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Expansion of Canopy-Forming Willows Over the Twentieth Century on Herschel Island, Yukon Territory, Canada

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Abstract Canopy-forming shrubs are reported to be increasing at sites around the circumpolar Arctic. Our results indicate expansion in canopy cover and height of willows on Herschel Island located at 70° north on the western Arctic coast of the Yukon Territory. We examined historic photographs, repeated vegetation surveys, and conducted monitoring of long-term plots and found evidence of increases of each of the dominant canopy-forming willow species (*Salix richardsonii*, *Salix glauca* and *Salix pulchra*), during the twentieth century. A simple model of patch initiation indicates that the majority of willow patches for each of these species became established between 1910 and 1960, with stem ages and maximum growth rates indicating that some patches could have established as late as the 1980s. Collectively, these results suggest that willow species are increasing in canopy cover and height on Herschel Island. We did not find evidence that expansion of willow patches is currently limited by herbivory, disease, or growing conditions.

Keywords Arctic · Tundra · Climate change · Willows (*Salix* spp.) · Shrub encroachment · Yukon

INTRODUCTION

Recent evidence indicates an expansion of canopy-forming shrubs at sites on the North Slope of Alaska (Sturm et al. 2001; Tape et al. 2006), on the coast of the Northwest Territories (Lantz et al. 2009), in Northern Quebec (B. Tremblay et al., pers. comm.) and in northern Russia (Forbes et al. 2010a). In Arctic Alaska, canopy cover of alder (*Alnus viridis* subsp. *crispa*) shrubs has increased by 14–20% on average within the last 40 years, with increases of up to 80% in some areas (Tape et al. 2006). In addition, studies of population structures of shrub and tree species indicate advancing of shrubs up slopes in alpine tundra ecosystems in subarctic Sweden (Hallinger et al. 2010) and sites Norway (Hofgaard et al. 2009). Local indigenous Nenets people in the western Russian Arctic report increasing willow shrubs (Forbes et al. 2010b) and similar observations of vegetation change by Inuit have been reported in Arctic Canada (Thorpe et al. 2002). Ecological disturbances such as fire and permafrost degradation (Lantz et al. 2009, 2010) or human disturbances (Johnstone and Kokelj 2008; Kemper and Macdonald 2009) are responsible for some observations of increasing shrub species; however, reports also show widespread changes in shrub cover in the absence of localized disturbances (Sturm et al. 2001; Tape et al. 2006).

Growing season temperatures are warming in Alaska and western Canada (Chapin et al. 2005; ACIA 2005), and on Herschel Island mean annual temperatures have increased over the last few decades (Burn and Zhang 2009). Willows (*Salix* spp.) are well adapted to invading ecosystems when conditions change. Pollen records indicate that willows were widespread in Arctic ecosystems during warmer periods after the last glacial maximum (Brubaker et al. 1983; Bigelow et al. 2003); therefore, we might project increases of these species with the current warming trend. However, temperatures on Herschel Island have not shown the same increase as annual temperatures (Myers-Smith 2011), and shrub growth is most sensitive to temperatures in the early growing season period of the year (Ainsworth et al. 2001).

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In addition to observations of changing shrub cover, modeling and experimental studies forecast future increases in shrub species in Arctic tundra. Ecological models project increases in graminoid and shrub functional groups (Euskirchen et al. 2009), and experiments have shown that graminoid and deciduous shrub species respond positively to warming and fertilization treatments (Chapin et al. 1995; Dormann and Woodin 2002; van Wijk et al. 2004; Hollister et al. 2005; Wahren et al. 2005; Walker et al. 2006). However, to extend our understanding of future shrub change, we need to look back as well as forward, and make use of historic datasets, photographs, and local knowledge of tundra ecosystems. Unconventional sources of ecological data could be able to fill in gaps in our understanding of how tundra ecosystems have responded to previous changes in climate.

In this study, we applied repeat photography, vegetation surveys, and annual growth ring analysis to quantify changes in canopy-forming shrub species on Herschel Island in the western Canadian Arctic. We tested the hypothesis that willow cover and canopy height have increased on Herschel Island. This site has a long human history, from Inuvialuit inhabitants, to a whaling settlement established in 1890, a mission established in 1897, police detachment in 1903, and the foundation of a Yukon Territorial Park in 1987 (Yukon Territorial Government, Heritage Branch 2001). The historic record over the past 100 years provides a unique source of data on vegetation changes on the island. The western Arctic coastlands were among the first parts of the Canadian Arctic to be documented by photographs, and these historic photographs can be used to study environmental and ecological change (Mackay and Burn 2011). Previous work at sites along the Yukon Coast has documented an increase of 1–5% cover for the graminoid species *Arctagrostis latifolia* on disturbed substrates between 1986 and 1999 (Kennedy et al. 2001). For willows, changes over an even longer period can be examined by using multiple lines of evidence. Our study addresses the primary goals of the International Polar Year "Back to the Future" project by identifying multi-decadal past changes in the structure and function of tundra ecosystems and establishing a baseline from which to assess future change.

MATERIALS AND METHODS

Study Site

Herschel Island (69.57N 138.91W) covers approximately 100 km^2 and reaches maximum height of 183 m above sea level. The soils are composed of glacial and marine deposits, underlain by ice-rich permafrost (Burn and Zhang 2009). Prominent geomorphic features include numerous retrogressive thaw slumps, most of which were activated by coastal erosion of ice-rich permafrost (Lantuit and Pollard 2008; Burn and Zhang 2009).

The flora of Herschel Island is lowland tundra composed of various vegetation types, which were described in the vegetation survey conducted during the establishment of Qikiqtaruk Territorial Park (Smith et al. 1989). The "Herschel" vegetation type consists primarily of tussocks of *Eriophorum vaginatum* L. with varying cover of the potentially canopy-forming willow species *Salix pulchra* Cham. The "Komakuk" vegetation type is made up of previously disturbed terrain where the ground cover is dominated by *Dryas integrifolia* Vahl., various forb species, such as *Lupinus arcticus* S. Wats., *Oxytropis* spp., *Pedicularis* spp., grasses, and mosses and the prostrate willow *Salix arctica* Pall. The canopy-forming willow *Salix glauca* L. is found on south-facing ridges. The "Orca" vegetation type is found on the alluvial floodplain near the Pauline Cove settlement (Fig. 1) and is dominated by the canopy-forming willow *Salix richardsonii* Hook., and various sedge and moss species. In this study, we visited sites in each of these three vegetation types, which were within walking distance of the Pauline Cove.

There are a variety of herbivore species on Herschel Island including musk oxen (*Ovibos moschatus* Zimm.), caribou (*Rangifer tarandus* L.), collared lemmings (*Dicrostonyx groenlandicus* Tr.), brown lemmings (*Lemmus sibiricus* Kerr.), tundra voles (*Microtus oeconomus* Pall.), and rock ptarmigan (*Lagopus muta* Montin). All these species can feed on willows, particularly if their preferred forage species are in low abundance or not available.

Repeat Photographs

We used repeat photography to quantify visual changes in canopy cover of shrubs. From the over 100 photographs that we located, 55 of which contained views of the tundra vegetation, we were able to locate and retake five photographs showing change in cover of canopy-forming willow species. The photographs included 11 historic photographs from 1898 to 1920 taken during the whalers occupation of Herschel Island, 22 from 1953 to 1956 taken by William McFarland and Jim Hickling when the RCMP were stationed on Herschel Island, and 22 from 1978 to 1987 taken during vegetation, soils and cultural surveys conducted prior to the establishment of the Territorial Park. We identified the locations of these sites and retook the photographs at the same angles using landscape features to compare between images. We visually identified willow patches on the photographs by outlining the canopy-forming willow cover. Exact photo retakes could not be achieved because landmarks had moved over time.

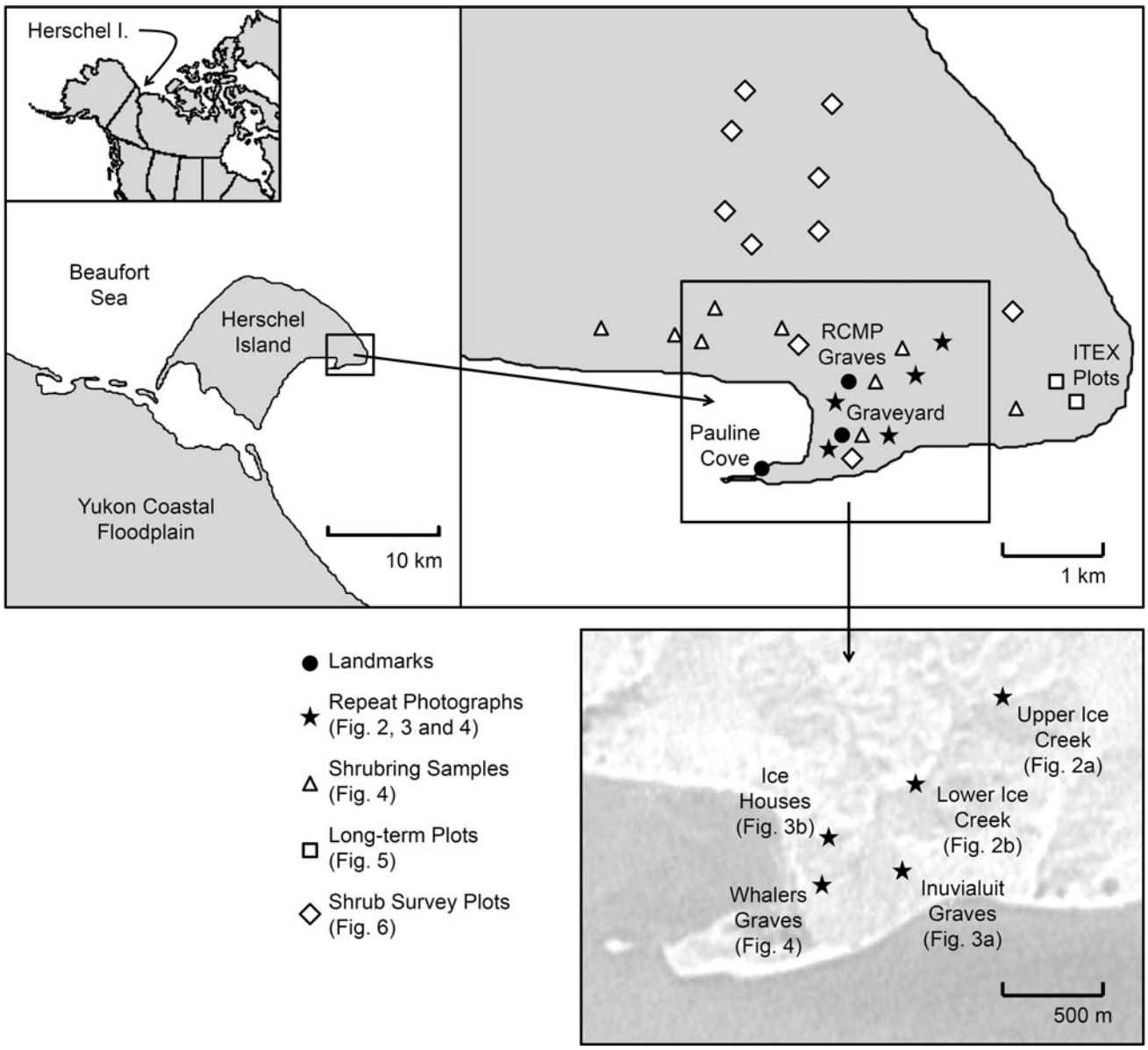

Fig. 1 The study site, Herschel Island, on the Arctic coast of the Yukon Territory

Permafrost-underlain soils have slumped, snow melt has eroded the creek banks, or graves have fallen down, been re-erected or rebuilt.

ITEX Long-Term Plots

The International Tundra Experiment (ITEX) is a scientific network of warming experiments focusing on the impact of climate change on plant species composition in tundra vegetation (Walker et al. 2006). To track changes in vegetation composition, long-term monitoring plots were established 10 years ago using the ITEX protocols (Molau and Mølgaard 1996). In 1999, twelve 1-m^2 plots were established in two sets of six plots in two areas representing the "Herschel" and "Komakuk" vegetation types near Collison Head, Herschel Island. In 1999, 2004, and 2009, plant cover and height in the plots was surveyed using a grid of 100-point intercepts within a fixed frame (for detailed methods see Molau and Mølgaard 1996). We used these data to compare changes in canopy height and cover of *S. pulchra*. In 1999 and 2004, height was recorded for only the tallest species growing at each of the 100 points in the sampling grid in each plot. In 2009, we additionally recorded the maximum height for *S. pulchra* when it was growing below the tundra canopy at each point in the sampling grid.

Vegetation Surveys

We conducted vegetation surveys to quantify the canopy height of the three dominant canopy-forming willow species. On April 20, 2008, we measured a transect of willow canopy height and snow depth on the "Orca" alluvial fan near Pauline Cove (Fig. 1). At 28 locations, located 20 m apart, we measured the canopy height of the *S. richardsonii* shrubs and conducted a visual estimate of the percent cover of willow canopy in circular plots of one and three m radii around each transect point. On 13–15 August 2009, we conducted surveys of willow canopy height for *S. pulchra* (50 m × 50 m plot, sample points every 10 m for a total of 36 points), *S. richardsonii* and *S. glauca* (90 m transects, sample points every 10 m for a total of 10 points, Fig. 1). At each of these survey points, we also measured the stem increment length of the current year's new growth on five arbitrarily chosen branchlets on stems growing within a 1 m radius of each sample point.

To compare previously collected data to the current willow extent on Herschel Island, we repeated vegetation surveys and measured canopy height in areas visited during the establishment of the Territorial Park. In 1985, 125 plots were sampled for vegetation classification across Herschel Island. These plots were circular and approximately 20 m in diameter (Smith et al. 1989). In 2008, we resurveyed the two vegetation classes with canopy-forming willows (the "Herschel" and "Orca" vegetation types) within walking distance of Pauline Cove. We surveyed 11 plots in the same general areas as 13 plots from the 1985 survey (Fig. 1). We made a visual estimate of the percent cover of each willow species following the protocol used in 1985 (Smith et al. 1989); however in 2008, we had two observers walk the plot area and make independent estimates to account for potential observer bias.

Annual Growth Rings

We conducted annual growth ring analysis to age willow stems of each of the dominant canopy-forming willow species. In 2008 and 2009, we sampled the largest stem from six individual shrubs located 10 or more meters apart at each of the nine plots (Fig. 1). We recorded the species, sex, width, height, and diameter of the largest stem for a total of 14 individuals of *S. richardsonii*, 9 individuals of *S. glauca*, and 13 individuals of *S. pulchra* (Table 1). To prepare samples for counting rings, we made thin sections of the willow stems, mounted the sections on glass slides, and took digital images. We counted and measured annual growth rings along four radii at 0°, 90°, 180°, and 270°, unless the placement of radii had to be moved or omitted due to growth deformities or rotten wood. Rings were counted and measured at a resolution of 0.0001 mm using digital tree-ring analysis software (WinDendro, QC, Canada). Stems and radii were visually cross dated to determine final stem age estimates. Partial rings were observed in ~60% of willows samples when cross dating the four measured radii. Missing rings were identified in five out of the 14 *S. richardsonii* and one of the 13 *S. pulchra* individuals sampled. The partial and missing rings were accounted for in the visual cross-dating of the ring counts.

Willow Patch Establishment

Canopy-forming willows form discrete patches in most of the habitats on Herschel Island. We were able to follow shallow root systems between stems, and therefore assume that each of the patches surveyed represented one establishment event. We measured the width and height of each of the individual patches surveyed, and were able to estimate the annual stem growth increment for each individual (see above). We calculated the maximum patch radius (R_{max}) by dividing the maximum patch width by two. We also sampled the largest stem of each of these individuals for annual growth ring analysis, and were able to estimate the patch age (see above). Using these data (Table 1; Supplementary Fig. 1), we created two simple models to estimate establishment dates for the willow patches surveyed in this study (Eqs. 1 and 2). The models assume that growth is radial and constant over the life of the individual—although this is a simplification of the growth of these species, we do not have data to parameterize a more complex growth model with multiple age classes or variable growth.

Table 1 Parameters for the shrub patch growth model: measured mean growth in 2009 for each species, estimated vertical growth per year and projected lateral growth, and shrub patch growth model projections

Species	Growth ring sample size	Mean height (cm)	Mean age (years)	Mean growth (mm)	Annual growth sample size	Estimated vertical growth (mm)	Estimated lateral growth (mm)
S. richardsonii	14	34 ± 4	25 ± 16	25 ± 3	10	14	21
S. glauca	9	43 ± 3	27 ± 12	25 ± 5	10	16	18
S. pulchra	13	32 ± 7	31 ± 9	13 ± 1	36	11	7

Values indicate the mean ± SE for measured values

PA_{mean} = Patch age estimate based on the mean measured annual stem elongation (years before 2008)

$$PA_{mean} = \frac{R_{max}}{\sqrt{\left(\frac{H_{max}}{S_{age}}\right)^2 + G_{mean}^2}} \quad (1)$$

PA_{min} = Patch age estimate based on the maximum measured annual stem elongation (years before 2008)

$$PA_{min} = \frac{R_{max}}{\sqrt{\left(\frac{H_{max}}{S_{age}}\right)^2 + G_{max}^2}} \quad (2)$$

where G_{mean} is the mean measured annual growth (cm/year); G_{max} the maximum measured annual growth (cm/year); R_{max} the maximum patch radius (cm); S_{age} the age of the largest stem (years); and H_{max} is the maximum patch height (cm).

The models make two different estimates: an older patch age estimate (PA_{mean}, Eq. 1) using the mean measured annual growth (G_{mean}), and the minimum patch age (PA_{min}, Eq. 2) using the maximum measured annual growth (G_{max}). The models estimate the patch age by dividing the maximum patch radius (R_{max}) by the estimated annual lateral growth. We used the Pythagorean Theorem to estimate annual lateral growth from an estimate of the vertical annual growth based on the age of the largest stem in the patch (S_{age}) and the measured maximum patch height (H_{max}) and the measured stem elongation (G_{mean} or G_{max}). Since we collected measurements of the maximum patch diameter only, we feel that using the measured minimum annual growth rate, we would overestimate the patch age, so we have not included this permutation of the model.

Statistical Analysis

Statistical analyses were conducted with the software R (version 2.10.1, R Development Core Team, Vienna). We used analysis of variance (ANOVA) and Tukey's tests to assess whether cover (point-frame hits) and height of *S. pulchra* had increased over time. We tested for differences between the variables patch width, canopy height, mean annual growth ring width, and stem age between species using multivariate analysis of variance (MANOVA) and Pillai's trace statistic to determine significance of the MANOVA as each of these variables were collected from the same individuals. We then used ANOVA on each of the significant variables and Tukey's tests to make pairwise comparisons to test for differences between species. To compare annual stem elongation between species, we used ANOVA and Tukey's tests as these data were collected from different individuals than in the previous comparison. The variables—shrub width, canopy height and patch size—were log transformed to meet the assumptions of normality and homoscedasticity.

RESULTS

Repeat Photographs

Repeat photographs showed expansion of individual willow patches in the shrubby habitats dominated by the species *S. richardsonii* at sites on the alluvial peninsula at Pauline Cove (Figs. 2, 3). Patches have increased in size and height (Figs. 2, 3) and cover has transitioned from discrete patches to nearly continuous cover (Fig. 4). Establishment of new patches is also suggested in some of these photograph comparisons (Fig. 3b).

Willow Species Growth Characteristics

Canopy cover and height of current patches of *S. richardsonii* were larger than *S. pulchra* patches in the individuals sampled for growth ring analysis (ANOVA, $F_{2,33} = 4.95$, $p = 0.01$, $n_{richardsonii} = 14$, $n_{pulchra} = 13$; Fig. 5a, b). During this sampling, we encountered some taller-statured *S. pulchra* individuals including one individual growing 76 cm tall, and as a result there was no significant difference in canopy height in the comparison of that data (Fig. 5a). However, in general *S. pulchra* plants were shorter in stature than the other willow species, with a mean canopy height of 13.3 ± 0.7 cm measured in the vegetation survey ($n = 36$) and 7.3 ± 0.9 cm in the 2009 monitoring of the ITEX plots ($n = 6$, Fig. 6). *S. pulchra* had shorter annual stem elongation than the other two species (ANOVA, $F_{2,53} = 13.3$, $p < 0.01$, $n_{richardsonii} = 10$, $n_{glauca} = 10$, $n_{pulchra} = 36$; Fig. 5c). *S. pulchra* ring widths were narrower than either *S. richardsonii* or *S. glauca* annual growth rings (ANOVA, $F_{2,33} = 6.10$, $p < 0.01$, $n_{richardsonii} = 14$, $n_{glauca} = 9$, $n_{pulchra} = 13$; Fig. 5d). Mean stem age for the largest stems of willows sampled in the different vegetation zones was 20–30 years old ($n_{richardsonii} = 14$, $n_{glauca} = 9$, $n_{pulchra} = 13$; Fig. 5e).

Repeat Vegetation Surveys

Point-intercept sampling indicated increases in canopy height for the canopy-forming willow *S. pulchra* in the six long-term plots located in the "Herschel" vegetation type (ANOVA, $F_{2,12} = 6.21$, $p = 0.01$, $n = 6$; Fig. 6). Even when using the plot mean height for canopy and below canopy measurements of *S. pulchra* in 2009, we found that this species was significantly taller than the canopy-only height measurements taken in 1999 (ANOVA,

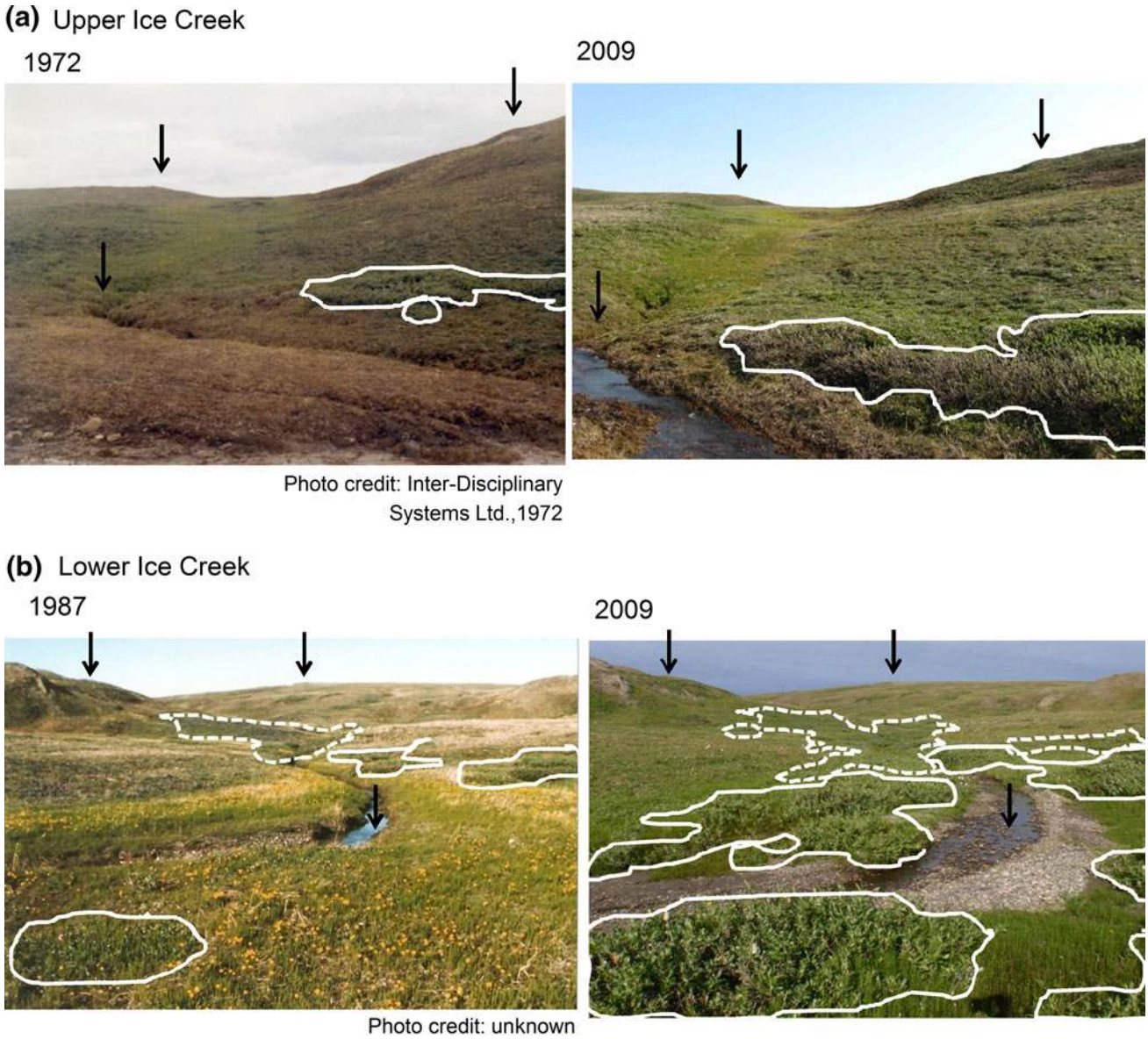

Fig. 2 Repeat photographs of *S. richardsonii* patch expansion and new recruitment (photo credit: Inter-Disciplinary Systems Ltd 1972). *White lines* indicate the boundaries of the patches, *dotted white lines* indicate areas of variable willow cover where patches cannot be determined from the photographs, and *black arrows* indicate features present between photographs. Owing to the low resolution of the early *black* and *white photographs*, we cannot conclusively determine if willow patches are absent

$F_{2,15} = 4.44$, $p = 0.03$, $n = 6$; repeat measures ANOVA, 1999–2004: $T_{6,18} = 1.92$, $p = 0.08$, 2004–2008: $T_{6,18} = 3.67$, $p < 0.01$; Fig. 6a).

We found no significant difference in abundance of *S. pulchra* over the 10 years of monitoring of the six ITEX plots located in the "Herschel" vegetation type (ANOVA, $F_{2,15} = 1.43$, $p = 0.27$, $n = 6$; Fig. 6b); however, abundance data were variable. Higher abundance of *S. pulchra* was recorded in four of the six plots in 2009 when compared with the first two sampling years (Fig. 6b). In contrast to the directional change in *S. pulchra*, we observed no significant change in abundance or height for the prostrate willow species present in the long-term monitoring plots (Fig. 6b).

Repeat vegetation surveys indicated an increase in the cover of *S. pulchra* between the mid 1980s and 2008 (ANOVA, $F_{1,15} = 12.17$, $p < 0.01$; Fig. 7e); however, the difference in cover between sample years was not significant for *S. richardsonii* (ANOVA, $F_{1,4} = 0.04$, $p = 0.84$; Fig. 7a).

Willow Patch Establishment

Modeled shrub patch expansion, based on measurements of annual stem elongation for each of the dominant

Fig. 3 Repeat photographs of *S. richardsonii* patch expansion and new recruitment continued (see Fig. 2)

canopy-forming willow species (Table 1), indicated that shrub patches were initiated between 1910 and 1960, and that current large diameter stems began growing in the late 1970s and early 1980s (Fig. 7). If maximum growth rates are used in the model, then shrub patches are estimated to have been established as late as 1974–1981, approximately the same time as the stem establishment dates (Table 2).

DISCUSSION

Multiple lines of evidence indicate increases in canopy cover and height of willows on Herschel Island (Fig. 7). Repeat photographs show an increase in the canopy cover of the willow *S. richardsonii*. The repeat vegetation surveys suggest greater cover of both *S. richardsonii* and *S. pulchra*. The long-term vegetation monitoring plots show increases in cover and height of *S. pulchra*. *S. glauca* stems growing near the police grave sites first established in shrub-free tundra in the 1950s. Annual growth ring analysis of these stems show them to be 25 ± 1 years old (mean ± SE), suggesting that these approximately 80-cm-tall willows have grown established and grown to this height over the last three decades. When repeating past vegetation surveys using different observers, there could be significant measurement error; however, the use of multiple

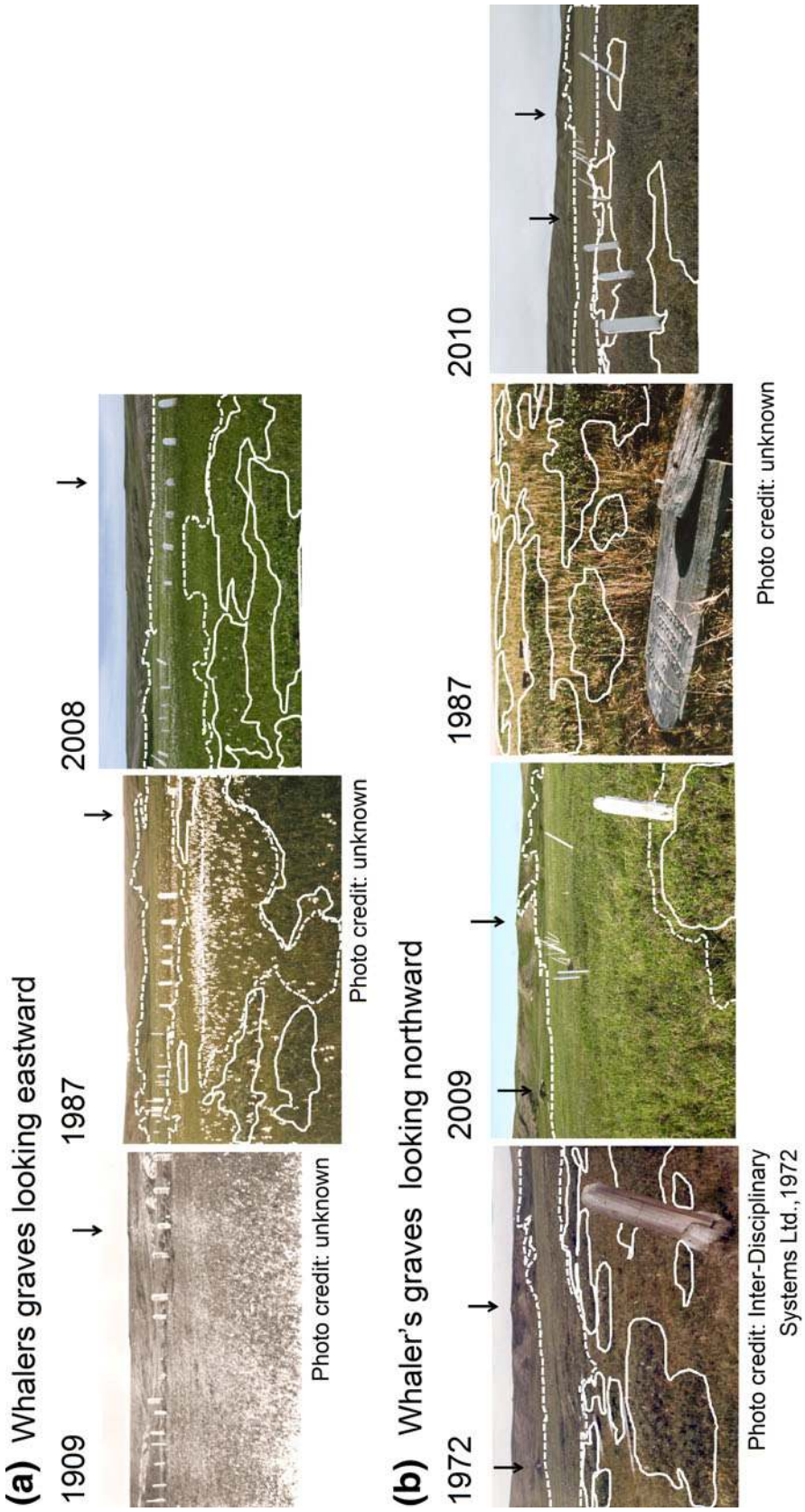

Fig. 4 Photographs illustrating filling in of *S. richardsonii* patches in the graveyard area of the alluvial fan near Pauline Cove. *White lines* indicate the boundaries of the patches, *dotted white lines* indicate areas of variable willow cover where patches cannot be determined from the photographs, and *black arrows* indicate features present between photographs. The photographs of the whaler's graves looking northward (**b**) show photographs taken close to the locations of the grave markers and show a change from discrete patches to more continuous cover of *S. richardsonii* in this area. Owing to the low resolution of the early *black* and *white photographs*, we cannot conclusively determine if willow patches are absent

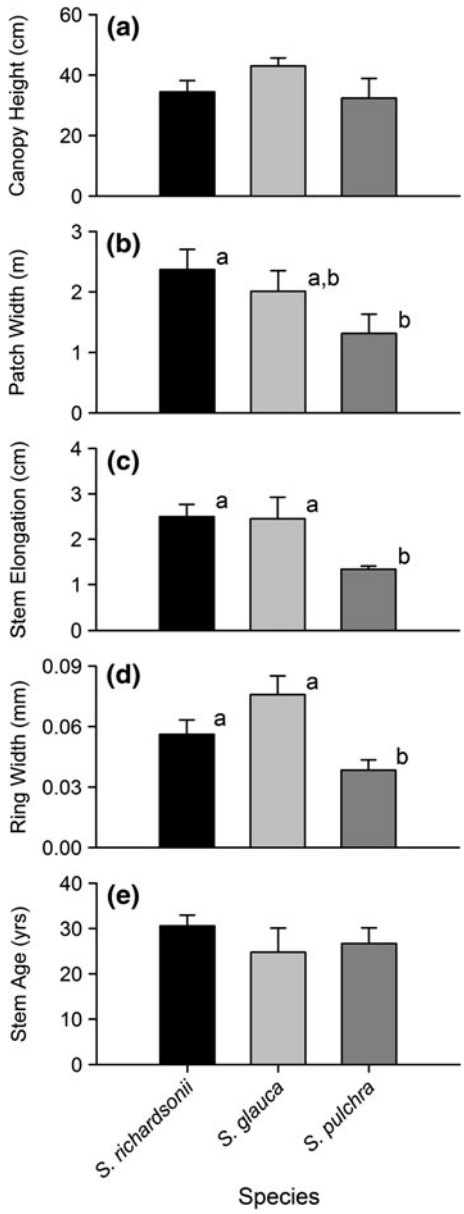

Fig. 5 Mean **a** canopy height, **b** patch width, **c** annual stem elongation, **d** ring width, and **e** stem age for the three dominant canopy-forming willow species sampled in 2008. *Error bars* indicate SE and *letters* indicate significant differences between species (MANOVA, Pillai's trace = 0.46, $F_{2,33} = 2.31$, $p = 0.03$)

lines of evidence including repeat photographs, vegetation surveys, and annual growth ring analysis increases the confidence that we have in these findings.

Growth of Shrubs

Both shrub and graminoid species have been found to increase in cover and height in warming experiments (Chapin et al. 1995; Dormann and Woodin 2002; van Wijk et al. 2004; Hollister et al. 2005; Wahren et al. 2005; Walker et al. 2006). Herbaceous species have been shown to have stronger and more consistent vegetative growth responses than woody species (Arft et al. 1999). However, these two functional groups should respond in different ways to improved growing conditions. In years with harsher growing conditions, the aboveground biomass of herbaceous species will reach lower canopy heights and cover than in warm years with long growing seasons. Regardless of growing conditions, stems of woody species will elongate incrementally unless reduced by herbivory, disease, or dieback from exposure to extreme conditions, though the annual growth increments will be larger in warmer growing seasons.

Recent studies have used annual growth ring analysis of shrub species growing in tundra ecosystems to link increased secondary growth of shrub species to growing season temperatures (Forbes et al. 2010a; Hallinger et al. 2010; Blok et al. 2011). We found that on Herschel Island, although willow growth is sensitive to temperature change, not all individuals have strong positive responses to warm growing season conditions (Myers-Smith 2011). In the absence of significant observed mortality, herbivory, or dieback, it is not surprising to observe increases in cover of these species. Recent synthesis of global Arctic and alpine plot monitoring data show that changes in cover and height of certain tundra functional groups and species are not correlated with warming growing season temperatures for many sites (S. Elmendorf, pers. comm.). Therefore, the observed changes in willow species do not relate directly to the observed increases in mean annual temperatures on Herschel Island (Burn and Zhang 2009) or to potentially improved growing season conditions in the western Canadian Arctic.

Willow species differ in growth characteristics between sexes. Willows are dioecious, having both male and female plants, and tundra willows of the Yukon Territory have been shown to have a uniformly female biased sex ratio of approximately 2:1 (unpubl. results). Size sexual dimorphism has been observed in some willow species and females have been found to allocate more resources to reproduction than males and in addition, differential resource use has sometimes been observed (Elmqvist et al. 1988; Dudley 2006). Owing to the biased sex ratio observed in these species, the majority of willows surveyed in this study on Herschel Island were female (*S. pulchra*: female = 3, male = 0, unidentified = 11, *S. richardsonii*: female = 8, male = 2, unidentified = 5, *S. glauca*: female = 9, male = 1, unidentified = 5). Our sampling was conducted in August; therefore, we missed the flowering time for the early-flowering *S. pulchra* and *S. richardsonii* and as a result identified fewer males of these species. We found no evidence that patch size, ring width, or age differed between sexes for these same species in the Kluane Region (Myers-Smith 2011). On Herschel Island, though the majority of the individuals sampled were female

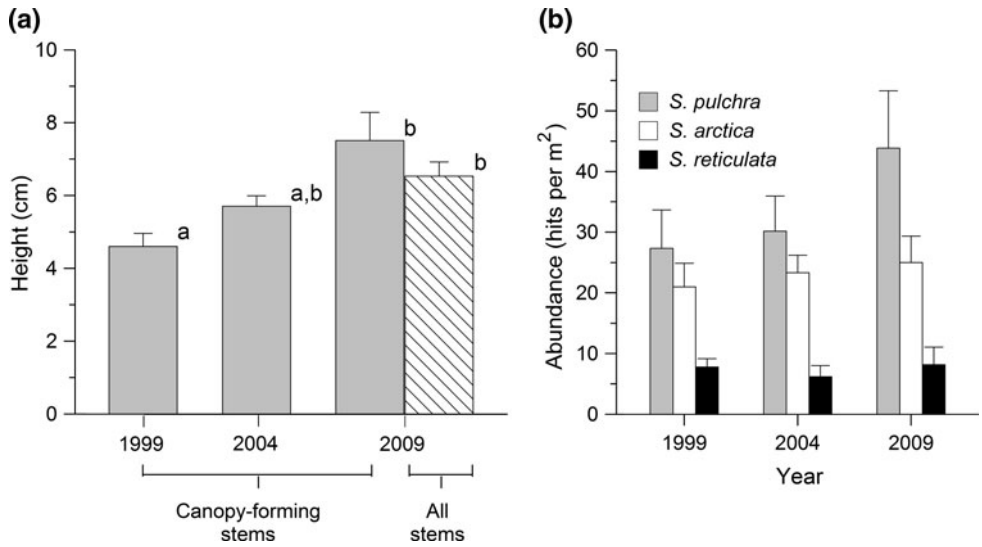

Fig. 6 Mean abundance (**a**) and canopy height (**b**) of the potentially canopy-forming willow species *S. pulchra* and the mean abundance of the prostrate dwarf willow species *S. arctica* and *S. reticulata* recorded in ITEX control plots from 1999 to 2009. Abundance was measured as the sum of all live leaf and stem interceptions recorded across 100 grid points within each of the six 100 cm × 100 cm plots. In **b**, *gray bars* indicate the mean height of canopy-forming *S. pulchra* individuals at each grid point. The *hatched bar* is the mean canopy height for all *S. pulchra* stems at each grid point in 2009. *Error bars* indicate SE, and *letters* indicate significant differences between monitoring years

or unidentified, we also observed no significant difference in growth characteristics between sexes. Sex ratio and the spatial pattern of female and male plants on the landscape could influence fertilization rates and seed set, but we do not believe that this is a significant factor explaining variation in growth rates between individuals.

Herbivory and Mortality

Herbivory controls new recruitment of shrub species and could limit or reduce shrub patch expansion on the landscape. Shrub encroachment in tundra ecosystems has been shown to be reduced or inhibited by herbivores in exclosure experiments (Post and Pedersen 2008; Olofsson et al. 2009). And herbivory by sheep and reindeer is thought to be the primary factor determining the height of the shrubby treeline ecotone at sites in northern Scandinavia (Hofgaard et al. 2010; Speed et al. 2010, 2011).

We observed little die back, mortality or herbivory in the 2008 and 2009 willow surveys. In three of the 46 willow individuals sampled for aging (two *S. richardsonii* and one *S. glauca*), we observed some evidence of scarring in the stem cross sections initiated between 1999 and 2003. Scarring could indicate past herbivory, as was observed in sections of willows from a site experiencing periodic lemming herbivory on the Kent Peninsula, Northwest Territories, Canada (Predavec and Danell 2001). The low occurrence of scarring does not indicate high levels of stem herbivory in recent decades on Herschel Island. We observed caribou and muskox feces and shed qiviuq (muskox wool) in and around the ITEX long-term monitoring plots; however, we did not observe any evidence of willow herbivory while surveying the plots in 2009.

There is no evidence of recent declines in herbivore populations on Herschel Island; instead, large herbivore presence has increased in the past 50 years (D. Reid, pers. comm.). Caribou populations were likely decimated by the whalers at the turn of the twentieth century, and their activity on Herschel has increased since the 1970s. Musk Ox were reintroduced to the Arctic National Wildlife Refuge during 1969–1970 and spread to Herschel Island during the following decades. Taken together, these data suggest that willow herbivory has historically been low on Herschel Island and might not be a significant factor determining rates of expansion of willow patches over the past century.

The Role of Disturbance

Disturbance has been identified as a key factor determining recruitment of woody species in tundra systems (Munier et al. 2010; Lantz et al. 2010). Furthermore. both fire (Lantz et al. 2010) and permafrost degradation (Lantz et al. 2009) have been positively associated with recruitment and growth in alder (*Alnus viridis* subsp. *fruticosa*). When examining changes in shrub abundance in tundra ecosystems, disturbances rather than climate warming could be the most important factor determining recruitment of new individuals. Furthermore, interactions among the disturbance regime, nutrient availability, herbivory, disease and

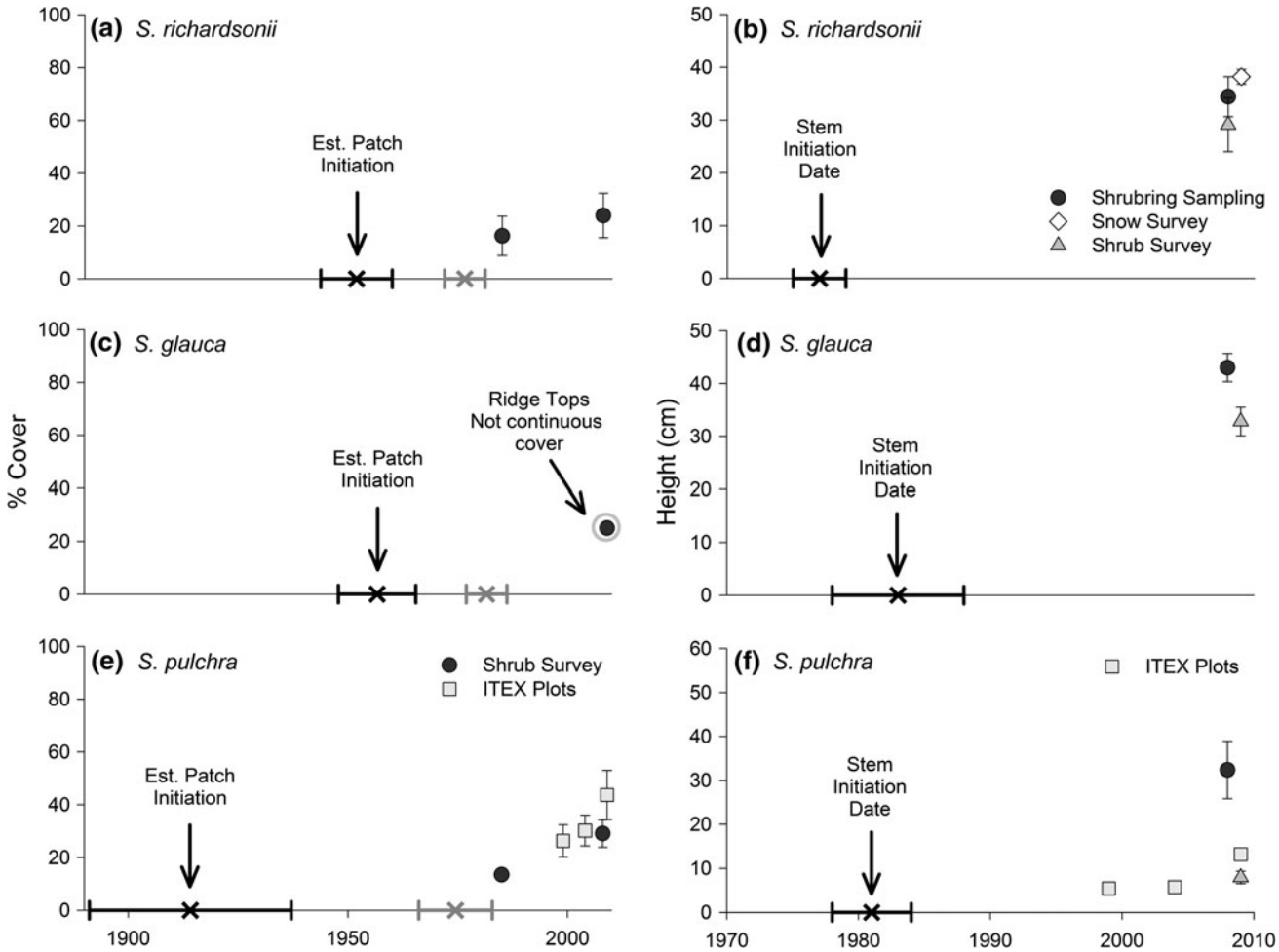

Fig. 7 Mean canopy cover and projected shrub initiation dates for percent cover of willow patches (**a**, **c,** and **e**) and mean canopy height and stem initiation dates (**b**, **d**, and **f**) for each of the three dominant canopy-forming willow species. *Black crosses* indicate the mean patch age estimated using the measured mean annual growth rate (PA_{mean}, Eq. 1), and *gray crosses* indicate the mean patch age estimated using the maximum measured annual growth (PA_{min}, Eq. 2). *Vertical* and *horizontal error bars* indicate SE

Table 2 Model estimates of patch and stem establishment dates

Species	Sample size	Mean age PA_{mean} Eq. 1	Minimum age PA_{min} Eq. 2	Stem age $\frac{H_{max}}{S_{age}}$
S. richardsonii	14	1951 ± 8	1975 ± 5	1976 ± 2
S. glauca	9	1956 ± 9	1981 ± 5	1982 ± 5
S. pulchra	13	1913 ± 23	1974 ± 8	1980 ± 3

Dates are mean estimates for all patches of each species ± SE

weather conditions might all influence the establishment and growth of woody tundra species.

A deeper active layer and more active permafrost degradation have been observed on Herschel Island over the last century (Lantuit and Pollard 2008; Burn and Zhang 2009). Greater disturbance of the surface terrain could provide microsites appropriate for establishment of new willow patches. Alder (*Alnus viridis* subsp. *fruticosa*) shrub encroachment has been previously observed in retrogressive thaw slumps in the Mackenzie Delta region of the Northwest Territories (Lantz et al. 2009). The previously observed increase in the graminoid species, *Arctagrostis latifolia* (R.Br.) Griseb, on disturbed terrain on Herschel Island was likely a result of vegetation succession (Kennedy et al. 2001). It could be that changes in the disturbance regime rather than growing season conditions are primarily responsible for the observed willow change on Herschel Island. The alluvial floodplain habitat, where *S. richardsonii* is dominant, experiences annual flooding during thaw, and the ridges where *S. glauca* is found show evidence of erosion. However, the "Herschel" vegetation type, the *Eriophorum* sedge tussock habitat where *S. pulchra* is found, is less disturbed. If *S. pulchra* is increasing in height and cover in this habitat, then this change is unlikely to have been induced by large-scale disturbance as is possible in the other habitats.

Recruitment of Willows

Clonal species can have extremely long lifespans and do not necessarily experience senescence over time (de Witte and Stöcklin 2010); therefore, willow patches, once established could continue to increase into the future. We assume that willow patches on Herschel Island have established from seed. We observed few dead stems, and little dieback or dead portions of willow patches indicating mature willow stands, as is common at sites farther south in the Yukon Territory. Adjacent to the coastline, dead *S. richardsonii* patches did occur, likely due to salt water inundation. In some higher elevation habitats, we observed dead tips of stems, potentially indicating winter dieback and exposure to cold temperatures and wind abrasion above the snowpack. However, the majority of canopy-forming willows growing on Herschel Island appear to be healthy and in good condition.

Our results suggest that the majority of the current patches of canopy-forming willow species found on Herschel Island today established between the 1920s and 1980s, and that these willow individuals have expanded incrementally over time. Because annual incremental growth of branches and stems were smaller for the species *S. pulchra*, this species is projected to have initiated earlier than the faster growing *S. richardsonii* and *S. glauca*. Our models do not take into account changes in growing conditions over time. If growing conditions have been more favorable in recent years, then we could be overestimating mean annual stem elongation in our model.

Our data do not definitively indicate when initial recruitment of these willow species occurred on Herschel Island. Reports of canopy-forming willows (likely *S. richardsonii*) on the alluvial floodplain adjacent to Pauline Cove exist from the 1970s (Hardy Associates Ltd. 1979), and photographs taken by Jim Hickling of the Royal Canadian Mounted Police show evidence of *S. pulchra* and *S. richardsonii* from two unknown locations on Herschel Island in the 1950s. This evidence of willow cover from over 30 years ago, suggests these canopy-forming shrubs species were prevalent before the middle of the twentieth century. However, the repeat photography and survey data that we present here indicate substantial increases in cover of all three species. In particular, *S. richardsonii* growing on the alluvial flood plain and *S. glauca* growing on the south-facing ridges around Pauline Cove appear to have increased in cover and stature in the last half century.

On the North Slope of Alaska, Tape et al. (2006) suggested that the initial recruitment resulting in the observed expansion of alder patches could have occurred coincident with the end of the Little Ice Age cool period in approximately 1850. This historic shift in climate could also be responsible for an expansion of willow cover on Herschel Island and the adjacent Arctic Coast of the Yukon. In addition to climate-driven shrub recruitment, disturbance can facilitate the establishment of new individuals. On Herschel Island, disturbance regime could interact with climate to create recruitment pulses, and patch expansion and increases in canopy height could proceed in the intervening years between these pulses.

Herschel Island is located near the northern extent of canopy-forming willow species (Argus et al. 1999). As individuals from the canopy-forming species *S. richardsonii*, *S. glauca*, and *S. pulchra* increase in size, they will likely increase in reproductive output. Increases in the production of viable seed could have implications for future recruitment at this site and the advance northward of these species.

CONCLUSION

In this study, we report evidence of increases in canopy cover and height of canopy-forming willows on Herschel Island in the Western Canadian Arctic. The long-term photographic, plot-based and growth ring data reported in this study provide multiple lines of evidence of shrub increase at this site. Continued monitoring of long-term vegetation plots, will improve our estimates of shrub change and rates of patch expansion. However, to better understand this changing tundra ecotone, the focus of future research should move beyond whether canopy-forming shrub patches are expanding clonally, to the identification of factors that are responsible for the recruitment of new individuals and the quantification of the impact of this canopy-cover change to the functioning of tundra ecosystems.

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