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Expansion of canopy-forming willows over the 20th 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 20th 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 (pers. comm. B. Tremblay, E. Lévesque and S. Boudreau) 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, growing season 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).

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 data sets, 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 amongst 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% to 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.

Material 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 that 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 1898–1920 taken during the whalers occupation of Herschel Island, 22 from 1953–56 taken by William McFarland and Jim Hickling when the RCMP were stationed on Herschel Island, and 22 from 1978–87 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. 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 Collinson 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 20 April 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 x 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 1m 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 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°, 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 treering analysis software (WinDendro, Québec, 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, Supplement 1), we created two simple models to estimate establishment dates for the willow patches surveyed in this study (Equations 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.

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

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

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

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

G_{mean} = mean measured annual growth (cm/year)

G_{max} = maximum measured annual growth (cm/year)

R_{max} = maximum patch radius (cm)

S_{age} = age of the largest stem (years)

H_{max} = 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 analysis of variance (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 and 3). Patches have increased in size and height (Figs. 2 and 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, $F_{2,33} = 4.95$, $p = 0.01$, $n_{richardsonii} = 14$, $n_{pulchra} = 13$; Figs. 5a and 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 to 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, $F_{2,15} = 4.44$, $p = 0.03$, 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 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, shrub patches are estimated to have been established as late as 1974–81, approximately the same time as the stem establishment dates.

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 past three decades. When repeating past vegetation surveys using different observers, there could be significant measurement error; however, the use of multiple lines of evidence including repeat photographs, vegetation surveys and annual growth ring analysis, increases the confidence 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 (pers. comm. S. Elmendorf). 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). Due 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 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 ageing (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 (pers. comm. D. Reid). Caribou populations were likely decimated by the whalers at the turn of the 20th century, and their activity on Herschel has increased since the 1970s. Musk Ox were reintroduced to the Arctic National Wildlife Refuge in 1969-70 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). And 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. And interactions among the disturbance regime, nutrient availability, herbivory, disease and 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 that 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, 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, 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 20th 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 northwards 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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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. Values indicate the mean ± SE for measured values.

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

Table 2. Model estimates of patch and stem establishment dates. Dates are mean estimates for all patches of each species ± SE.

Species	Sample Size	Mean Age PA_{mean} Eq. 1	Minimum Age PA_{min} Eq. 2	Stem Age $\frac{\mathbf{H}_{\mathbf{max}}}{\mathbf{S}_{\mathbf{age}}}$
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

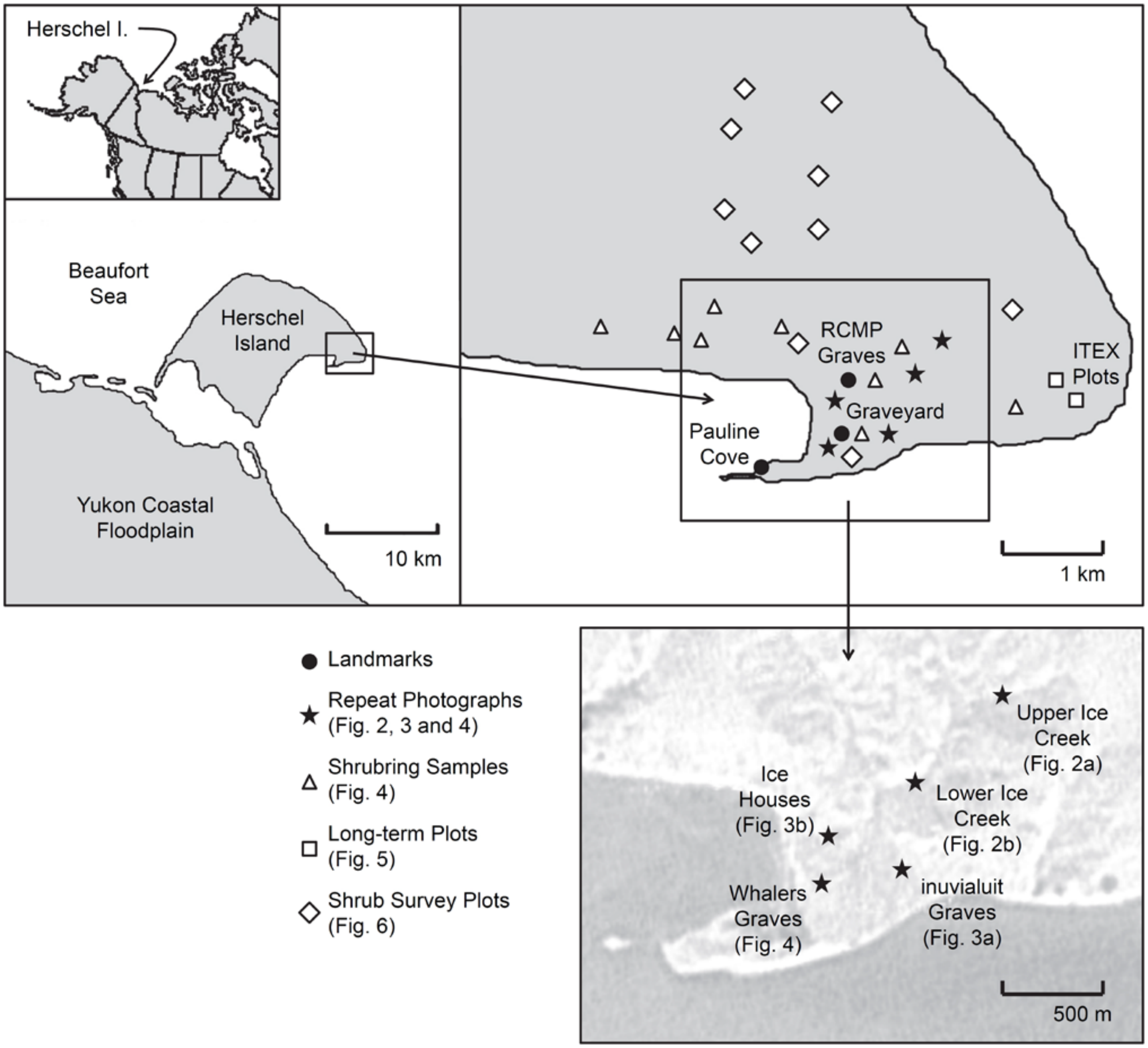


Fig. 1. The study site, Herschel Island, on the arctic coast of the Yukon Territory.

a) Upper Ice Creek

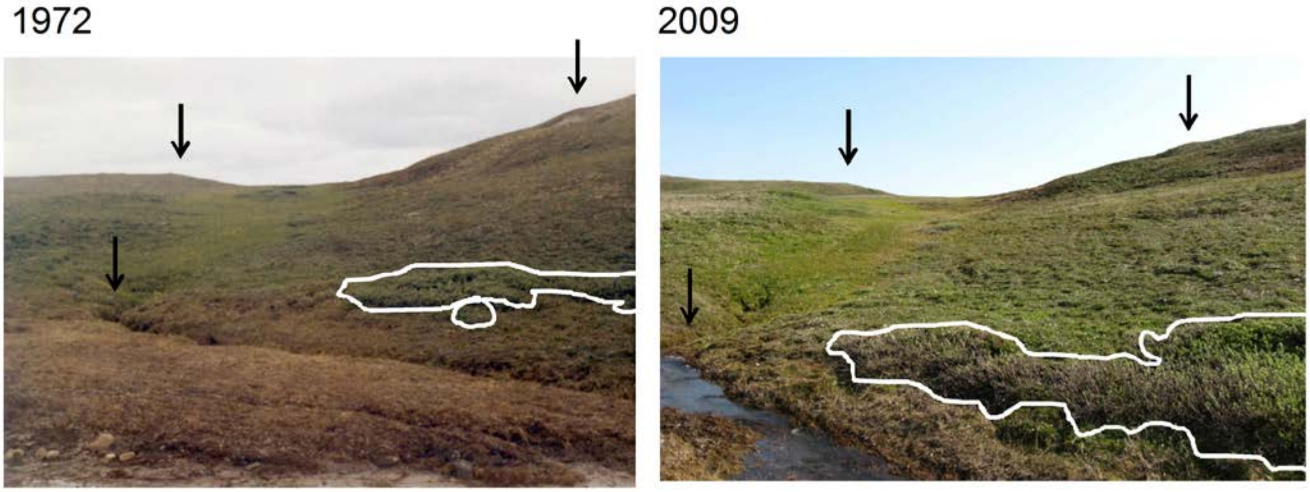


Photo credit: Inter-Disciplinary Systems Ltd.,1972

b) Lower Ice Creek

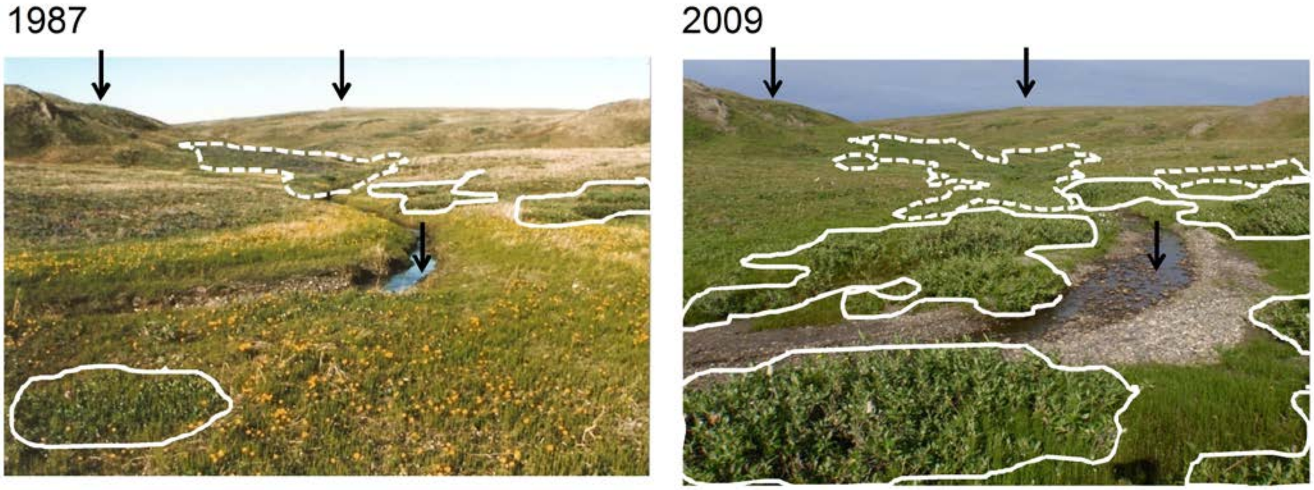


Photo credit: unknown

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. Due to the low resolution of the early black and white photographs, we cannot conclusively determine if willow patches are absent.

a) Graveyard

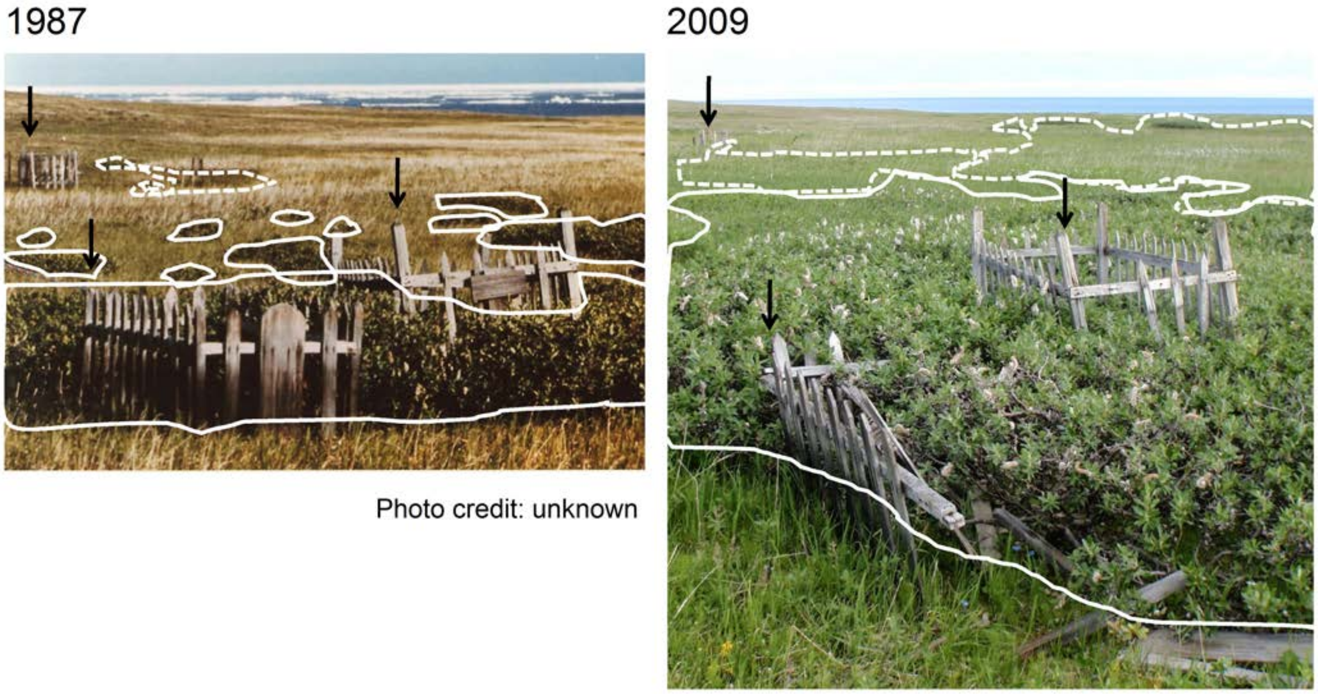


Photo credit: unknown

b) Ice Houses

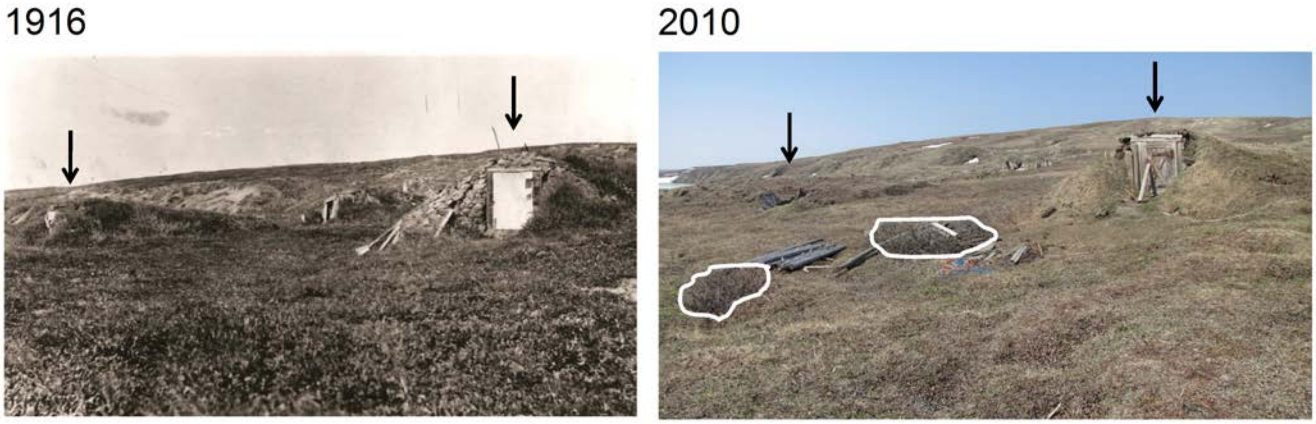


Photo credit: unknown

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

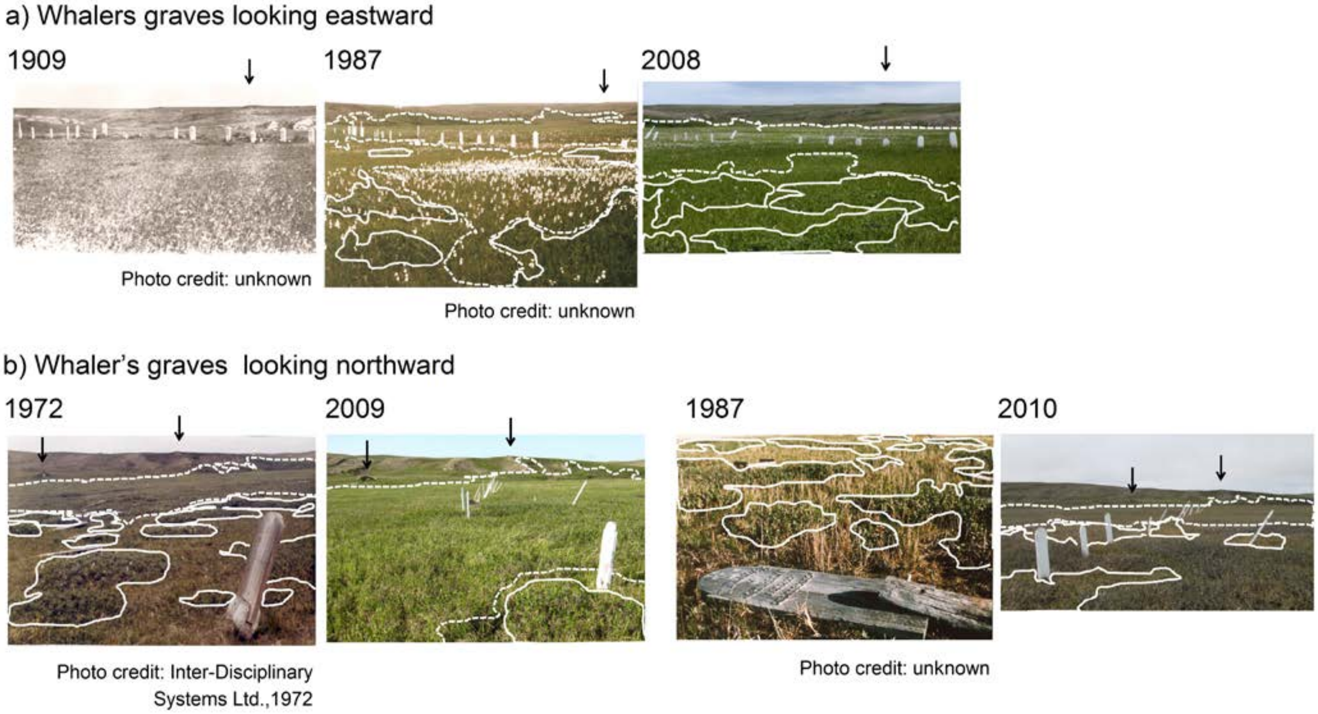

a) Whalers graves looking eastward

Photo credit: unknown

Photo credit: unknown

b) Whaler's graves looking northward

Photo credit: Inter-Disciplinary Systems Ltd.,1972

Photo credit: unknown

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. Due to the low resolution of the early black and white photographs, we cannot conclusively determine if willow patches are absent.

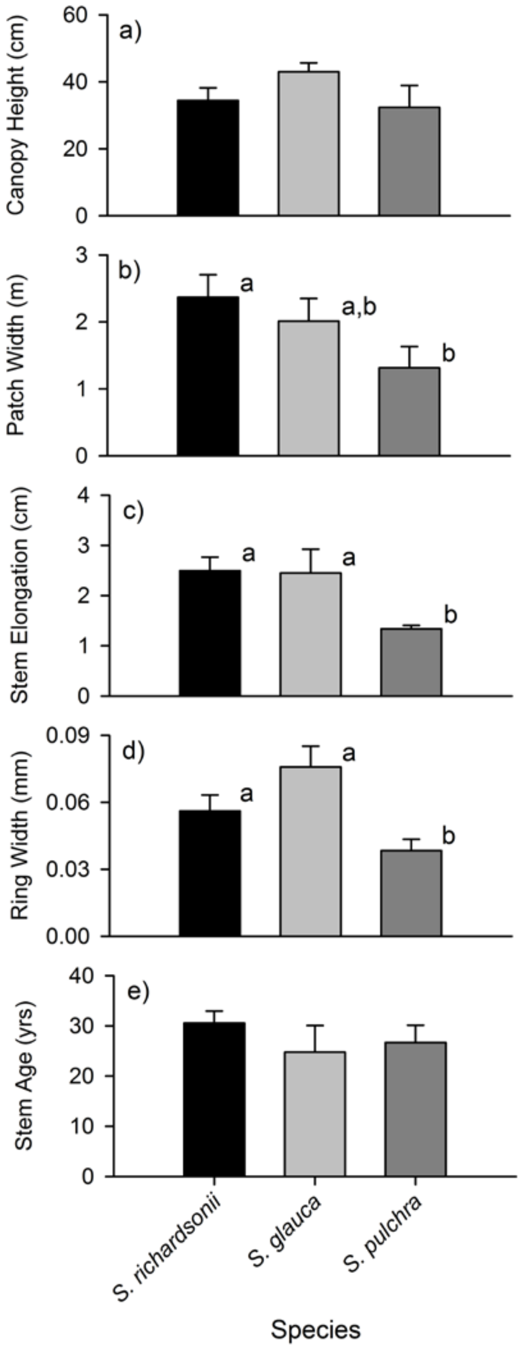


Fig. 5. Mean a) canopy height, b) patch width, c) annual stem elongation, d) ring width, and e) stem age for the three dominant canopy-forming willow species sampled in 2008. Error bars indicate SE and letters indicate significant differences between species (MANOVA, Pillai's trace = 0.46, $F_{2,33}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

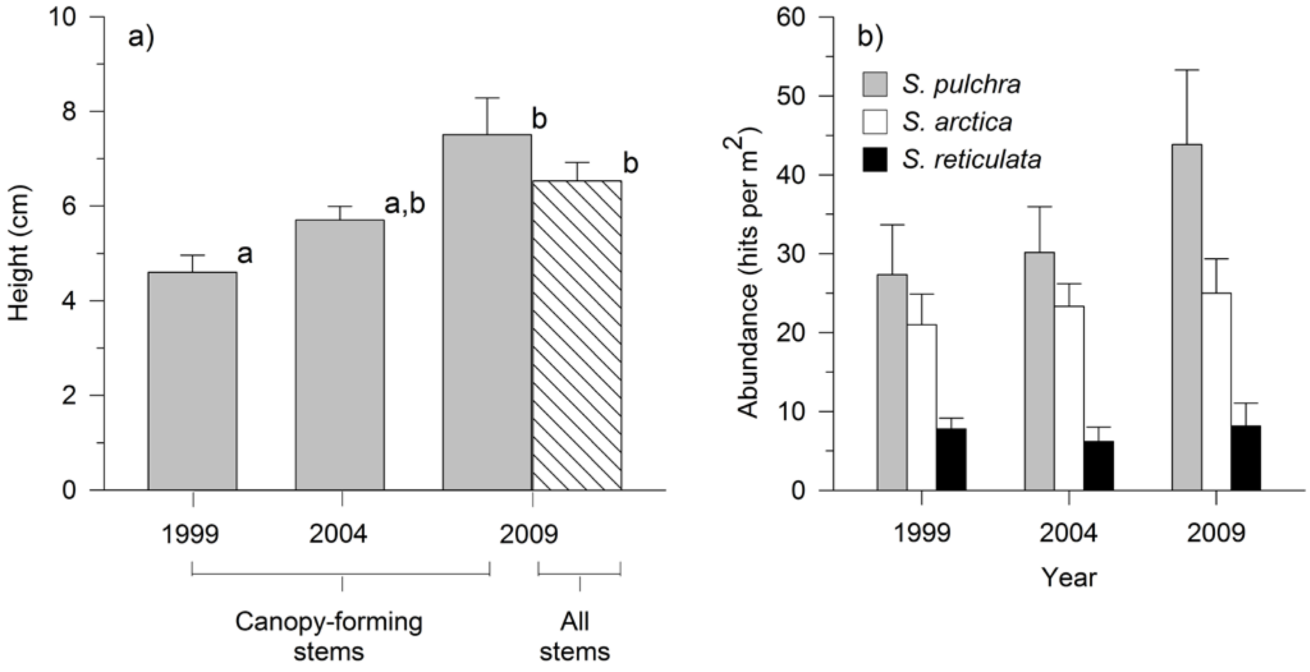


Fig. 6. Mean abundance (a), and canopy height (b) of the potentially canopy-forming willow species *S. pulchra* and the mean abundance of the prostrate dwarf willow species *S. arctica* and *S. reticulata* recorded in ITEX control plots from 1999 to 2009. Abundance was measured as the sum of all live leaf and stem interceptions recorded across 100 grid points within each of the six 100 cm x 100 cm plots. In panel b, grey 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.

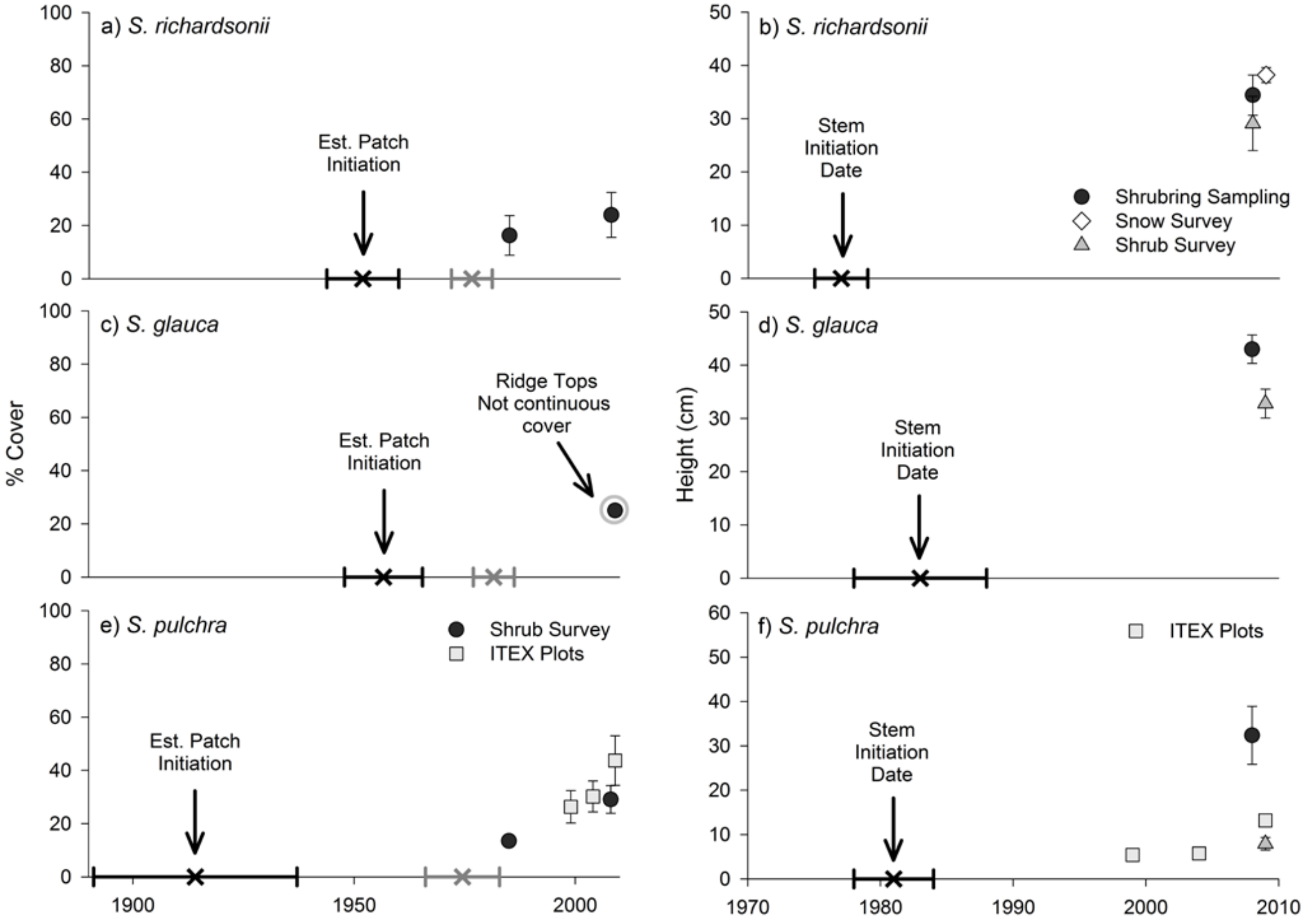
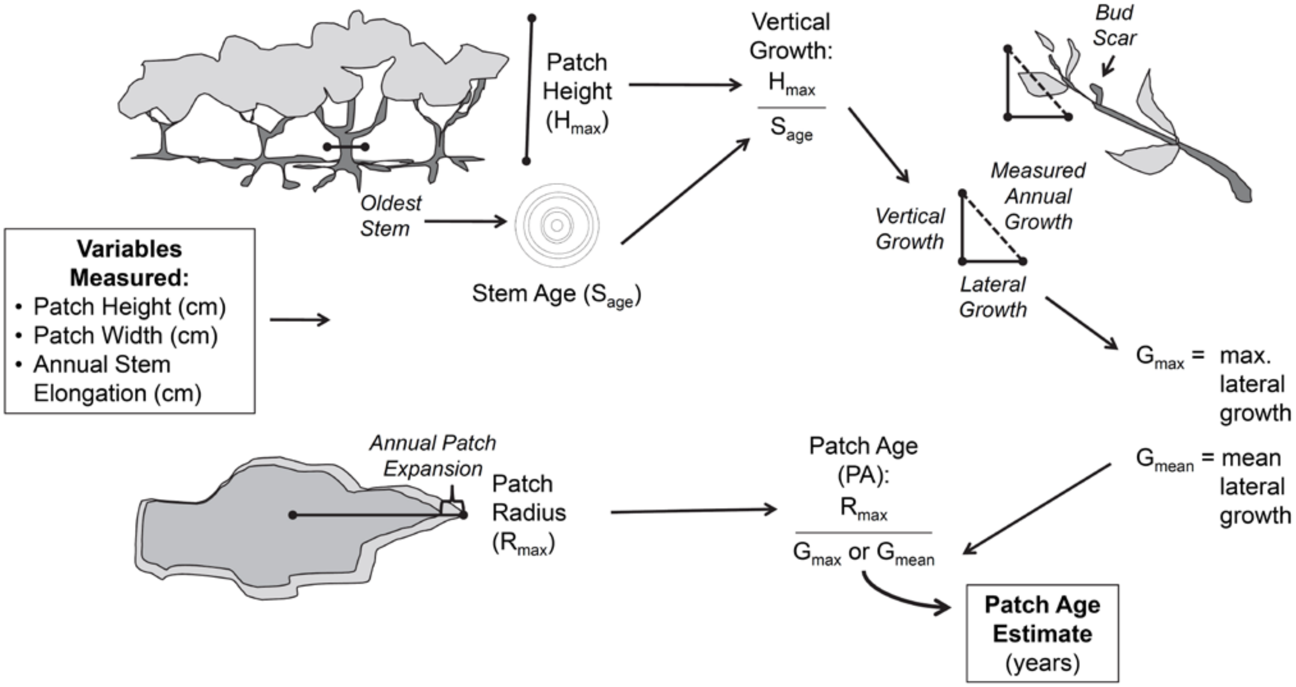


Fig. 7. Mean canopy cover and projected shrub initiation dates for percent cover of willow patches (a, c and e) and mean canopy height and stem initiation dates (b, d and f) for each of the three dominant canopy-forming willow species. Black crosses indicate the mean patch age estimated using the measured 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.

Supplement 1. Diagram of model parameters to calculate patch age.



Supplement 2. Coordinates for all plot locations on Herschel Island, using the UTM grid and decimal degrees (Lat/Lon hddd.ddddd°) and the datum NAD83.

Data Set	Name	Description	UTM Position	N	W	Ele.
ITEX Long-term plot	ITEXH1	12-AUG-09 11:11:27AM	7 W 583214 7719921	69.57488	138.86307	76
ITEX Long-term plot	ITEXH2	12-AUG-09 11:21:06AM	7 W 583210 7719921	69.57489	138.86317	78
ITEX Long-term plot	ITEXH3	12-AUG-09 11:21:57AM	7 W 583199 7719920	69.57488	138.86347	80
ITEX Long-term plot	ITEXH4	12-AUG-09 11:22:45AM	7 W 583186 7719917	69.57486	138.86379	80
ITEX Long-term plot	ITEXH5	12-AUG-09 11:23:07AM	7 W 583183 7719917	69.57486	138.86387	81
ITEX Long-term plot	ITEXH6	12-AUG-09 11:23:36AM	7 W 583175 7719917	69.57486	138.86407	81
ITEX Long-term plot	ITEXK1	10-AUG-09 10:17:30AM	7 W 583009 7720085	69.57642	138.86818	73
ITEX Long-term plot	ITEXK2	10-AUG-09 3:13:02PM	7 W 583011 7720083	69.5764	138.86812	73
ITEX Long-term plot	ITEXK3	10-AUG-09 3:14:55PM	7 W 583026 7720090	69.57646	138.86774	75
ITEX Long-term plot	ITEXK4	10-AUG-09 3:15:55PM	7 W 583030 7720091	69.57647	138.86764	74
ITEX Long-term plot	ITEXK5	10-AUG-09 3:17:16PM	7 W 583043 7720096	69.57651	138.8673	74
ITEX Long-term plot	ITEXK6	10-AUG-09 3:18:15PM	7 W 583055 7720101	69.57654	138.867	74
Long-term Shrub Monitoring Plot	HE SP 1 NE	13-AUG-09 3:49:19PM	7 W 582901 7720449	69.57971	138.87064	80
Long-term Shrub Monitoring Plot	HE SP 1 NW	13-AUG-09 1:37:14PM	7 W 582851 7720450	69.57974	138.87192	85
Long-term Shrub Monitoring Plot	HE SP 1 SE	14-AUG-09 4:23:35PM	7 W 582907 7720403	69.5793	138.87052	80
Long-term Shrub Monitoring Plot	HE SP 1 SW	14-AUG-09 4:56:30PM	7 W 582857 7720399	69.57928	138.87179	84
Long-term Shrub Monitoring Transect	ST Glauc1	15-AUG-09 1:06:34PM	7 W 581720 7719792	69.57419	138.90153	22
Long-term Shrub Monitoring Transect	ST Glauc2	15-AUG-09 1:07:52PM	7 W 581729 7719787	69.57414	138.90129	19
Long-term Shrub Monitoring Transect	ST Glauc3	15-AUG-09 1:09:18PM	7 W 581742 7719781	69.57409	138.90097	18
Long-term Shrub Monitoring Transect	ST Glauc4	15-AUG-09 1:12:13PM	7 W 581759 7719775	69.57403	138.90054	16
Long-term Shrub Monitoring Transect	ST Glauc5	15-AUG-09 1:14:53PM	7 W 581783 7719769	69.57396	138.89993	16
Long-term Shrub Monitoring Transect	ST Glauc6	15-AUG-09 1:15:42PM	7 W 581783 7719781	69.57407	138.89992	16
Long-term Shrub Monitoring Transect	ST Glauc7	15-AUG-09 1:17:11PM	7 W 581791 7719768	69.57396	138.89971	13
Long-term Shrub Monitoring Transect	ST Glauc8	15-AUG-09 1:18:43PM	7 W 581792 7719761	69.5739	138.8997	13
Long-term Shrub Monitoring Transect	ST Glauc9	Not marked				
Long-term Shrub Monitoring Transect	ST Glauc10	Not marked				
Long-term Shrub Monitoring Transect	ST Rich1	15-AUG-09 12:49:31PM	7 W 581869 7719439	69.57098	138.89801	5
Long-term Shrub Monitoring Transect	ST Rich2	15-AUG-09 12:51:04PM	7 W 581865 7719452	69.57111	138.89809	4
Long-term Shrub Monitoring Transect	ST Rich3	15-AUG-09 12:52:46PM	7 W 581865 7719470	69.57127	138.89807	5
Long-term Shrub Monitoring Transect	ST Rich4	15-AUG-09 12:54:02PM	7 W 581862 7719485	69.57139	138.89814	8
Long-term Shrub Monitoring Transect	ST Rich5	15-AUG-09 12:55:09PM	7 W 581859 7719500	69.57153	138.89821	7
Long-term Shrub Monitoring Transect	ST Rich6	15-AUG-09 12:56:28PM	7 W 581856 7719514	69.57166	138.89828	5
Long-term Shrub Monitoring Transect	ST Rich7	15-AUG-09 12:57:38PM	7 W 581850 7719529	69.57179	138.89841	4
Long-term Shrub Monitoring Transect	ST Rich8	15-AUG-09 12:58:52PM	7 W 581844 7719541	69.57191	138.89856	5
Long-term Shrub Monitoring Transect	ST Rich9	15-AUG-09 1:00:02PM	7 W 581841 7719556	69.57204	138.89862	5
Long-term Shrub Monitoring Transect	ST Rich10	Not marked				
Repeat Shrub Survey	SC1	07-AUG-08 2:56:34PM	7 W 582167 7719882	69.57831	138.94448	28
Repeat Shrub Survey	SC2	07-AUG-08 4:13:39PM	7 W 582122 7719939	69.57539	138.89107	10
Repeat Shrub Survey	SC3	07-AUG-08 6:39:22PM	7 W 581279 7720224	69.5782	138.91245	67
Repeat Shrub Survey	SC4	09-AUG-08 11:00:46AM	7 W 580502 7720576	69.58159	138.93209	56
Repeat Shrub Survey	SC5	09-AUG-08 12:07:46PM	7 W 580813 7721509	69.58986	138.92328	78
Repeat Shrub Survey	SC6	09-AUG-08 12:24:05PM	7 W 580884 7722156	69.59564	138.9209	93
Repeat Shrub Survey	SC7	09-AUG-08 12:35:43PM	7 W 580917 7722557	69.59922	138.9197	78
Repeat Shrub Survey	SC8	09-AUG-08 1:39:20PM	7 W 581117 7723458	69.60723	138.91378	76
Repeat Shrub Survey	SC9	09-AUG-08 3:13:55PM	7 W 581698 7722306	69.59673	138.89986	67
Repeat Shrub Survey	SC10	09-AUG-08 3:36:56PM	7 W 581667 7721567	69.59012	138.9013	80
Repeat Shrub Survey	SC11	09-AUG-08 3:57:59PM	7 W 581618 7721020	69.58523	138.90305	77

Shrubring Samples	HA	09-AUG-08 1:39:20PM	7 W 581117 7723458	69.60723	138.91379	76
Shrubring Samples	HB1	08-AUG-08 10:51:35AM	7 W 581705 7719317	69.56994	138.90233	2
Shrubring Samples	HB2	08-AUG-08 11:15:03AM	7 W 581715 7719315	69.56992	138.90206	1
Shrubring Samples	HB3	08-AUG-08 11:13:30AM	7 W 581729 7719315	69.56992	138.90171	-2
Shrubring Samples	HB4	08-AUG-08 11:20:23AM	7 W 581743 7719313	69.56989	138.90134	-1
Shrubring Samples	HB5	08-AUG-08 11:31:45AM	7 W 581754 7719312	69.56988	138.90105	0
Shrubring Samples	HB6	08-AUG-08 11:37:50AM	7 W 581764 7719312	69.56987	138.90081	-1
Shrubring Samples	HG1	07-AUG-08 2:10:58PM	7 W 582218 7719869	69.57473	138.88866	35
Shrubring Samples	HG2	07-AUG-08 2:26:27PM	7 W 582206 7719870	69.57474	138.88897	31
Shrubring Samples	HG3	07-AUG-08 2:33:45PM	7 W 582197 7719873	69.57477	138.88921	31
Shrubring Samples	HG4	07-AUG-08 2:41:17PM	7 W 582189 7719873	69.57477	138.88942	32
Shrubring Samples	HG5	07-AUG-08 2:47:39PM	7 W 582178 7719875	69.57479	138.8897	30
Shrubring Samples	HG6	07-AUG-08 2:56:34PM	7 W 582167 7719882	69.57486	138.88996	28
Shrubring Samples	HGPOL1	07-AUG-08 4:23:34PM	7 W 582090 7719970	69.57568	138.89188	8
Shrubring Samples	HGPOL2	07-AUG-08 4:25:00PM	7 W 582091 7719980	69.57576	138.89182	10
Shrubring Samples	HGPOL3	07-AUG-08 4:31:32PM	7 W 582099 7719993	69.57588	138.89162	19
Shrubring Samples	HGRET2	07-AUG-08 4:03:56PM	7 W 582160 7719882	69.57487	138.89015	27
Shrubring Samples	HGRET3	07-AUG-08 4:04:49PM	7 W 582150 7719884	69.57489	138.89041	21
Shrubring Samples	HGUNK1	07-AUG-08 4:41:41PM	7 W 582113 7720015	69.57607	138.89122	42
Shrubring Samples	HGUNK2	07-AUG-08 4:59:04PM	7 W 582109 7720041	69.5763	138.89132	36
Shrubring Samples	HH1	10-AUG-08 1:04:44PM	7 W 581042 7721234	69.58733	138.91766	84
Shrubring Samples	HH2	10-AUG-08 1:21:49PM	7 W 581028 7721237	69.58736	138.91801	84
Shrubring Samples	HH3	10-AUG-08 1:38:37PM	7 W 581022 7721249	69.58746	138.91815	85
Shrubring Samples	HH4	10-AUG-08 1:43:48PM	7 W 581007 7721256	69.58753	138.91852	83
Shrubring Samples	HH5	10-AUG-08 1:46:03PM	7 W 580996 7721257	69.58755	138.9188	84
Shrubring Samples	HH6	10-AUG-08 1:53:24PM	7 W 580989 7721263	69.5876	138.91899	81
Shrubring Samples	HK1	07-AUG-08 5:53:45PM	7 W 581337 7720211	69.57806	138.91097	57
Shrubring Samples	HK2	07-AUG-08 6:00:08PM	7 W 581325 7720212	69.57808	138.91129	65
Shrubring Samples	HK3	07-AUG-08 6:13:23PM	7 W 581314 7720214	69.5781	138.91156	65
Shrubring Samples	HK4	07-AUG-08 6:23:53PM	7 W 581302 7720216	69.57812	138.91186	64
Shrubring Samples	HK5	07-AUG-08 6:32:57PM	7 W 581295 7720223	69.57819	138.91205	68
Shrubring Samples	HK6	07-AUG-08 6:39:22PM	7 W 581279 7720224	69.5782	138.91244	67
Shrubring Samples	HNIPH1	08-AUG-08 2:32:02PM	7 W 582385 7719656	69.57276	138.88457	49
Shrubring Samples	HNIPH3	09-AUG-08 11:17:54AM	7 W 580514 7720571	69.58154	138.93179	57
Shrubring Samples	HNIPH4	11-AUG-08 4:59:26PM	7 W 578115 7719633	69.57385	138.99414	4
Shrubring Samples	HNIPH5	11-AUG-08 5:07:48PM	7 W 578129 7719641	69.57392	138.99379	9
Shrubring Samples	HNIPH6	11-AUG-08 5:13:31PM	7 W 578155 7719647	69.57397	138.9931	15
Shrubring Samples	HNYPH2	09-AUG-08 11:00:46AM	7 W 580502 7720576	69.58159	138.93208	56
Shrubring Samples	HPOL3	10-AUG-08 6:01:07PM	7 W 580360 7720169	69.57798	138.93608	43
Shrubring Samples	HSC1	10-AUG-08 4:07:23PM	7 W 580093 7720170	69.57807	138.94292	41
Shrubring Samples	HSC3	10-AUG-08 4:39:53PM	7 W 580080 7720175	69.57813	138.94328	51
Shrubring Samples	HSC4	10-AUG-08 4:46:18PM	7 W 580069 7720174	69.57812	138.94355	43
Shrubring Samples	HSC6	10-AUG-08 5:09:05PM	7 W 580057 7720181	69.57818	138.94384	45
Shrubring Samples	HSC7	10-AUG-08 5:15:47PM	7 W 580041 7720185	69.57823	138.94425	46
Shrubring Samples	HSC8	10-AUG-08 5:22:11PM	7 W 580032 7720194	69.57831	138.94449	50
Snow-Canopy Transect	300-44	20/04/2008 16:39	7 W 581558 7719148	69.56848	138.90625	0
Snow-Canopy Transect	301-34	20/04/2008 16:42	7 W 581575 7719184	69.56879	138.90577	-3
Snow-Canopy Transect	302-14	20/04/2008 16:43	7 W 581591 7719220	69.56911	138.90532	-2
Snow-Canopy Transect	303-25	20/04/2008 16:44	7 W 581610 7719256	69.56942	138.90481	-2
Snow-Canopy Transect	304-21	20/04/2008 16:49	7 W 581628 7719291	69.56973	138.90432	0
Snow-Canopy Transect	305-18	20/04/2008 16:51	7 W 581646 7719327	69.57005	138.90383	-1
Snow-Canopy Transect	306-50	20/04/2008 16:53	7 W 581660 7719365	69.57038	138.90342	1

Snow-Canopy Transect	307-41	20/04/2008 16:54	7 W 581677 7719400	69.5707	138.90296	2
Snow-Canopy Transect	308-45	20/04/2008 16:56	7 W 581695 7719437	69.57102	138.90247	3
Snow-Canopy Transect	309-22	20/04/2008 16:57	7 W 581712 7719474	69.57134	138.90201	3
Snow-Canopy Transect	310-16	20/04/2008 16:59	7 W 581730 7719508	69.57165	138.9015	4
Snow-Canopy Transect	311-25	20/04/2008 17:04	7 W 581748 7719544	69.57197	138.90101	1
Snow-Canopy Transect	312-26	20/04/2008 17:06	7 W 581765 7719581	69.57229	138.90055	3
Snow-Canopy Transect	313-39	20/04/2008 17:07	7 W 581783 7719617	69.57261	138.90006	6
Snow-Canopy Transect	314-44	20/04/2008 17:08	7 W 581801 7719653	69.57292	138.89955	4
Snow-Canopy Transect	315-31	20/04/2008 17:10	7 W 581821 7719688	69.57323	138.89903	5
Snow-Canopy Transect	316-52	20/04/2008 17:14	7 W 581844 7719720	69.57351	138.8984	6
Snow-Canopy Transect	317-58	20/04/2008 17:16	7 W 581870 7719733	69.57362	138.89773	6
Snow-Canopy Transect	318-40	20/04/2008 17:18	7 W 581908 7719747	69.57373	138.89673	8
Snow-Canopy Transect	319-100	20/04/2008 17:21	7 W 581945 7719763	69.57386	138.89577	10
Snow-Canopy Transect	320-18	20/04/2008 17:24	7 W 581981 7719777	69.57398	138.89482	16
Snow-Canopy Transect	321-12	20/04/2008 17:26	7 W 582033 7719772	69.57392	138.89349	21
Snow-Canopy Transect	322-17	20/04/2008 17:27	7 W 582073 7719771	69.57389	138.89248	20
Snow-Canopy Transect	323-11	20/04/2008 17:29	7 W 582114 7719770	69.57388	138.89143	24
Snow-Canopy Transect	324-18	20/04/2008 17:30	7 W 582154 7719767	69.57384	138.8904	28
Snow-Canopy Transect	325-27	20/04/2008 17:32	7 W 582195 7719760	69.57376	138.88936	33
Snow-Canopy Transect	326-8	20/04/2008 17:33	7 W 582232 7719747	69.57363	138.88842	41
Snow-Canopy Transect	327-6	20/04/2008 17:34	7 W 582271 7719737	69.57353	138.88741	43

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