

High incidence and correlates of dioecy in the flora of the Canadian Arctic Archipelago

Peter G. Kevan and Becky Godglick

Abstract: In comparing the incidence of dioecy in North American floras, we report a strong, positive correlation with increasing latitude. Dioecy in the High Arctic is highly correlated with woodiness, as elsewhere. It is significantly correlated with fleshy, zoochorous fruits as well documented elsewhere. Correlation with floral inconspicuousness, which we define in terms of attractiveness to pollinators (i.e., functionality to pollination), is weak and statistically insignificant. Published findings on that correlation are equivocal; different authors variously defined inconspicuousness in ways that may or may not reflect functionality in pollination. Although we acknowledge that for some diverse taxa (e.g., *Salix* spp.) the relative importances of anemophily, zoophily (entomophily), and ambophily are unknown, we assigned species to (a) anemophily if evidence for entomophily could not be invoked and (b) entomophily if insect pollination was considered possible (i.e., counts for entomophily include possibly ambophilous species). We found no correlation between dioecy and anemophily/entomophily. The view that insularity favours establishment of dioecious taxa may be invoked by considering localized and disjoint post-glacial colonization. The view that dioecy, as a form of xenogamy, has evolved in response to offsetting the adverse consequences of inbreeding and accumulation of mutations may apply under High Arctic conditions, further eroding ideas that short, harsh, active seasons promote self-fertilization (autogamy), agamospermy, and vegetative reproduction while disfavouring xenogamy by insect or wind pollination.

Key words: plant sexual reproduction, latitudinal gradient, pollination, anemophily, floral characters, fleshy fruit, woodiness.

Résumé : En comparant l'incidence de dioécie chez les flores nord-américaines, nous constatons une corrélation positive étroite avec une latitude croissante. La dioécie dans le Haut-Arctique est hautement corrélée avec la lignification, comme ailleurs. Elle est significativement corrélée avec les fruits charnus, « zoochorous », aussi documentés ailleurs. La corrélation avec l'aspect discret floral, que nous définissons en matière d'attrait aux pollinisateurs (c.-à-d. la fonctionnalité à la pollinisation), est faible et statistiquement sans importance. Les conclusions publiées sur cette corrélation sont ambiguës; les différents auteurs ont défini l'aspect discret de différentes façons qui peuvent ou ne peuvent pas refléter la fonctionnalité à la pollinisation. Bien que nous reconnaissons que pour certains taxa (p. e. *Salix* spp.) les importances relatives de la pollinisation anémophile, zoophile (entomophile) et ambophile (par le vent et les insectes) sont inconnues, nous avons assigné des espèces à (a) l'anémophilie si la preuve de l'entomophilie ne pouvait pas être invoquée et à (b) l'entomophilie si la pollinisation d'insecte a été considérée possible (c.-à-d. les dénombrements pour entomophilie comprennent possiblement les espèces ambophiles). Nous n'avons trouvé aucune corrélation entre la dioécie et l'anémophilie ou l'entomophilie. La perspective que l'insularité favorise l'établissement de taxa dioïques peut être invoquée en considérant la colonisation postglaciaire localisée et disjointe. La perspective que la

Received 11 July 2016. Accepted 2 May 2017.

P.G. Kevan and B. Godglick. School of Environmental Sciences, University of Guelph, Guelph, ON N1G 2W1, Canada.

Corresponding author: Peter G. Kevan (email: pkevan@uoguelph.ca).

This article is open access. This work is licensed under a Creative Commons Attribution 4.0 International License (CC BY 4.0) http://creativecommons.org/licenses/by/4.0/deed.en_GB.

dioécie, comme une forme de xénogamie, s'est développée en réponse au contrebalancement des conséquences défavorables de croisement consanguin et à l'accumulation de mutations peut s'appliquer sous les conditions du Haut-Arctique nuisant davantage à l'idée que des saisons courtes, dures, actives promeuvent l'autofécondation (autogamie), l'agamosperme et la reproduction végétative tout en défavorisant la xénogamie par le biais de la pollinisation par insecte ou par le vent. [Traduit par la Rédaction]

Mots-clés : reproduction sexuée des plantes, gradient latitudinal, pollinisation, anémophilie, types floraux, fruit charnu, lignification.

Introduction

Dioecious plants bear male and female flowers on separate plants. It has been estimated that 3%–4% (Yampolsky and Yampolsky 1922) or 6% of all flowering plants are dioecious (Renner and Ricklefs 1995). Several evolutionary pathways to dioecy have been investigated, including through hermaphroditism, gynodioecy, monoecy, and heterostyly (Lewis 1942; Maynard Smith 1978; Bawa 1980; Lloyd 1982; Thomson and Brunet 1990; Richards 1997). The main selective pressure favouring dioecy has been suggested to be the advantages of outcrossing and genetic heterogeneity. The incidence of dioecy has been correlated with various botanical and biogeographical factors, including woodiness, fleshy fruits, anemophily, small and pale flowers and associated pollination by small insects (entomphily), insularity, and latitude. Steiner (1988) provided an ample review of the botanical correlates ascribed to dioecy that Vamosi et al. (2003), Vamosi and Vamosi (2004), and Sabath et al. (2016) used to address the question of phylogenetic biases and possibly constraints (McKittrick 1993).

It may be suggested that dioecy would not be well represented in Arctic floras because of the perceived lack of insect pollinators and also restricted opportunity for interplant pollen transfer by wind (anemophily). However, it is now known that anthophiles are abundant in the Arctic regions (Mosquin and Martin 1967; Hocking 1968; Kevan 1972, 1973; Danks 1978, 1986; Swales 1979; Tikhmenev 1984; Philipp et al. 1990; Elberling and Olesen 1999; Lundgren and Olesen 2005; Olesen et al. 2008; Franzen and Ockinger 2012; Høye et al. 2013; Schmidt et al. 2016) and effective in pollination (Kevan 1972, 1973; Philipp et al. 1990). Moreover, Fox (1985) noted that the incidence of dioecy increases with northerly latitude in North America, even to the Alaskan North Slope. More recently, Godin (2014) noted that 35% of the woody flora of Siberia is dioecious and that dioecy is correlated with harsh alpine and Arctic conditions there. Fox (1985) considered some of the correlates of dioecy with pollination, seed dispersal, and growth form. In particular, he found that the incidence of dioecy increases northward in woody plants but that floral characteristics (which he equated with pollination mechanism or syndrome) and means of seed dispersal (zoochory versus anemochory) were not correlated with dioecy in the north. He classified floral characteristics as follows: having simple, small flowers (all “open” flowers having petals under 5 mm long, regardless of floral display) or showy flowers (larger open blossoms, and all tubular or campanulate and most zygomorphic flowers). His floral classification is overly simplistic because it did not take into functional account how potentially pollinating insects would perceive the anthia (attractive floral units (Faegri and van der Pijl 1966)) such as inflorescences or arrays of flowers (see Kevan 1970; Vamosi et al. 2003). With more information on the pollination systems and floral attributes of the High Arctic flora of the Canadian Arctic Archipelago at our disposal (Kevan 1970), we decided to test if the correlates to dioecy (listed in Table 1) apply to that flora and then discuss if the idea of evolutionary pressure favouring dioecy (incidence of outcrossing) has merit.

Table 1. Classification of flora of the Canadian Arctic Archipelago by sexual state, growth form, fruit type, floral (anthial) conspicuousness, and inferred pollination mechanism (entomophily (including ambophily) versus anemophily).

Growth form or inferred pollination mechanism	Fruit type	Anthial conspicuousness	Dioecious	Nodioecious	Proportion dioecious
Woody	Fleshy	Conspicuous	0	2	0
		Inconspicuous	1	2	0.33
Herbaceous	Dry	Conspicuous	13	9	0.59
		Inconspicuous	3	2	0.6
	Fleshy	Conspicuous	2	0	1
		Inconspicuous	0	0	
Entomophilous	Dry	Conspicuous	6	182	0.032
		Inconspicuous	4	130	0.030
Anemophilous		Conspicuous	19	236	0.081
		Inconspicuous	5	49	0.102

Note: Associated categories for classification for each species considered are included in the supplementary material¹.

Although dioecy is well known in the Arctic flora (Murray 1987), few studies have quantified its frequency and its relationships between the common correlates. Dioecy has been studied in the Arctic willows (Salicaceae), primarily in *Salix arctica*; however, the scope of those studies has been broad, including the importance of sex and habitat in gas exchange (Jones et al. 1999), sex ratios in *Salix polaris* and *Salix herbacea* (Crawford and Balfour 1983), stomatal water conductance and the spatial segregation of sexes (Dawson and Bliss 1989), differences in catkin warmth between sexes (Kevan 1990), and growth response with respect to snow precipitation (Schmidt et al. 2010). Studies on dioecy in other Arctic taxa are wanting although it is recorded that some species that are dioecious in southerly locations may tend, in the north, to hermaphroditism (e.g., *Empetrum nigrum*) or be single-sexed female agamosperms (e.g., *Antennaria* spp.) (Porsild 1964).

Our first objective was to assemble a compendium (supplementary material¹) of the flowering plants (Spermatophyta: Angiospermae) of the Canadian High Arctic (the Canadian Arctic Archipelago) and note whether or not dioecy can be invoked. We included the unisexual and agamospermous *Antennaria* spp. as dioecious just as we have included nonsexually reproducing agamosperms and other apomicts as nondioecious if dioecy cannot be invoked. With that compendium, our aim was to document the incidence of dioecy in the flora and to compare that with the incidence of dioecy published for other floras of North America (north of Mexico). We then ascribed to each species characteristics that have been positively associated with dioecy (correlates) with the objective of assessing whether or not those correlates are positively associated with dioecy in the High Arctic flora of North America. Our final objective is to discuss the characteristics in terms of their possible ecological and evolutionary functionality in the sexual reproduction, especially xenogamy, in the High Arctic flora.

Methods

To examine the prevalence of dioecy in the flora of the Canadian Arctic Archipelago as well as the correlates of plant species diversity, plant growth form, and mating systems with dioecy, we used Porsild (1964) and Nature dataset of the Flora of the Canadian Arctic

¹Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/as-2016-0030>.

Archipelago (Aiken et al. 2007) to delimit the flora. The data set includes 356 angiosperm species (supplementary material¹). We also consulted the floras of Greenland, the circumpolar Arctic, and the circumpolar plants for information pertaining to basic floral morphology (Polunin 1959; Hultén 1962; Böcher et al. 1968). We reviewed modern and older literature to determine breeding and mating systems (Warming 1886; Murray 1987; Richards 1997) and pollination mechanisms (references in Kevan 1970, 1972, 1973). Web resources were additionally considered, although most did not return any additional, relevant information.

In assembling our database (supplementary material¹), we took the 356 species and first classified species by mating system (xenogamy, autogamy, or mixed). Dioecy was noted by a thorough search of pertinent literature (noted above). If information pertaining to mating systems could not be found, the species were classified by default as non-dioecious. A few species mentioned in the various sources consulted were noted as polygamous and partially xenogamous. They are classified as possibly dioecious in the supplementary material¹.

Pollination mechanisms, whether by entomophily or anemophily, were determined or inferred from published information. For some species, categorization was difficult. An extreme example is noted for the genus *Antennaria* (Asteraceae) for which the taxonomy is difficult; dioecy and hermaphroditism are recorded in some species but only agamosperous female plants are known from the Canadian High Arctic (Porsild 1964). Even so, insects are known to visit the capitulae in some species elsewhere (Willis and Burkill 1903; Bierzychudek 1987) so that entomophily might reasonably be inferred. *Oxyria digyna* may have unisexual plants in some parts of its range but is generally hermaphrodite (Mooney and Billings 1961) and anemophilous. The willows (*Salix* spp. Salicaceae) are all dioecious but at least some High Arctic species in some places are entomophilous (e.g., *Salix arctica*) (Kevan 1972) and others seem to be anemophilous (e.g., *Salix polaris*) (Yeloff et al. 2008); ambophily (pollination by both wind and insects (Stelleman and Meeuse 1976)) may be widespread in the genus (Peeters and Totland 1999; Culley et al. 2002; Karrenberg et al. 2002). Despite those problems, we categorized the dioecious and nondioecious species as anemophilous (54 species) or entomophilous with published records or, at least, with characteristics that indicated that entomophily (i.e., floral visitation by insects, not necessarily pollination by insects) could be reasonably considered (255 species) with 47 species as unknown.

We assigned species to the categories herbaceous or woody according to the data set of Aiken et al. (2007) as well as by visual inspection of living plants, herbarium specimens, and photographs. Woodiness is defined by perennial growth and lignified secondary xylem above ground. Woody species of the Arctic tundra are chamaephytes and include all shrubs, including dwarf shrubs (0.1 m or less) and cushion plants. Cryptophytes and hemicryptophytes are listed as herbaceous. There are almost no annuals (therophytes) in the Arctic flora (Billings and Mooney 1968).

The types of the fruit at maturity (fleshy or dry) were also classified from information in the same data set (Aiken et al. 2007) as well as by visual inspection of living plants, herbarium specimens, and photographs.

To assess the possible conspicuousness of inflorescences, we combined floral colours and anthial sizes to categorize anthia as conspicuous to anthophilous insects or inconspicuous. Flower colours were noted from published records (especially Kevan 1972; Aiken et al. 2007), visual inspection of living plants, herbarium specimens, and photographs. Whitish to yellow-green flowers were especially noted because pale colouring has been associated with dioecy. The sizes of anthia (floral arrays) in respect to pollination are sometimes difficult to assess. In general, the larger the array (whether a single flower or an inflorescence)

the more attractive it is to floral visitors (Kevan 1970, 1973; Dafni et al. 1997). Aiken et al. (2007) classified flowers as small (corolla <5 mm diameter), medium (corolla diameter >5 and <15 mm), and large (corolla diameter >15 mm). By combining Kevan's (1970) data on floral measurements with those from Aiken et al. (2007) and other sources, visual inspection of living plants, herbarium specimens, and photographs, we scored the conspicuousness of the anthia and considered it as a possible correlate of dioecy. Inconspicuous anthia are those with no apparent optical attraction to insect pollinators. Conspicuous blossoms and anthia include dish- to bowl-, bell- or funnel-, head- or brush-, gullet-, flag-, or tube-shaped flowers that are presented singly or in lax inflorescences. Although the individual flowers (or florets) of *Salix* spp., *Bistorta vivipara*, and Asteraceae are small, they combine to make conspicuous anthia. In this study, anthia that are neutral, greenish, or dark were typically classified as inconspicuous, regardless of size (small or medium) (e.g., monocotyledons, *Betula*, *Oxyria*, some *Salix* spp.).

To test the hypothesis that dioecy is at least as well represented in the flora of the Canadian Arctic Archipelago as elsewhere, we compared our findings with those from other parts of North America. We used only data from regional floras of North America (see Fox 1985) and our own. Those data were ranked in order of latitude. On noting that dioecy is well represented in the Canadian High Arctic flora, we tested the hypothesis that there is a gradient of increasing dioecy with latitude by using the Spearman's rank correlation coefficient (Zar 2009; www.socscistatistics.com/tests/spearman/Default.aspx, accessed 2 February 2017). In our statistical approach to testing the hypotheses that woodiness, fruit type, anthial conspicuousness, and anemophily/entomophily are associated with dioecy, we applied χ^2 contingency tests and Fisher's exact test (Zar 2009; www.socscistatistics.com/tests/chisquare/Default2.aspx and <http://www.socscistatistics.com/tests/fisher/Default2.aspx>, accessed 2 February 2017) using the null hypothesis (rejected at $\alpha = 0.05$) that the correlate is proportionately equally represented in dioecious and nondioecious species in the flora of the Canadian High Arctic.

Results

In the Canadian Arctic Archipelago, the incidence of dioecy is 8.1%, i.e., 29 of 356 species. Although that is quite similar to the incidence found in other floras of the world (see Steiner 1988), it seems that the incidence of dioecy increases northward in North America and is most prevalent in the Arctic floras (Fig. 1), even exceeding the maximum given in Fox (1985). This correlation is statistically significant (Spearman's rank correlation coefficient $R_s = 0.89$, $p = 0.019$) for data corresponding to the Carolinas, California, northeastern United States, Alaska, the Alaskan North Slope, and the Canadian Arctic Archipelago.

Table 1 summarizes our data (supplementary material¹) for the flora of the Canadian Arctic Archipelago by sexual state (dioecious or not), growth form (woody versus herbaceous), fruit type (fleshy or dry), and floral conspicuousness. Table 2 presents the results of χ^2 and Fisher's contingency tests in which the incidence of dioecy is parsed by various characteristics noted above. The exclusion of *Antennaria* spp. from consideration does not alter the statistical conclusions. Dioecy is much more prevalent in species that are woody than in those that are herbaceous. Even though there are only a few plants (seven) that produce fleshy fruits in the High Arctic, a statistically significant disproportionate number (three) are dioecious. There is no statistically significant correlation between dioecy and plants that have inconspicuous anthia even though there is a weak association between floral inconspicuousness and dioecy. There is no correlation between entomophily/anemophily and dioecy. We do note that within the herbaceous plants, there is a statistically significant correlation of fleshy fruits with dioecy but that is not the case for

Fig. 1. Rank correlation of the relationship between latitude and the incidence of dioecy (including female unisexuality in *Antennaria* spp., a genus that is usually dioecious) in North America from south to north for the Carolinas (Conn et al. 1980), California, northeastern United States, boreal Alaska, Alaskan North Slope (Fox 1985), and Canadian Arctic Archipelago (supplementary material¹).

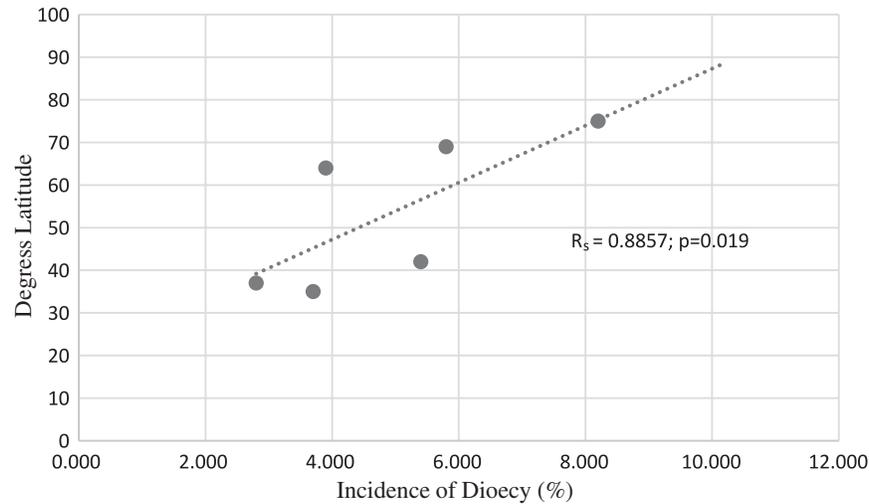


Table 2. Correlative association of dioecy with woodiness, fleshy fruit, anthial conspicuousness, and entomophily (i.e., insect visitation to flowers documented or inferred) versus anemophily by 2×2 chi-square contingency statistics (χ^2) and by Fisher's exact test with probability values that the null hypothesis (the correlate is proportionately equally represented in dioecious and nondioecious species in the flora of the Canadian High Arctic) holds.

Correlate	χ^2	<i>p</i> value	<i>p</i> by Fisher's exact test
Woodiness	99.1	<0.0001	<0.0001
Fleshy fruit	19.2	<0.0001	0.014
Conspicuousness	2.75	0.10	0.17
Entomophily	0.20	0.66	0.59
Woody with fleshy fruits:			0.16
dioecious versus nondioecious	Not valid, some values too small	Not valid, some values too small	
Herbaceous with fleshy fruits:			0.001
dioecious versus nondioecious	Not valid, some values too small	Not valid, some values too small	

woody plants. We made no attempt to examine for autocorrelations of traits associated with dioecy, as did Steiner (1988), or to test for phylogenetic biases as did Vamosi et al. (2003), Vamosi and Vamosi (2004), and Sabath et al. (2016).

Discussion

Our analysis indicates a significant positive correlation between increasing latitude and the incidence of dioecy. We first address issues to do with plant reproductive strategies, (1) fruiting and fruit dispersal, and (2) floral biology, especially floral conspicuousness and anemophily/entomophily before considering the evolutionary and genetic consequences of woodiness and longevity as factors favouring xenogamy in general and dioecy in particular.

One of the most argued correlates of dioecy is fleshy fruits or seeds dispersed by frugivores (Bawa 1980; Givnish 1980; Muenchow 1987; Steiner 1988; Thomson and Brunet 1990; Vamosi and Vamosi 2004). Both Bawa (1980) and Givnish (1980) agreed that fleshy fruits play a causal role in the evolution of dioecy through disproportionate gains in female fitness with an increase in the reproductive effort. In the High Arctic, the association of dioecy with zoochory seems also to apply. Certainly, there are various migratory birds, a few residential birds, and some mammals present in the High Arctic that disperse fleshy fruits. Baker (1984) and Baker and Cox (1984) explained that several seeds being dispersed as a group, through zoochory, to a given place (e.g., islands) would allow establishment of breeding populations, as dioecy prescribes. The highly disjunct, bipolar populations of *Empetrum* spp. (dioecy is documented for *Empetrum nigrum*) are proposed to have resulted from a single long-distance dispersal event mediated by birds (Popp et al. 2011). The same suggestion would apply to other elements of the Canadian High Arctic flora that became locally established and then widespread only in Holocene time following deglaciation.

The probable relationships between dioecy and pollination are not simple to explain. Inconspicuousness of flowers has been a central point in this part of the debate (Steiner 1988; Vamosi et al. 2003; Vamosi and Vamosi 2004), but inconspicuousness has been variously defined by flower sizes, floret size, and coloration without regard to the functionally attractive floral unit for pollinators. Fox's (1985) floral dimensions (inferred improperly to represent pollination syndromes) make a case in point. Muenchow (1987) used floral colour (green versus not green) to distinguish between conspicuous and inconspicuous flowers but concluded that green flowers did not distinguish dioecious plants from nondioecious. Although it is known in general that small, inconspicuous flowers tend to be pollinated by small, generalist insects (Proctor et al. 1996; Willmer 2011), it is those co-occurring conditions that some researchers have suggested favour the evolution of dioecy. The mechanism proposed whereby dioecy is favoured through constraints in pollination purports that small and generalist flower visitors frequently effect self-pollination, leading to inbreeding depression and so favouring the establishment of xenogamy, including dioecy. Although Renner and Feil (1993) rejected that pathway for the tropical flowering plants they surveyed, noting dioecy is well represented in taxa with specialized pollinators and pollination mechanisms, Bawa (1994) countered that view with an explanation of its flaws. The countervailing, yet plausible, effect is that small, pale-coloured flowers represent the ancestral condition (i.e., phylogenetic constraint) of self-compatibility in some plant taxa and that condition favours autogamy and geitonogamy (Lewis 1942; Lloyd 1982). Our analysis also suggests that the association of dioecy with inconspicuous antheria is weak in the High Arctic.

Turning to abiotic pollination, Stebbins (1950, pp. 299–324) stated that the adaptation to anemophily is likely responsible for the evolution of imperfect, monoecious, and dioecious flowers, made possible through the reduction of perianth parts (inconspicuousness) and the separation of sexes. Indeed, positive relationships have been documented between anemophily and dioecy in flowering plants (Kaplan and Mulcahy 1971; Freeman et al. 1980a, 1980b; Muenchow 1987; Steiner 1988; Vamosi and Vamosi 2014). Environmental conditions that allow for anemophily include clumped distributions of plants, definitive physical cues (seasonality to diel periodicities in microclimate), and opportunities for pollen to move rapidly (Whitehead 1983; Culley et al. 2002; Montoya-Pfeiffer et al. 2016). Those same conditions, which occur in almost all environments including the Arctic, would then also favour dioecy via the sort of evolutionary pathway invoked by Stebbins (1950). The lack of correlation we report between anemophily and dioecy in the High Arctic seems neither to support nor detract from Stebbins' (1950) evolutionary ideas. Anemophily and dioecy are

probably taxonomic synapomorphies successfully carried into the High Arctic in Holocene time following deglaciation.

We conclude that the proposed relationship between inconspicuousness of flowers and dioecy does not apply in the Arctic. The sizes, colours, scents, etc., of individual flowers are not indicators of conspicuousness to pollinators that respond to anthia in floral displays. The abundance or sizes, or both together, displayed by anemophilous inflorescences (i.e., conspicuousness to air currents) reflect both male and female function.

The strong positive relationship between aboveground woodiness and dioecy in the High Arctic (and other harsh northerly environments (Fox 1985; Godin 2014)) is remarkable. One may ask why that is so, and why the converse of disproportionate paucity of dioecy in geophytes and hemicryptophytes is evident. Steiner (1988) and others noted that the association between dioecy and woodiness may be related to plant size and particularly to longevity. He stated, as Stebbins (1958) and Maynard Smith (1978) also noted, that populations of plants with long life spans are more likely to suffer restricted recombination because of limitations to genetic diversity and exchange over protracted durations. Over evolutionary time, xenogamy through dioecy might be favoured to reduce the adverse effects of inbreeding. At the same time, sexual and gender biases to male reproductive function, as noted by Richards (1997), would further assure mating, but detailed studies on seasonal or annual resource allocation to sexual function in plants are wanting despite the commonly held view that female function is the more costly (Charnov 1982). Additionally, there are positive relationships between plant age (noted as stature by Scofield and Schultz 2006), the incidence of intraplant mutations, and selective pressures for outbreeding. That idea could apply to intragenet mutations in long-lived clonal species, but de Witt and Stöcklin (2010) noted little intergenet genetic variation even in Arctic plants. Regardless, there appears to be agreement that woodiness is positively associated with dioecy (Fox 1985; Steiner 1988; Vamosi et al. 2003; Vamosi and Vamosi 2004), as it is in Siberia (Godin 2014) and the High Arctic. Our result may be strongly influenced by the willows (*Salix* spp., 16 species), all of which are woody and dioecious. Steiner (1988), Richards (1997), Vamosi et al. (2003), Vamosi and Vamosi (2004), and Sabath et al. (2016) noted taxonomic bias in correlates with dioecy. Previous reviews, as cited, on the incidence of dioecy do not make phylogenetic comparisons with other breeding systems, especially those that promote xenogamy, and so this shortcoming remains for further study.

Dioecy is a breeding system that favours xenogamy no matter the nature of the pollen vectors. It seems to have evolved in various floras as a response to offset the adverse consequences of inbreeding and that seems to apply just as well, if not better, under High Arctic conditions as elsewhere. Xenogamy promoted by other breeding systems (dichogamy, herkogamy, heterostyly, and self-incompatibility (Warming 1886; Kevan 1970, 1972, 1973; Murray 1987; Grundt et al. 2005)) is not as well represented in the Arctic as elsewhere, but surveys and reviews are wanting. In some Arctic plants, breeding systems favouring xenogamy have been, or may have been, lost (e.g., *Antennaria* spp. are agamosperous (Porsild 1964), *Empetrum nigrum* seems to favour hermaphroditism in northern parts of its range (Porsild 1964), *Primula* spp. and *Silene* spp. in the Arctic seem to be homostylous (Philipp et al. 1990), but loss of heterostyly in Arctic populations of *Menyanthes trifoliata* has been questioned (Oleson 1987), the incidence of autogamy seems to vary geographically in some species such as *Saxifraga oppositifolia* and *Dryas integrifolia* (Kevan 1972; Philipp et al. 1990), and production of vegetative propagules is well known in some Arctic taxa). Evolutionary departure from xenogamy would presumably be favoured in plants that became locally established in isolated small populations and then widespread in Holocene time following deglaciation. Despite the foregoing examples and suggestions,

the relatively high incidence of dioecy in the High Arctic certainly erodes the generally upheld view that short, harsh, active seasons promote self-fertilization (autogamy), agamospermy, and vegetative reproduction while disfavoring xenogamy by insect or wind pollination.

Acknowledgements

We are grateful for the helpful comments provide during the process of review. Support for this study was provided by a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to P.G.K and through the Canadian Pollination Initiative (NSERC-CANPOLIN) Strategic Network. This study is No. 145 from NSERC-CANPOLIN.

References

- Aiken, S.G., Dallwitz, M.J., Consaul, L.L., McJannet, C.L., Boles, R.L., Argus, G.W., Gillett, J.M., Scott, P.J., Elven, R., LeBlanc, M.C., Gillespie, L.J., Brysting, A.K., Solstad, H., and Harris, J.G. 2007. Flora of the Canadian Arctic Archipelago: descriptions, illustrations, identification, and information retrieval. NRC Research Press, National Research Council of Canada, Ottawa, Ont. <http://nature.ca/aaflora/data> [accessed 6 January 2017].
- Baker, H.G. 1984. Some functions of dioecy in seed plants. *Am. Nat.* **124**: 149–158. doi: [10.1086/284260](https://doi.org/10.1086/284260).
- Baker, H., and Cox, P.A. 1984. Further thoughts on dioecism and islands. *Ann. Mo. Bot. Gard.* **71**: 244–253. doi: [10.2307/2399068](https://doi.org/10.2307/2399068).
- Bawa, K.S. 1980. Evolution of dioecy in flowering plants. *Annu. Rev. Ecol. Evol. Syst.* **11**: 15–39. doi: [10.1146/annurev.es.11.110180.000311](https://doi.org/10.1146/annurev.es.11.110180.000311).
- Bawa, K.S. 1994. Pollinators of tropical dioecious angiosperms: a reassessment? No, not yet. *Am. J. Bot.* **81**: 456–460. doi: [10.2307/2445495](https://doi.org/10.2307/2445495).
- Bierzychudek, P. 1987. Pollinator increase the cost of sex by avoiding female flowers. *Ecology*. **68**: 444–447. doi: [10.2307/1939276](https://doi.org/10.2307/1939276).
- Billings, W.D., and Mooney, H.A. 1968. The ecology of Arctic and alpine plants. *Biol. Rev.* **43**: 481–529. doi: [10.1111/j.1469-185X.1968.tb00968.x](https://doi.org/10.1111/j.1469-185X.1968.tb00968.x).
- Böcher, T., Wittrock, K.H., and Jakobsen, K. 1968. The flora of Greenland. Haase, Copenhagen, Denmark.
- Charnov, E.L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.
- Conn, J.S., Wentworth, T.R., and Blum, U. 1980. Patterns of dioecism in the flora of the Carolinas. *Am. Midl. Nat.* **103**: 310–315. doi: [10.2307/2424628](https://doi.org/10.2307/2424628).
- Crawford, R.M.M., and Balfour, J. 1983. Female predominant sex ratios and physiological differentiation in Arctic willows. *J. Ecol.* **71**: 149–160. doi: [10.2307/2259968](https://doi.org/10.2307/2259968).
- Culley, T.M., Weller, S.G., and Sakai, A.K. 2002. The evolution of wind pollination in angiosperms. *Trends Ecol. Evolut.* **17**: 361–369. doi: [10.1016/S0169-5347\(02\)02540-5](https://doi.org/10.1016/S0169-5347(02)02540-5).
- Dafni, A., Lehrer, M., and Kevan, P.G. 1997. Spatial flower parameters and insect spatial vision. *Biol. Rev. Cambridge Philos. Soc.* **72**: 239–282. doi: [10.1017/S0006323196005002](https://doi.org/10.1017/S0006323196005002).
- Danks, H.V. 1978. Canada and its insect fauna. Entomological Society of Canada, Ottawa, Ont.
- Danks, H.V. 1986. Insect plant interactions in Arctic regions. *Rev. Entomol. Que.* **31**: 52–75.
- Dawson, T.E., and Bliss, L.C. 1989. Patterns of water use and tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. *Oecologia*. **79**: 332–343. doi: [10.1007/BF00384312](https://doi.org/10.1007/BF00384312). PMID: 23921398.
- de Witt, L.C., and Stöcklin, J. 2010. Longevity of clonal plants: why it matters and how to measure it. *Ann. Bot.* **106**: 859–870. doi: [10.1093/aob/mcq191](https://doi.org/10.1093/aob/mcq191). PMID: 20880935.
- Elberling, H., and Olesen, J.M. 1999. The structure of a high latitude plant-flower visitor system: the dominance of flies. *Ecography*. **22**: 314–323. doi: [10.1111/j.1600-0587.1999.tb00507.x](https://doi.org/10.1111/j.1600-0587.1999.tb00507.x).
- Faegri, K., and van der Pijl, L. 1966. The principles of pollination ecology. Pergamon Press, Toronto, Ont.
- Fox, J.F. 1985. Incidence of dioecy in relation to growth form, pollination and dispersal. *Oecologia*. **67**: 244–249. doi: [10.1007/BF00384293](https://doi.org/10.1007/BF00384293). PMID: 28311318.
- Franzen, M., and Ockinger, E. 2012. Climate-driven changes in pollinator assemblages during the last 60 years in an Arctic mountain region in Northern Scandinavia. *J. Insect Physiol.* **16**: 227–238. doi: [10.1007/s10841-011-9410-y](https://doi.org/10.1007/s10841-011-9410-y).
- Freeman, D.C., Harper, K.T., and Charnov, E.L. 1980a. Sex change in plants: old and new observations and new hypotheses. *Oecologia*. **47**: 222–232. doi: [10.1007/BF00346825](https://doi.org/10.1007/BF00346825). PMID: 28309476.
- Freeman, D.C., Harper, K.T., and Ostler, W.K. 1980b. Ecology of plant dioecy in the intermountain region of western North America. *Oecologia*. **44**: 410–417. doi: [10.1007/BF00545246](https://doi.org/10.1007/BF00545246). PMID: 28310298.
- Givnish, T.J. 1980. Ecological constraints on the evolution of breeding systems in plants: dioecy and dispersal in gymnosperms. *Evolution*. **34**: 959–972. doi: [10.2307/2408001](https://doi.org/10.2307/2408001).
- Godin, V.N. [Годин, В.Н.]. 2014. Половые формы и их экологические корреляции у древесных голосеменных и покрытосеменных растений Сибири [Sexual forms and their ecological correlates of woody gymnosperms and angiosperms in Siberia]. Вестник Томского государственного университета. Биология [Tomsk State Univ. J. Biol.]. **4**: 17–36.

- Grundt, H.H., Elven, R., and Brochmann, C. 2005. A rare case of self-incompatibility in Arctic plants: draba palanderiana (*Brassicaceae*). *Flora*. **200**: 321–325. doi: [10.1016/j.flora.2004.10.001](https://doi.org/10.1016/j.flora.2004.10.001).
- Hocking, B. 1968. Insect-flower associations in high Arctic with special reference to nectar. *Oikos*. **19**: 359–387. doi: [10.2307/3565022](https://doi.org/10.2307/3565022).
- Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K., and Forchhammer, M.C. 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nat. Clim. Change*. **3**: 759–763. doi: [10.1038/nclimate1909](https://doi.org/10.1038/nclimate1909).
- Hultén, E. 1962. The circumpolar plants. Almqvist & Wiskell, Stockholm, Sweden.
- Jones, M.H., MacDonald, S.E., and Henry, G.H. 1999. Sex and habitat specific responses of a high Arctic willow, *Salix arctica*, to experimental climate change. *Oikos*. **87**: 129–138. doi: [10.2307/3547004](https://doi.org/10.2307/3547004).
- Kaplan, S.M., and Mulcahy, D.L. 1971. Mode of pollination and floral sexuality in *Thalictrum*. *Evolution*. **25**: 659–668. doi: [10.2307/2406946](https://doi.org/10.2307/2406946).
- Karrenberg, S., Kollmann, J., and Edwards, P.J. 2002. Pollen vectors and inflorescence morphology in four species of *Salix*. *Plant Syst. Evol.* **235**: 181–188. doi: [10.1007/s00606-002-0231-z](https://doi.org/10.1007/s00606-002-0231-z).
- Kevan, P.G. 1970. High Arctic insect–flower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, Northwest Territories, Canada. Doctoral dissertation, University of Alberta, Edmonton, Alta.
- Kevan, P.G. 1972. Insect pollination of high Arctic flowers. *J. Ecol.* **60**: 831–847. doi: [10.2307/2258569](https://doi.org/10.2307/2258569).
- Kevan, P.G. 1973. Flowers, insects and pollination ecology in the Canadian high Arctic. *Polar Rec.* **16**: 667–674. doi: [10.1017/S0032247400063609](https://doi.org/10.1017/S0032247400063609).
- Kevan, P.G. 1990. Sexual differences in temperatures of blossoms on a dioecious plant, *Salix arctica*: significance for life in the Arctic. *Arct. Alp. Res.* **22**: 283–289. doi: [10.2307/1551591](https://doi.org/10.2307/1551591).
- Lewis, D. 1942. The evolution of sex in flowering plants. *Biol. Rev.* **17**: 46–67. doi: [10.1111/j.1469-185X.1942.tb00431.x](https://doi.org/10.1111/j.1469-185X.1942.tb00431.x).
- Lloyd, D.G. 1982. Selection of combined versus separate sexes in seed plants. *Am. Nat.* **120**: 571–585. doi: [10.1086/284014](https://doi.org/10.1086/284014).
- Lundgren, R., and Olesen, J.M. 2005. The dense and highly connected world of Greenland's plants and their pollinators. *Arct. Alp. Res.* **37**: 514–520. doi: [10.1657/1523-0430\(2005\)037\[0514:TDAHWCW\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2005)037[0514:TDAHWCW]2.0.CO;2).
- Maynard Smith, J. 1978. Evolution of sex. Cambridge University Press, New York.
- McKittrick, M. 1993. Phylogenetic constraint in evolutionary theory: has it any explanatory power? *Annu. Rev. Ecol. Syst.* **24**: 307–330. doi: [10.1146/annurev.es.24.110193.001515](https://doi.org/10.1146/annurev.es.24.110193.001515).
- Montoya-Pfeiffer, P.M., Kevan, P.G., González-Chaves, A., Pereira Queiroz, E., and Dec, E. 2016. Explosive pollen release, stigma receptivity and pollen dispersal pattern of *Boehmeria caudata* Sw. (Urticaceae) in a Brazilian rain forest. *Botany*. **94**: 607–614. doi: [10.1139/cjb-2016-0031](https://doi.org/10.1139/cjb-2016-0031).
- Mooney, H.A., and Billings, W.D. 1961. Comparative physiological ecology of Arctic and alpine populations of *Oxyria digyna*. *Ecol. Monogr.* **31**: 1–29. doi: [10.2307/1950744](https://doi.org/10.2307/1950744).
- Mosquin, T., and Martin, J.E.H. 1967. Observations on the pollination biology of plants on Melville Island, N.W.T., Canada. *Can. Field Nat.* **81**: 201–205.
- Muenchow, G.E. 1987. Is dioecy associated with fleshy fruit? *Am. J. Bot.* **74**: 287–293. doi: [10.2307/2444031](https://doi.org/10.2307/2444031).
- Murray, D.F. 1987. Breeding systems in the vascular flora of Arctic North America. Pages 239–262 in K.M. Urbanska, ed. Differentiation patterns in higher plants. Academic Press, London, UK.
- Olesen, J.M. 1987. Heterostyly, hornostyly, and long-distance dispersal of *Menyanthes trifoliata* to Greenland. *Can. J. Bot.* **65**: 509–511. doi: [10.1139/b87-064](https://doi.org/10.1139/b87-064).
- Olesen, J.M., Bascompte, J., Elberling, H., and Jordano, P. 2008. Temporal dynamics in a pollination network. *Ecology*. **89**: 1573–1582. doi: [10.1890/07-0451.1](https://doi.org/10.1890/07-0451.1). PMID: 18589522.
- Peeters, L., and Totland, Ø. 1999. Wind to insect pollination ratios and floral traits in five alpine *Salix* species. *Can. J. Bot.* **77**: 556–563. doi: [10.1139/b99-003](https://doi.org/10.1139/b99-003).
- Philipp, M., Böcher, J., Mattesen, O., and Woodell, S.R.J. 1990. A quantitative approach to the sexual reproductive biology and population structure in some Arctic flowering plants: *Dryas integrifolia*, *Silene acaulis* and *Ranunculus nivalis*. *Meddel. Grønland*. **274**: 1–60.
- Polunin, N. 1959. Circumpolar Arctic flora. Clarendon Press, Oxford, UK.
- Popp, M., Mirr, V., and Brochmann, C. 2011. A single Mid-Pleistocene long-distance dispersal by a bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*). *Proc. Natl. Acad. Sci. USA*. **108**: 6520–6525. doi: [10.1073/pnas.1012249108](https://doi.org/10.1073/pnas.1012249108). PMID: 21402939.
- Porsild, A.E. 1964. Illustrated flora of the Canadian Arctic Archipelago. Bulletin of the National Museum of Canada 146.
- Proctor, M., Yeo, P.F., and Lack, A. 1996. The natural history of pollination. Timber Press, Portland, Ore.
- Renner, S.S., and Feil, J.P. 1993. Pollinators of tropical dioecious angiosperms. *Am. J. Bot.* **80**: 1100–1107. doi: [10.2307/2445757](https://doi.org/10.2307/2445757).
- Renner, S.S., and Ricklefs, R.E. 1995. Dioecy and its correlates in the flowering plants. *Am. J. Bot.* **82**: 596–606. doi: [10.2307/2445418](https://doi.org/10.2307/2445418).
- Richards, A.J. 1997. Plant breeding systems. 2nd ed. Chapman Hall, London, UK.
- Sabath, N., Goldberg, E.E., Glick, L., Einhorn, M., Ashman, T.L., Ming, R., Otto, S.P., Vamosi, J.C., and Mayrose, I. 2016. Dioecy does not consistently accelerate or slow lineage diversification across multiple genera of angiosperms. *New Phytol.* **209**: 1290–1300. doi: [10.1111/nph.13696](https://doi.org/10.1111/nph.13696). PMID: 26467174.

- Schlessman et al. (unpublished). From Vary, L.B., Gillen, D.L., Randrianjanahary, M., Lowry, P.P., Sakai, A.K., and Weller, S.G. 2011. Dioecy, monoecy, and their ecological correlates in the littoral forest of Madagascar. *Biotropica*. **43**: 582–590. doi: [10.1111/j.1744-7429.2010.00742.x](https://doi.org/10.1111/j.1744-7429.2010.00742.x).
- Schmidt, N.M., Baittinger, C., Kollmann, J., and Forchhammer, M.C. 2010. Consistent dendochronological response of the dioecious *Salix arctica* to variation in local snow precipitation across gender and vegetation types. *Arct. Alp. Res.* **42**: 471–475. doi: [10.1657/1938-4246-42.4.471](https://doi.org/10.1657/1938-4246-42.4.471).
- Schmidt, N.M., Mosbacher, J.B., Nielsen, P.S., Rasmussen, C., Toke, T., Høye, T.T., and Roslin, T. 2016. An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography*. **39**: 1250–1252. doi: [10.1111/ecog.02261](https://doi.org/10.1111/ecog.02261)
- Scofield, D.G., and Schultz, S.T. 2006. Mitosis, stature and evolution of plant mating systems: low- Φ and high- Φ plants. *Proc. Biol. Sci.* **273**: 275–282. doi: [10.1098/rspb.2005.3304](https://doi.org/10.1098/rspb.2005.3304). PMID: [16543169](https://pubmed.ncbi.nlm.nih.gov/16543169/).
- Stebbins, G.L. 1950. Variation and evolution in plants. Columbia University Press, New York.
- Stebbins, G.L. 1958. Longevity, habitat and release of genetic variability in higher plants. *Cold Spring Harb. Symp. Quant. Biol.* **23**: 365–378. doi: [10.1101/SQB.1958.023.01.035](https://doi.org/10.1101/SQB.1958.023.01.035). PMID: [13635568](https://pubmed.ncbi.nlm.nih.gov/13635568/).
- Steiner, K.E. 1988. Dioecism and its correlated in the Cape flora of South Africa. *Am. J. Bot.* **75**: 1742–1754. doi: [10.2307/2444689](https://doi.org/10.2307/2444689).
- Stelleman, P., and Meeuse, A.D.J. 1976. Anthecological relations between reputedly anemophilous flowers and syrphid flies. I. The possible role of syrphid flies as pollinators of *Plantago*. *Tijdschr. Entomol.* **119**: 15–31.
- Swales, D. 1979. Nectararies of certain Arctic and subarctic plants with notes on pollination. *Rhodora*. **81**: 363–407.
- Thomson, J.D., and Brunet, J. 1990. Hypotheses for the evolution of dioecy in seed plants. *Trends Ecol. Evol.* **5**: 11–16. PMID: [21232310](https://pubmed.ncbi.nlm.nih.gov/21232310/).
- Tikhmenev, E.A. 1984. Pollination and self-pollinating potential of entomophilic plants in Arctic and mountain tundras of the northeastern U.S.S.R. *Soviet J. Ecol.* **15**: 166–172.
- Vamosi, J.C., and Vamosi, S.M. 2004. The role of diversification in causing the correlates of dioecy. *Evolution*. **58**: 723–731. doi: [10.1111/j.0014-3820.2004.tb00405.x](https://doi.org/10.1111/j.0014-3820.2004.tb00405.x). PMID: [15154548](https://pubmed.ncbi.nlm.nih.gov/15154548/).
- Vamosi, J.C., Otto, S.P., and Barrett, S.C.H. 2003. Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *J. Evol. Biol.* **16**: 1006–1018. doi: [10.1046/j.1420-9101.2003.00559.x](https://doi.org/10.1046/j.1420-9101.2003.00559.x). PMID: [14635916](https://pubmed.ncbi.nlm.nih.gov/14635916/).
- Warming, E. 1886. Om bygningen og den formodede bestøvningsmaade af nogle grønlandske blomster. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger. Bianco Lunos Kgl. Hof-Bogtrykkeri (F. Dreyer). København.
- Whitehead, D.R. 1983. Wind pollination: some ecological and evolutionary perspectives. Pages 97–109 in L. Real, ed. *Pollination biology*. Academic Press, Orlando, Fla.
- Willis, J.C., and Burkill, I.H. 1903. Flowers and insects of Great Britain. Part II. *Ann. Bot.* **17**: 313–350. doi: [10.1093/oxfordjournals.aob.a088919](https://doi.org/10.1093/oxfordjournals.aob.a088919).
- Willmer, P. 2011. *Pollination and floral ecology*. Princeton University Press, Princeton, N.J.
- Yampolsky, E., and Yampolsky, H. 1922. Distribution of sex forms in the phanerogamic flora. *Bibliogr. Genet.* **3**: 1–62.
- Yeloff, D., Blokker, P., Boelent, P., and Rozema, J. 2008. Is pollen morphology of *Salix polaris* affected by enhanced UV-B irradiation? Results from a field experiment in high Arctic tundra. *Arct. Alp. Res.* **40**: 770–774. doi: [10.1657/1523-0430\(07-045\)\[YELOFF\]2.0.CO;2](https://doi.org/10.1657/1523-0430(07-045)[YELOFF]2.0.CO;2).
- Zar, J.H. 2009. *Biostatistical analysis*. 5th ed. Prentice Hall, Upper Saddle River, N.J.