanum dulcamara L.	P	A	H	MR
S. nigrum L.	A	A	H	MR
THELYPTERIDACEAE				
Phegopteris connectilis (Michx.) Watt	P	N	HS (M)	CI
TYPHACEAE				
Typha latifolia L.	P	N	M	MR
URTICACEAE				
Urtica dioica L. subsp. *gracilis* (Aiton) Seland.	P	A	M	MR, MS
VIOLACEAE				
Viola cucullata Aiton	P	N	H	HI, CI
V. macloskeyi F.E. Lloyd subsp. *pallens* (Banks *ex* Ging) M.S. Baker	P	N	H	CI, MS