Dendroecology of the dwarf shrub *Dryas integrifolia* near Churchill, Manitoba

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Abstract

Shrubs have generally been overlooked in dendrochronology and little information exists on allometric relationships in dwarf shrubs. In this study, the dimensions (mat, stem and root) of the shrub, *Dryas integrifolia* M. Vahl., were measured and anatomical slides containing annual growth rings were prepared for each individual. The first objective was to compare allometric relationships among descriptors of shrub dimension and between these descriptors and shrub age in four populations of *D. integrifolia*. Secondary objectives included the documentation of maximum age and evaluation of a potential for cross-dating among individual shrubs. A strong, consistent allometric relationship between mat and stem diameter was observed in individuals among sites, although relationships with root length were more variable. Moreover, growth rates in individuals varied within and between sites and were much higher for the significantly younger *D. integrifolia* from site-A. *Dryas integrifolia* from Churchill, Manitoba could be cross-dated. The radial growth – climate association was found to be similar to that of white spruce, black spruce and tamarack regarding the impact of October climatic conditions. Snow accumulation and onset of the growing season appear to be the most important factors controlling *D. integrifolia* growth. These findings suggest that past climatic information can be obtained from the dwarf shrub, *D. integrifolia*, in areas where meteorological data are lacking such as in the Canadian arctic.

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1.0 Introduction

Dendrochronology can be applied to those plants capable of secondary growth and production of annual growth, they include trees, shrubs and dwarf shrubs (Schweingruber 1996). However, dendrochronology has been mainly confined to the use of trees. Although there are more than 1,200 species of prostrate woody plants in the world (Kolishchuk 1990), the majority of shrubs and dwarf shrubs have generally been overlooked (Beschel and Webb 1963; Schweingruber 1996; Schweingruber and Dietz 2001a) and little information exists on their allometric relationships (Martinez and Lopez-Portillo 2003).

Dendroclimatology has been widely used to analyze the annual growth rings in trees and to construct chronologies capable of yielding past climatic information, especially in regions where tree growth is sensitive and limited by some climatic factor (Fritts 1976). A network of chronologies from these long-lived natural climatic indicators can reveal regional climatic data. In these instances, long meteorological records can be compared with long sequences of tree-ring measurements from the same period (Schweingruber 1996) and thereby be used to reconstruct past climatic variations from past variations in ring-widths (Fritts 1976). However, arctic and alpine regions are often devoid of trees and therefore, tree-ring chronologies cannot be developed. Instead, dwarf shrubs producing a small amount of growth every year are often found in these extreme environments (Wilson 1964; Woodcock and Bradley 1994). These prostrate woody plants are able to spread beyond the treeline as a result of being protected by snow in the winter season (Kolishchuk 1990). Grace *et al.* (2002) reported that temperatures were 5-

10 ºC higher in microclimates that developed over and within dwarf shrubs during the daytime than those of the air above.

Schweingruber and Dietz (2001a) indicated that wood anatomy in dwarf shrubs do not greatly deviate from that of known trees. The pattern of growth rings was commonly found to be more consistent among species within the Caryophyllaceae, Lamiaceae and Rosaceae. Moreover, dendrochronological techniques have successfully been applied to perennial herbs (Dietz and Ullmann 1998; Dietz and Schweingruber 2002) as well as to dwarf shrubs (Milton *et al.* 1997; Schweingruber and Dietz 2001a; Rayback and Henry 2005). Thus, shrubs have great potential in the reconstruction of past climatic events, especially in areas containing sparse vegetation with few or no trees.

Gordon (1991) indicated that the relatively shallow-rooted habit of shrubs in contrast to more deeply rooted trees may make the former more suitable for ring-width analysis in relation to precipitation. However, this may also make shrubs more susceptible to microsite effects and thus be more difficult to cross-date. Beschel and Webb (1963) hypothesized that cross-dated arctic willow (*Salix arctica* Pall.) tree-ring series would be correlated with meteorological records in the vicinity. However, cross-dating difficulties were encountered because of the higher likelihood of eccentric positions of the pith and missing and discontinuous rings in older specimens (Bär 2005). Woodcock and Bradley (1994) observed the same difficulties in *S. arctica* but added that these problems could be overcome when good increment series were available. They indicated that weather information could also be derived from establishment periods, which coincide with

favorable conditions. In addition, ring-width of *S. arctica* was found to vary considerably although growth-rate decreased with age (Wilson 1964). However, some older specimens close to 60 years of age were reported to still have vigorous growth rates on Ellesmere Island (Woodcock and Bradley 1994). Nonetheless, the ring-widths of shrubs in arid regions were shown to be attributable to water availability (Milton *et al.* 1997) and to late winter/early spring precipitation (Gordon 1991). The ring-widths of an arctic dwarf shrub have also been used to reconstruct mean summer air temperature (Rayback and Henry in press). Other studies have described dwarf shrubs as having good potential for dendroclimatological work (Woodcock and Bradley 1994; Schweingruber and Dietz 2001a; Bär 2005; Rayback and Henry 2005).

Dendrochronological techniques can also be used to assess the long-term growth of woody plants (Nilsen and Orcutt 1996). For example, mean growth rate can be inferred through the comparison of total annual rings (age) and stem diameter. Although vegetative reproduction has been found to be problematic in the age-size determination of some dwarf shrubs (Molau 1997), Beschel and Webb (1963) indicated that shrub diameters were useful indicators of glacier forelands of the Alps and West Greenland for dating substrates within the last hundred years. Moreover, maximum cushion diameter of the arctic perennial plant, *Silene acaulis* (L.), provided minimum age estimates for 75-100 year-old substrates (Benedict 1989). The largest cushions of *S. acaulis* were also estimated to be in excess of 300 years of age (Morris and Doak 1998) and at least 400 years for the slow-growing evergreen perennial, *Diapensia lapponica* (L.) (Molau 1997). Another study found that the maximum ages of surviving *Salix glauca* (L.) and *S.*

candida (Fluegge) revealed the minimum dates for the displacement of the shoreline at distances along the eastern side of Hudson Bay, Quebec (Mörs and Bégin 1993).

1.1 Ecology of *Dryas integrifolia*

Entire-Leaved Mountain Avens (*Dryas integrifolia* M. Vahl.) in the Rosaceae is a perennial shrub, widely distributed across the northern half of North America, the coasts of Greenland (Porsild 1955; Porsild and Cody 1980) and all around the Hudson and James Bays (Johnson 1987) (Appendix A). The low growing or mat-forming species *D. integrifolia* has been described as a dwarf shrub with alternate, simple leaves characterized by lateral rooting branches (Porsild 1964), or rooting of low shoots (Harper 1978) (Appendix B). Its prostrate mat form is a result of slow radial development, although a vertical development of up to 15 cm has been observed in southern populations (Hart 1988). Median mat sizes were found to range from 208 cm^2 to 717 cm^2 at study sites in the Alexandra Fiord lowland, Ellesmere Island (Hart and Svoboda 1994) and mat sizes up to 9505 cm^2 were recorded at more recently colonized sites in Churchill, Manitoba (Hart 1988). Stem growth relative to the pith has been reported to be eccentric and generally greater on the side of horizontal branches closest to the ground (Miller 1975). Buds develop in the autumn prior to the flowering season (S rensen 1941). Solitary flowers appear on the shrub mid-June to early August and have evolved a number of adaptations to overcome the harsh, short growing season including faster flowering time and orientation of the flower towards the solar noon sun (Krannitz 1996). Although the flowers of *D. integrifolia* on Ellesmere Island were shown to be heliotropic for part of the day (Kevan 1975), this ability was absent for those studied at both Igloolik

and Pangnirtung (Krannitz 1996). When the flower heads are ripe, masses of plumed achenes are dislodged together and carried by the wind (Hart 1988). Lemmings feed on the seeds of *D. integrifolia* and contribute to their dissemination (Porsild 1955).

Dryas integrifolia is a pioneer, calciphilous species commonly occurring on barren, rocky, or gravelly substrates (Porsild 1947; Tremblay and Schoen 1999) where adventitious roots and vegetative reproduction assist in its colonization of the substrate (Porsild 1955). *Dryas integrifolia* mats are green only on the surface above old leaves that remain attached years after they die creating a more suitable microenvironment for the establishment of other species by providing a cache of moisture and organic debris (Svoboda 1974; Hart and Svoboda 1994). *Dryas integrifolia* has also been described as the dominant early colonizer of lime-rich gravel pits in the Churchill region (Scott 1995) as well as one of the most important stabilizers of marine beaches and gravel regions within the arctic (Johnson 1987). It has colonized nearly all arctic land surfaces previously occupied by ice within North America (Porsild 1947). Firlotte (1998) indicated that early colonizers such as *D. integrifolia* could be used to revegetate open gravel pits. She reported that a redistribution of overburden immediately after gravel mining would enhance the quality of the substrate for seedling establishment. Alternatively, large cobbles hindered seedling germination and did not retain water as well as a finer substrate such as sand.

White dryad (*Dryas octopetala* L.), a similar species occurring in Yukon, Alaska and Europe (Porsild and Cody 1980), has been reported to function as a nurse plant primarily

for a sub-set of species in alpine and arctic environments (Klanderud and Totland 2004). Species composition differed inside and outside of *D. octopetala* mats. Facilitation from the shrub appeared to favor bryophytes and some other species within the mat while vascular plants and lichens seemed to occur more frequently outside. Facilitation was found to occur most often in environments conducive to high levels of plant stress, irrespective of age, size or density. Similarly, establishing willow populations were shown to facilitate the germination of conifer seedlings at sub-arctic Quebec by trapping snow which acted as a protective barrier (Grégoire and Bégin 1993).

Lawrence *et al.* (1967) observed that *Dryas drummondii* (Richards.) rapidly prevents erosion, initiates the development of a humus layer and along with *D. integrifolia*, has root nodules which contain nitrogen-fixing bacteria. The authors also suggested that the presence of *D. drummondii* sped up succession approximately 20-30 years and that the current forest productivity in Glacier Bay, Alaska may have been lower without its presence.

Previous studies have also focused on the physiology of *D. integrifolia*. Maximum net CO_2 assimilation was found to occur during the night in the early growing season and later on during the daytime as light conditions diminished (Mayo *et al.* 1973). Lower net assimilation rates were reported as the season progressed. Hartgerink and Mayo (1976) showed that the leaves of *D. integrifolia* have the ability to sustain a constant turgor pressure over a highly variable range of water potentials during the growing season. They indicated that this ability to maintain turgor pressure may be vital for the continued

assimilation of CO_2 and overall growth. No studies to our knowledge have investigated the allometric relationships of *D. integrifolia*, its growth rate, or potential use in dendrochronology.

1.2 Objectives

The first objective of this study was to compare allometric relationships in four populations of *D. integrifolia* growing in the Churchill region, sub-arctic Manitoba. The relationships among descriptors of shrub dimension (mat, stem and root) and between these descriptors and shrub age were determined. A secondary objective included the documentation of maximum shrub age and evaluation of the potential for cross-dating among individual plants. Attempts were also made to correlate the *D. integrifolia* chronology to climatic data obtained from the Churchill meteorological station.

This study will have particular relevance and implications for the field of restoration ecology as we develop our understanding of early-colonizing shrubs in the sub-arctic. Allometric relationships derived from the study and age determination could supplement this field by providing information on shrub growth to aid in site remediation.

2.0 Material and Methods

2.1 Study area

The Churchill region is located in the northeastern corner of Manitoba on the western shore of Hudson Bay (Figure 1). The study area is located southeast of the town of Churchill (58°44' N and 94°04' W) within the Hudson Bay Lowland Ecoregion and York Factory Ecodistrict (Smith *et al.* 1998) (Figure 1). The area lies at the junction of three prominent natural regions: the Arctic Tundra, Boreal Forest and Arctic Marine biomes (Johnson 1987) and is within the High Sub-arctic Ecoclimatic region (Scott 1995).

The coastal calcareous substrates east of Churchill have less than 2000 years profile development due to the isostatic rebound of Hudson Bay (Scott 1995) and have begun to rise approximately 0.5 m per century (Dredge and Nixon 1992). Precambrian, Ordovician and Silurian bedrock underlie the region (Dredge and Nixon 1992). Continuous permafrost prevents water from draining away in some places producing bogs and muskeg while it may be deeper or absent from tidal zones and beach ridges (Johnson 1987). At these beach ridges, limited water-holding capacities and a low store of nutrients (Smith *et al.* 1998) severely restrict the vegetation able to inhabit these areas. Sandy, imperfectly to well-drained Regosols are found on beach ridges, while poorly drained Rego Gleysols are associated with clayey brackish tidal flats (Smith *et al.* 1998).

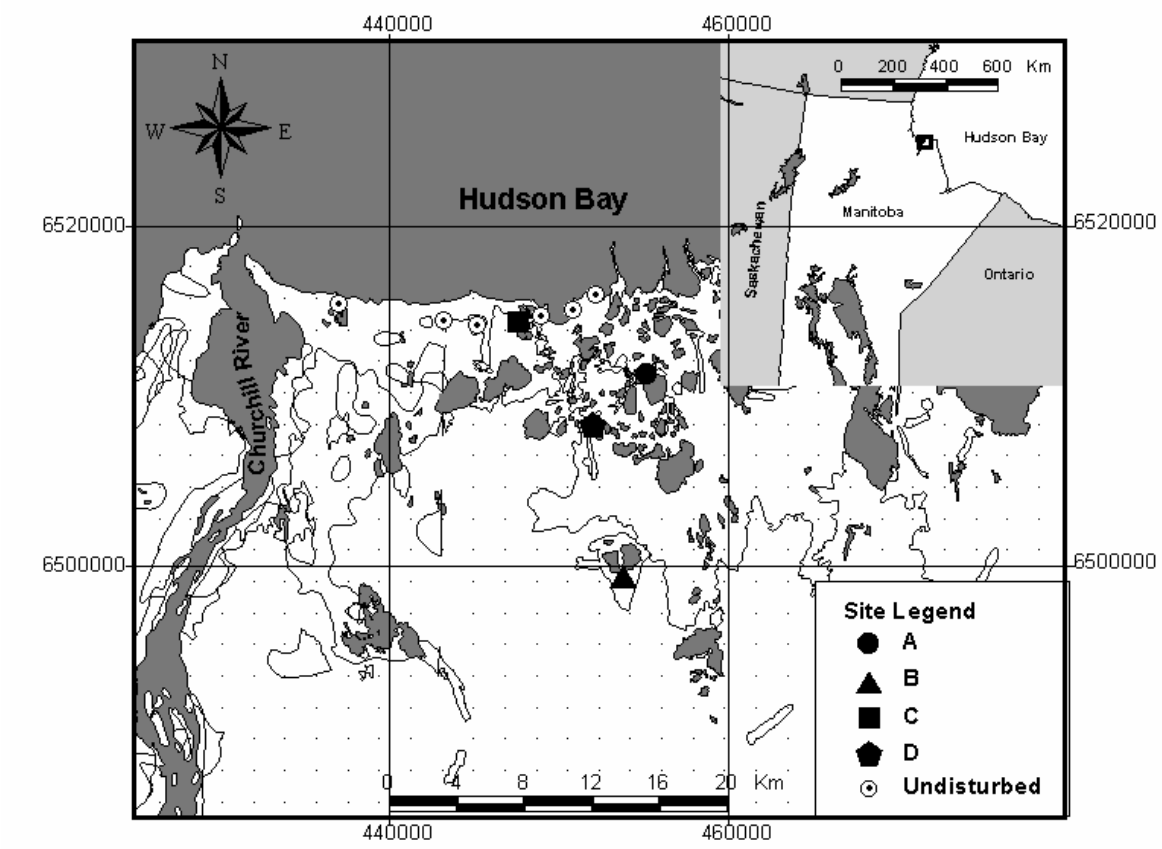

Figure 1. Map of the Churchill region, northeastern Manitoba, showing locations of sites where *Dryas integrifolia* were sampled in August 2004.

Scott (1995) reported that east of the town of Churchill, shrub tundra communities occur along the shorelines adjacent to Hudson Bay. On exposed ridges where vegetation cover is discontinuous, *D. integrifolia* and *Saxifraga tricuspidata* (Rottb.) are abundant, while dwarf shrubs such as *Arctostaphylos alpina* (L.), *Vaccinium uliginosum* (L.) and krummholz forms of *Betula glandulosa* (Michx.) dominate where cover is continuous. Well-developed shrub communities can propagate in sheltered areas where *Salix* spp. are able to reach 3 m in height. The region is mainly comprised of three tree species: black spruce (*Picea mariana* (Mill.) BSP.), white spruce (*Picea glauca* (Moench) Voss) and tamarack (*Larix laricina* (Du Roi) K. Koch). White spruce communities are found on well-drained elevated regions and gravel ridges, black spruce is usually associated with sphagnum moss over peat deposits and tamarack is distributed with both of these species (Brook 2001; Monson 2003).

Although Churchill is situated at the boundary between the true arctic and sub-arctic zones, its climate is considered sub-arctic because it has higher summer temperatures than more northerly latitudes such as Chesterfield Inlet (63°N) (Johnson 1987). The Hudson Bay causes much colder conditions to extend further south. As a consequence, long cold winters and short cool summers dominate the region. The Churchill meteorological station (58°44’ N and 94°03’ W) situated at 28.7 masl showed a mean annual daily average temperature of –6.9°C for the period from 1971-2000 (Environment Canada 2004). Of the 431.6 mm that falls as total annual precipitation in Churchill, 264.4 mm falls as rain and 191 mm as snow (Appendix C).

2.2 Sampling sites

In August 2004, four disturbed sites (A-D) (Appendix D) were selected along roads or gravel openings (Figure 1). The substrate in these four sites was weakly developed and had originated from anthropogenic activities. Moreover, gravel may have been placed at sites -A and -B from a nearby extraction pit (G. Scott, personal communication, 2006). In each of these four sites, individual *D. integrifolia* mats were distinguishable from one another. Site-A was located near the edge of a recent road constructed in 1994 (C. Paddack, personal communication, 2004). This site was characterized by small to medium-sized gravel with little organic material. Scattered white spruce and *Salix* spp. were found in adjacent locations. Site-B was located between an ATV road and a forest of tamarack and *P. glauca*. The substrate was composed of medium-sized gravel over sand. Site-C was centered on a past gravel extraction pit with some legumes mixed with *D. integrifolia*. Here, gravel was also medium-sized. Site-D was located north of Twin Lakes on a shallow gravel pit (Figure 1). Mat sizes varied from small to continuous in places. The substrate generally consisted of small to medium-sized gravel underlain by sand. *Picea glauca* and *L. laricina* bordered the edge of the pit.

Maps and aerial photographs were consulted to determine the approximate period immediately prior to when each of the four sites were disturbed. A map from 1972 of Norton Lake, Manitoba from the Mapping and Charting Establishment Department of National Defense, Canada, showed that site-A was undeveloped at this date. Similarly, aerial photographs published in 1971 by the Survey's Branch, Mines and Natural Resources, indicated that sites -B and -D were undeveloped in the Churchill region

during 1956. However, Range road was previously constructed in the vicinity of site -C during this time and it is not clear whether gravel extraction was already in process there. In addition to the four disturbed sites, a total of 26 *D. integrifolia* shrubs were collected from a series of undisturbed sites to assess the maximum age of the species. These sites were defined as where individual *D. integrifolia* mats came into contact forming a continuous ground cover of vegetation.

2.3 Field sampling

In the disturbed sites (A-D), *D. integrifolia* were chosen systematically according to different mat diameter size classes and an effort was made to collect at least two replicates for each size class (Appendix E). An individual mat bearing flowers and another without were sampled for each diameter class where feasible. The mat axis with the longest diameter (MD1) was used to select and assign each shrub to a particular diameter class. It was not always possible to find two individuals for each size class or flowering class due to site heterogeneity. Consequently, some size classes were more abundant at certain sites. A mean of 25 *D. integrifolia* were sampled at each disturbed site (Appendix E).

The following measurements (Appendix F) were directly taken in the field for each *D. integrifolia*: the longest mat diameter (MD1) and a second diameter taken perpendicular to MD1 (MD2). Dividing MD2 over MD1, later created the variable, Mat symmetry (MS). In addition, dieback estimation within each mat was quantitatively estimated. Mat dieback was estimated as the percentage mat area not currently occupied by the living

shrub. This included area within the mat occupied by leaf litter, rock and dead or discolored portions of mat. The number of flowers was then determined for each individual. Presence of lateral rooting branches (LRB) and richness of vascular and non-vascular plants growing within the mat perimeter was also recorded.

A measuring tape was placed adjacent to each *D. integrifolia* and a digital photo was taken in order to later derive other measurements (see laboratory section) before taproots were extracted. The taproot diameter (TRD) for each shrub was then excavated and measured for diameter and length. However, with the exception of *D. integrifolia* at site-A, entire roots were collected only for *D. integrifolia* with a MD1 up to 25 cm. The taproot length (TRL) measurements of *D. integrifolia* at site-A that contained a MD1 exceeding 25 cm were removed later to even out sampling sizes between sites. The excavated taproots were retained for laboratory analysis. Lateral roots and belowground biomass were not taken or estimated.

2.4 Laboratory analyses

2.4.1 Image analysis

In the laboratory, each digital photograph of *D. integrifolia* was analyzed to derive additional measurements (Appendix F). First, the percentage mat dieback for each *D. integrifolia* was re-estimated to compare with that estimated in the field and a Mean dieback value was calculated using both estimations. Second, the software *WinFolia Pro* 2005b (Régent Instruments, Inc. 2005) was used to calculate parameters related to mat dimension: mat area (MA), mat perimeter (MP), longest mat diameter (D1) and mat diameter perpendicular to D1 (D2). The color analysis option was used to calculate these variables after carefully overlaying each mat with an orange color, which contrasted sharply with the background colors effectively eliminating unrelated objects from being included in the analysis. Each picture was individually calibrated using both vertical and horizontal graduations, in centimeters, from the measurement tape.

2.4.2 Sectioning of *Dryas integrifolia* stems

To determine the age of each sample and to assess if a shrub-ring chronology could be developed, a microscope slide of the stem was prepared for each shrub specimen. Before sectioning, the diameter (or radius when the root split unexpectedly) of each sample was measured to the nearest tenth of a millimeter. Longest stem diameter (SD1) and the diameter perpendicular to this (SD2) were measured using a digital caliper (Appendix F).

In order to ease the process of making anatomical slides, *D. integrifolia* samples were kept refrigerated until sectioning so that the wood remained soft. As a result, no boiling or softening solution was required. The slides of stems were transversally sectioned at the stem bases of the or as close to the root-stem interfaces as possible (Figure 2). The macrosection was then cut about 2 cm below this interface to form a 2 cm long chunk that could fit easily into the microtome clamp. Previous studies on dwarf shrubs extracted stem sections just above the root collar (Woodcock and Bradley 1994) or at soil level (Milton *et al.* 1997) with acceptable results. Samples were cleaned using paper towels, water and forceps before sectioning to remove clay and sand particles clinging to each sample and to prevent nicking the razor blade. Macrosections of larger stems were cut with a coping saw and a razor blade was used for smaller stems. Slide sections were made from the side of the macrosection closer to the aboveground portion of the plant.

Branches of shrubs from disturbed sites (A-D) were occasionally sectioned when root portions were not in a suitable condition. In each of these cases, the largest branch would be selected with the portion that was closest to the root being selected for sectioning. For many individuals at the undisturbed sites, the two largest branches were sectioned in place of the highly degraded root portion. It has been observed that the stems of woody plants growing in extreme environments often split longitudinally (Milton *et al.* 1997) or have rotten centers (Kuivinen and Lawson 1982).

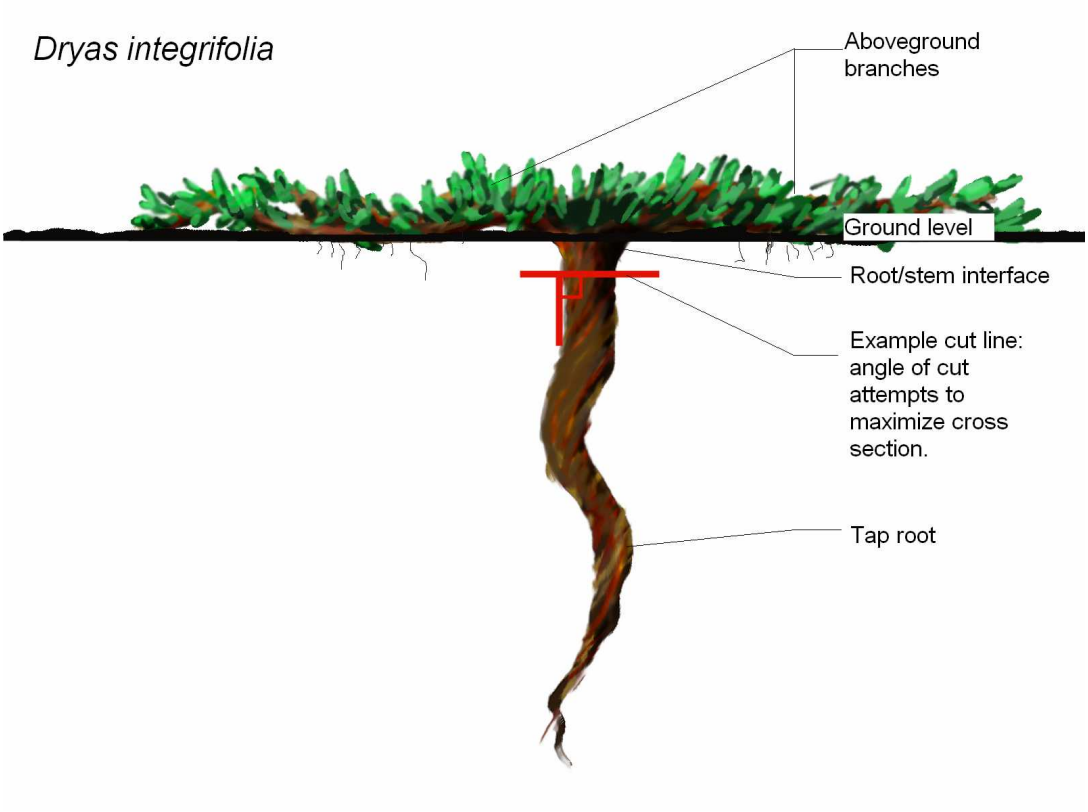

Figure 2. Lateral view of *Dryas integrifolia* indicating the general location where macrosections were taken. Illustration by Brin Jones.

A sledge microtome with Feather S35 blades was used for microsectioning stems. The blade was angled between 2-15° depending on the particular piece of wood. A small paintbrush with natural bristles was used to remove sections from the blade after each cutting. The sections taken from each specimen were mounted onto a slide with as many that could reasonably be placed without overlap. A single slide usually displayed 8-10 sections of varying thickness between 6 and 16 microns to offer a range for analysis. All sections were stained with 1% Safranin O solution and then cleared with 50% ethanol, 95% ethanol, reagent alcohol and a citrus-based clearing solvent, or D-limonene. On average, each bath would last from 2-5 minutes for each chemical. Clearing consisted of immersing sections in successive baths of the chemicals (2 with 50% ethanol and 3 or 4 with the 95% and 100% concentrations) while still on the slide. The fourth bath was necessary in order to clear sections more prone to clouding.

After clearing, a few drops of Permount® (Fisher Scientific, Fairlawn, N.J.) were applied to mount sections on microscope slides. Slides were labeled and secured to a metal tray with flat magnets to discourage bubbling underneath the cover slip. Once a metal tray was full (roughly 20 slides) it was placed in a drying oven at 40°C for at least two days. After this heating period, any excess glue on the slides was removed with a razor or additional D-limonene. All slides were then stored flat on trays for at least one month until glue was properly set.

2.4.3 Age determination and growth ring measurement

The annual growth rings contained in transverse sections of each *D. integrifolia* (Figure 3) were counted by two people using a Nikon E200 Eclipse microscope in order to determine the age for each plant. Each person counted the ages of three sections per slide (shrub) containing the most clearly defined rings and highest quality stem sections. If a discrepancy in age was found, the slide was re-examined by both people until a consensus was reached (Appendix G).

The ring-widths of 24 *D. integrifolia* (above a minimum age of 15 years) were cross-dated by F. Conciatori (technician) using the skeleton plot method to determine pointer years. Cross-dating ensured that patterns of ring-widths were matched among several series to identify the correct date of formation for every ring in all the samples (Swetnam *et al.* 1985). A Velmex slide stage micrometer interfaced with a DOS-based computer was used to record the ring-widths of these 24 *D. integrifolia* with a precision of 0.001 mm. Cross-dating and ring-width measurements were validated using COFECHA (Holmes 1983).

2.5 Statistical analyses

2.5.1 Population comparisons and allometric relationships

Several measurements were taken in the field and laboratory to determine: mat diameter, stem diameter and percent dieback in *D. integrifolia*. Field and laboratory measurements describing a given variable were compared using Pearson correlation analysis. The

Figure 3. A cross-section of a *Dryas integrifolia* stem showing annual growth increments. Outer stem segments often became isolated from one another in older individuals as a result of cambial division directed at only select locations. This particular individual was determined to be 40 years of age.

highest correlated variable for each measurement was retained for subsequent analysis while the others were discarded.

Since the *D. integrifolia* samples contained frequent instances of highly variable values, the use of non-parametric statistics was indicated. The characteristics of the four *D. integrifolia* populations (A-D) were compared using the non-parametric Kruskall-Wallis analysis of variance. In cases where the parametric single-factor ANOVA is not applicable, the Kruskal-Wallis single factor analysis of variance by ranks may be applied to test for the presence of a statistical difference between two or more groups (Zar 1996). The Mann-Whitney U test was employed for those variables shown to be statistically significant by the Kruskal-Wallis test to determine which specific pairwise comparisons were statistically significant (Sheskin 1997).

2.5.2 Growth rates and their relationships with dimensions

Growth rate and ratios were produced by dividing mat dimension (MD1, MA, MP, MSD, TRL) and status variables (Mean dieback, Richness, Flower abundance and MS) by age. The variable MD1 was also divided by MSD, TRL, MA and MP to produce allometric ratios. Finally, the ratios flower abundance over MA as well as over Live Area (LA) were created. The latter ratio represented the number of flowers in proportion to LA only, excluding dieback. The variable LA was calculated from the equation: LA = MA - ((Mean dieback/100) $\times$ MA). Following the same approach as the comparisons between *D. integrifolia* dimensions among the four populations (see section 2.5.1), the Kruskall-

Wallis analysis of variance was also applied to the series of derived growth ratios and the Mann-Whitney U test was employed to discern differences in the pairwise comparisons.

Finally, allometric relationships were developed by comparing the similarities and differences between dimensions across sites. The relationships between age and dimensions and status were investigated as well. Linear and non-linear regression analyses were used to model the relationships between selected variables. Statistical analysis were conducted with Systat (v. 11) for Windows (SYSTAT 2004a). All regressions were calculated using SigmaPlot (v. 9.01) for Windows (SYSTAT 2004b).

2.5.3 Chronology development and its association with climate

A *D. integrifolia* chronology was developed from 24 growth-ring measurement series after standardization using the program ARSTAN (Cook 1985). Standardization transforms measurement series into tree-ring indices to provide comparable means and variances for all indices. A cubic-spline function of 100% of the series length was applied to each measurement series to remove unwanted signals related to individual *D. integrifolia* growth and to maximize the common variation given the short length of the measurement series. As a standard practice in dendroclimatology, a residual chronology was then developed by removing temporal autocorrelation from each standardized measurement series using autoregressive modeling (Cook and Holmes 1986; Girardin *et al.* 2005) and a biweight robust mean was used to enhance the common signal of the residual chronology (Tardif and Bergeron 1997).

To assess the association between the residual chronologies of tree species and climate, Pearson correlations were calculated between the residual chronology and monthly climate data obtained from the Churchill meteorological station for the period from 1933-1999 (Girardin *et al.* 2005). In our study, correlations between *D. integrifolia* and climate were calculated for the period 1978-2004, corresponding to the establishment of a minimum sampling depth of twelve series. The weather variables included total monthly snowfall, total monthly precipitation, mean monthly minimum temperature and mean monthly maximum temperature for a 17-month period from May of the year prior to (t-1) ring formation to September of the year (t) during ring formation. Some missing data occurred between 2000 and 2004, these were not estimated.

The second component in our climate analysis was to construct a growth model where radial growth of *D. integrifolia* would be explained by monthly climate data. Accordingly, we developed a reconstructed tree-ring index following a forward stepwise multiple regression model. This used the residual chronology and climatic variables during the 17-month period between 1978 and 2004. All variables with a p-value < 0.05 were entered in the model. The multiple regression was calculated in Systat (v. 11) for Windows (SYSTAT 2004a).

3.0 Results

3.1 Cross-correlations among variables describing shrub dimensions

All mat diameter measurements taken in the field and in the laboratory were significantly cross-correlated. The weakest coefficient was 0.973 (Appendix H). The variable MD1 measured in the field was used in all subsequent analysis because it was the simplest to generate and highly correlated. The variable MSD had the highest correlation with all other stem diameter measurements. This variable was kept for further analysis. Similarly, the Mean dieback variable had the highest cross-correlations in its category and was also used from this point onwards (Appendix H).

3.2 Descriptive characteristics

Five variables (MSD, TRL, Mean dieback, Presence of LRB and age) showed significant differences among individuals in the four disturbed populations (Table 1). *Dryas integrifolia* from site-A consistently had the lowest mean values for these variables. In site-A, *D. integrifolia* were significantly younger, with shorter taproots and less dieback than the other populations. Site-A contained individuals with a mean age of less than one-quarter that of other sites even though mat dimensions for *D. integrifolia* at site-A did not differ significantly from those at the other disturbed sites (Table 1). It should be noted that the characteristics of undisturbed sites were not included in the Kruskal-Wallis tests of significance because they were not included in the initial sampling strategy. Rather, sampling mainly reflected the aim of identifying the maximum age of

Table 1. Descriptive statistics for each of the four disturbed and pooled undisturbed *Dryas integrifolia* populations (n=124).

	A			B			C			D			KW	Undisturbed**		
Variable	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**P***	**N**	**Mean**	**SD**
MD1 (cm)	25	17.89	15.42	19	39.53	40.98	24	28.76	21.79	30	25.77	25.12	0.148	3	71.50	33.78
MA (cm^2)	21	361.86	527.34	19	2006.57	4087.24	24	646.79	1152.81	30	755.41	1669.94	0.363	3	3158.02	2514.17
MP (cm)	21	110.55	77.67	19	206.01	201.21	24	201.75	153.43	30	160.70	165.03	0.205	3	332.36	184.26
MSD (mm)	23	3.75a	2.83	19	6.51b	4.59	24	6.18b	3.37	30	4.59ab	3.10	**0.031**	26	10.91	4.52
TRL (cm)	23	32.09a	25.08	10	41.68ab	23.36	10	65.09b	36.18	0	-	-	**0.028**	0	-	-
TRL (cm) [1]	17	20.30a	14.63	10	41.68b	23.36	10	65.09b	36.18	0	-	-	**0.002**	0	-	-
Mean dieback %	23	3.47a	7.51	19	38.36b	16.84	24	42.98b	17.25	30	44.37b	15.41	**0.000**	6	12.50	13.96
Richness	23	0.52	0.79	18	1.39	2.70	24	0.88	0.80	30	0.97	1.03	0.324	16	5.63	3.86
Flower number	25	23.40	51.70	19	7.79	13.27	24	8.08	12.05	30	17.73	31.68	0.498	3	239.33	127.62
Presence of LRB	23	0.35a	0.49	19	0.79b	0.42	24	0.58ab	0.50	30	0.73b	0.45	**0.011**	3	1.00	0.00
Age	23	5.17a	3.79	19	27.16bc	8.28	24	29.96c	11.46	30	24.27b	8.84	**0.000**	25	41.04	14.39
MS	25	0.88	0.10	19	0.84	0.09	24	0.83	0.13	30	0.81	0.13	0.260	3	0.87	0.02

MD1: Longest Mat Diameter; MA: Mat Area; MP: Mat Perimeter; MSD: Mean Stem Diameter; TRL: Taproot Length; LRB: Lateral Rooting Branches and MS (Mat symmetry): MD2/ MD1. KW: Kruskal-Wallis; SD: standard deviation; P: probability value.

*. All p-values exclude undisturbed sites.

**. All the undisturbed sites were pooled together forming the column "Undisturbed".

[1] For this variable, only samples within the range of a MD1 of 0-25cm were kept (Six cases were deleted from site-A to even out sampling sizes between groups).

All variables that were significant (p-value ≤ 0.05) appear in bold. Pairwise comparisons between populations calculated from the Mann-Whitney U test having different letters are statistically significant (p-value ≤ 0.05).

NB: although the summation of individuals from all sites is 124, there were often missing data for particular variables at certain sites. Therefore, summing the highest number at each site will result in 124 individuals.

D. integrifolia. The oldest shrub was found among undisturbed sites and had an age of 68 years (data not shown).

The comparison of growth rates and ratios among the four populations indicated that at least one population differed from the others for these variables: MD1/age, MP/age, MSD/age, TRL/age, Mean dieback/age, MS/age, MD1/TRL and MD1/MP (Table 2). Ratios from site-A were different than other sites for the majority of significantly different cases. *Dryas integrifolia* from site-A were found to hold the highest mean values among disturbed sites except for Mean dieback/age and MD1/MP. This indicated that *D. integrifolia* from this site had much faster growth rates (i.e. mat size growth rates) relative to those of other sites.

3.3 Allometric relationships

The relationships between variables describing mat dimension in *D. integrifolia* indicated that a constant relationship was maintained among sites (Figure 4ab). The relationship between MD1 and MP was best approximated by a linear regression (adj. r^2: 0.933; $p < 0.001$, n= 97) whereas the association between MD1 and MA was best approximated by a third-order polynomial equation (adj. r^2: 0.984; $p < 0.001$, n= 97). In contrast, the relationship between TRL and either MD1 or MSD was found to be more variable among sites (Figure 4cd). As previously indicated (Table 1), *D. integrifolia* from site-A have shorter TRLs than those at other sites for any given mat dimension. The linear relationship illustrated in Figure 4cd indicates that a larger mat size is supported by a

Table 2. Selected ratios calculated for disturbed and undisturbed sites and derived from the 124 sampled *Dryas integrifolia*.

	A			B			C			D			KW	Undisturbed**		
Variable	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**N**	**Mean**	**SD**	**P***	**N**	**Mean**	**SD**
MD1/ age	23	3.26b	1.75	19	1.22a	0.95	24	0.88a	0.50	30	0.99a	0.84	**0.000**	3	3.00	0.74
MA/age	21	46.35	52.77	19	52.94	98.00	24	17.51	27.06	30	25.75	52.15	0.096	3	112.82	22.36
MP/age	21	19.91b	10.34	19	6.46a	4.77	24	6.13a	3.86	30	6.19a	5.90	**0.000**	3	13.60	3.15
MSD/age	23	0.69b	0.35	19	0.22a	0.10	24	0.21a	0.08	30	0.18a	0.09	**0.000**	25	0.30	0.16
TRL/age[1]	17	5.17b	3.15	10	1.86a	0.88	10	3.07b	1.03	0	-	-	**0.002**	0	-	-
Mean dieback/age	23	0.54a	1.15	19	1.42b	0.51	24	1.48b	0.49	30	2.06c	1.16	**0.000**	6	0.34	0.33
Richness/age	23	0.09	0.16	19	0.04	0.07	24	0.03	0.02	30	0.04	0.04	0.900	15	0.16	0.10
Flower abundance /age	23	3.05	6.29	19	0.21	0.32	24	0.25	0.39	30	0.65	1.11	0.692	3	9.69	1.58
MS/age	23	0.14b	0.07	19	0.02a	0.01	24	0.02a	0.03	30	0.02a	0.02	**0.000**	3	0.03	0.02
MD1/ MSD	23	4.83	0.80	19	5.02	2.09	24	4.30	2.02	30	4.81	1.91	0.245	3	6.75	3.14
MD1/ TRL[1]	17	0.56c	0.17	10	0.36b	0.26	10	0.19a	0.06	0	-	-	**0.000**	0	-	-
MD1/ MA	21	0.35	0.53	19	0.16	0.23	24	0.22	0.39	30	0.29	0.49	0.328	3	0.03	0.01
MD1/ MP	21	0.18bc	0.03	19	0.19c	0.02	24	0.16a	0.05	30	0.16ab	0.02	**0.001**	3	0.22	0.02
Flower abundance / area	21	0.03	0.05	19	0.01	0.01	24	0.01	0.02	30	0.03	0.03	0.186	3	0.09	0.02
Flower abundance / LA	21	0.03	0.05	19	0.01	0.02	24	0.03	0.03	30	0.06	0.06	0.142	3	0.09	0.02

MD1: Longest Mat Diameter; MA: Mat Area; MP: Mat Perimeter; MSD: Mean Stem Diameter; TRL: Taproot Length; MS: Mat symmetry and LA: Live Area. KW: Kruskal-Wallis; SD: standard deviation; P: probability value.

*. All p-values exclude undisturbed sites.

**. All the undisturbed sites were pooled together forming the column "Undisturbed".

[1] For this variable, only samples within the range of a MD1 of 0-25cm were kept (Six cases were deleted from site-A to even out sampling sizes between groups).

All variables which were significant (p-value ≤ 0.05) appear in bold. Pairwise comparisons calculated from the Mann-Whitney U test having different letters are statistically significant (p-value ≤ 0.05).

NB: although the summation of individuals from all sites is 124, there were often missing data for particular variables at certain sites. Therefore, only summing the highest number of cases at each site will yield 124 individuals.

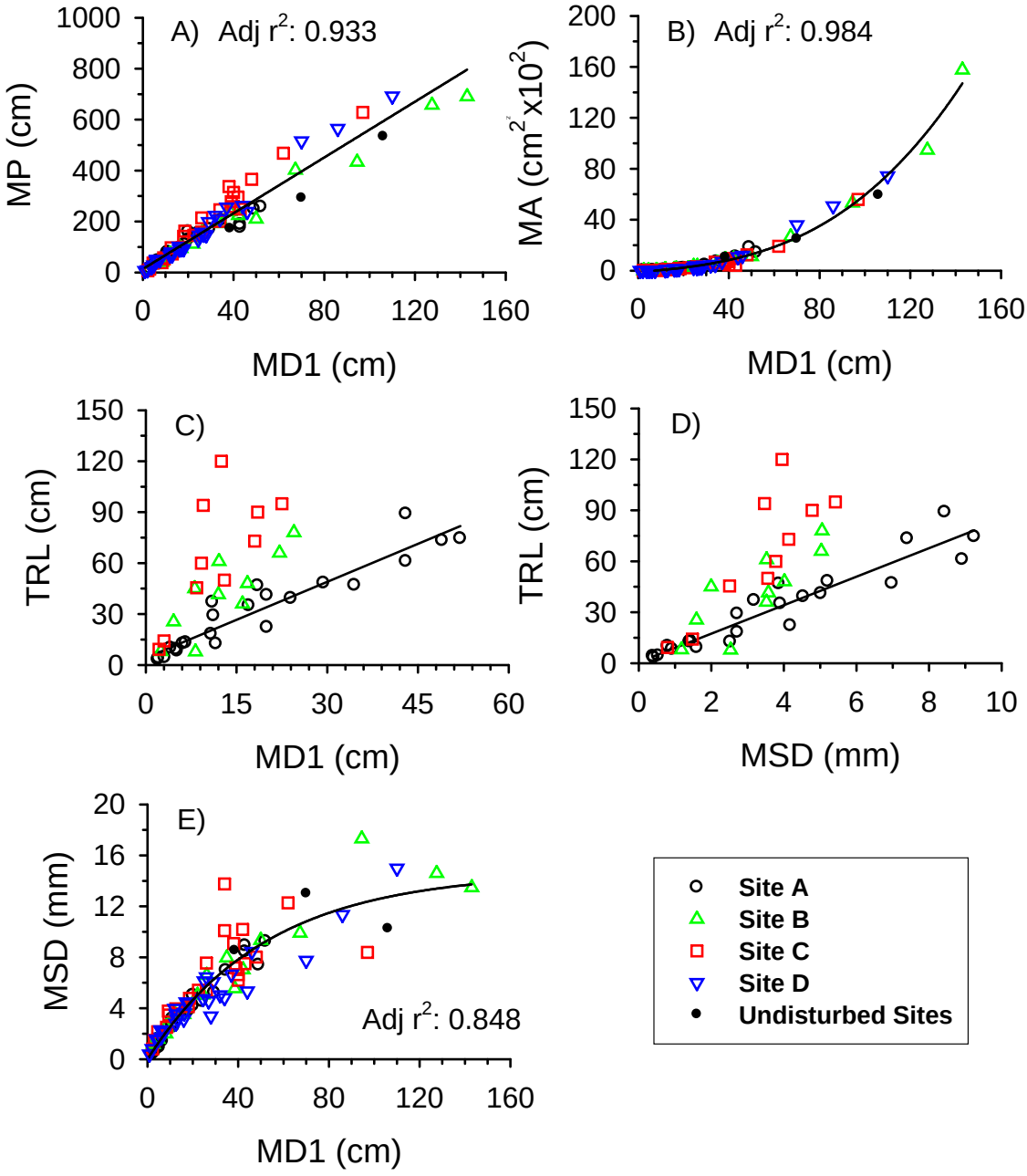

Figure 4. Allometric relationships for *Dryas integrifolia* (A-E). MD1: Longest Mat Diameter; MSD: Mean Stem Diameter; MA: Mat Area; MP: Mat Perimeter and TRL: Taproot Length. Individuals from both disturbed and undisturbed sites are indicated. Linear regressions in sub-figures (C) and (D) only used data from site-A.

shorter TRL for individuals from site-A compared to those of other sites. The relationship between MD1 and MSD was found to be consistent across all four populations although residuals become increasingly important among *D. integrifolia* with MD1s greater than 50 cm (Figure 4e). This relationship was best approximated by an exponential rise to max, single, 2-parameter regression equation (adj. r^2: 0.848; $p < 0.001$, n= 99).

3.4 Age related relationships

The relationships between *D. integrifolia* age and various descriptive variables of shrub dimension and status indicate that individuals from site-A have higher growth rates than in all other sites (Figure 5abc). Compared to the other sites, *D. integrifolia* from site-A showed a linear increase in MD1, MSD and TRL with age whereas this relationship becomes absent and more variable within and between sites -B, -C and -D. For example, the MD1 for *D. integrifolia* at site-D fluctuated with age and individuals of equal age at this site had highly variable mat sizes (Figure 6). For sites -B, -C and -D, a third-order polynomial regression best approximated age and MD1 (adj. r^2: 0.412; $p < 0.001$, n= 73), MSD (adj. r^2: 0.547; $p < 0.001$, n= 73) and TRL (adj. r^2: 0.496; $p < 0.01$, n= 22). Moreover, MSD and age increased consistently at sites -B, -C and -D as well as at undisturbed sites. It should be noted that at site-A, there was one outlier 20 years of age that exceeded the ages of all the other *D. integrifolia* at this site. In addition, the relationship between Mean dieback and age (Figure 5d) was also best approximated by a third-order polynomial equation (adj. r^2: 0.703; $p < 0.001$, n= 96). However, Mean

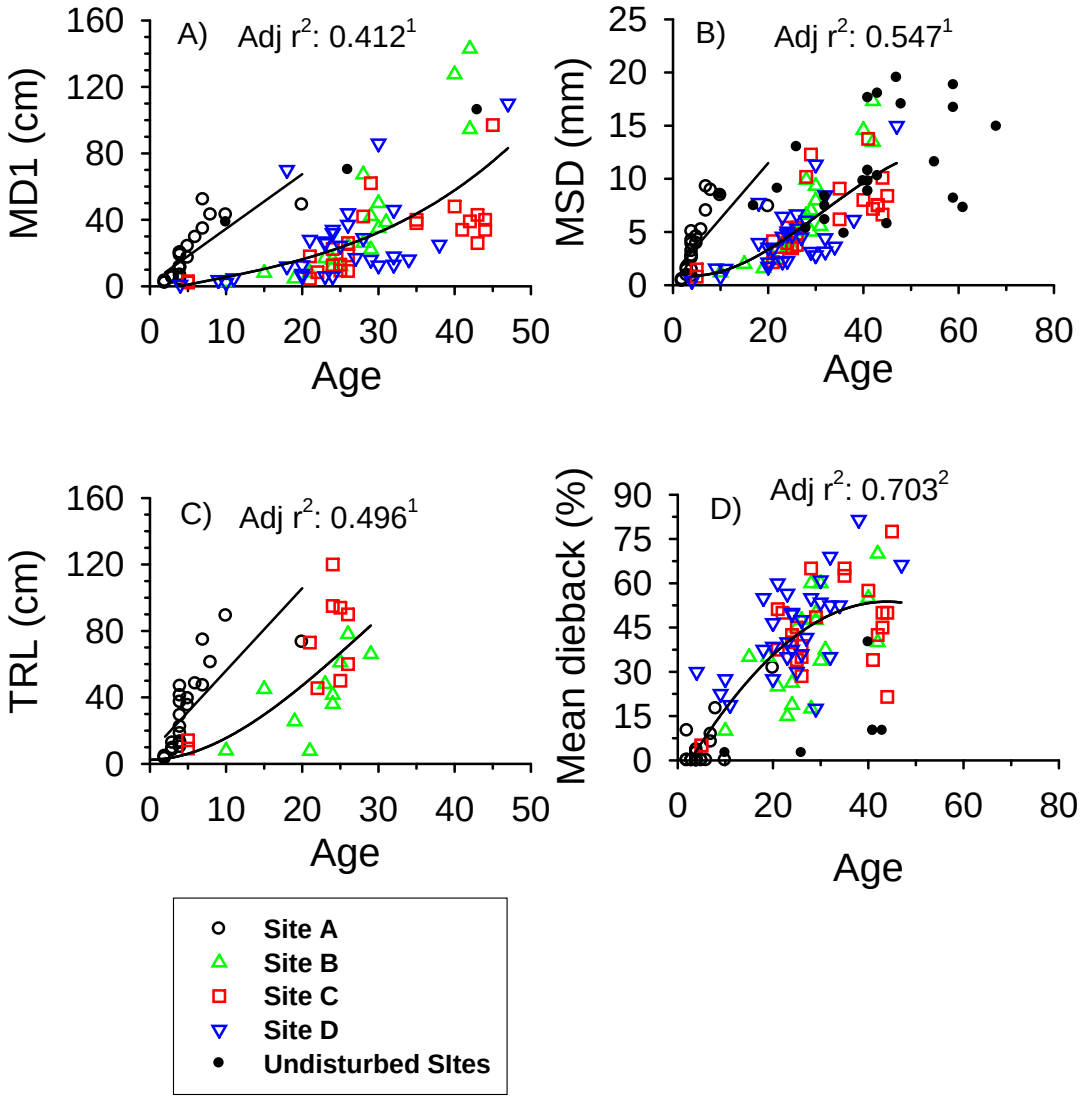

Figure 5. Relationships between age of *Dryas integrifolia* and MD1 (A), MSD (B), TRL (C) and Mean dieback (D). MD1, Longest Mat Diameter; MSD, Mean Stem Diameter and TRL, Root Length. Individuals from both disturbed and undisturbed sites are indicated. Linear regressions only used data from site-A. The regressions in these sub-figures have r-square values of 0.620(A), 0.486 (B) and 0.562 (C).
[1] These third-order polynomial regressions were calculated excluding *D. integrifolia* from both site-A and undisturbed sites.
[2] This cubic polynomial regression was calculated with data from all disturbed sites excluding undisturbed sites.

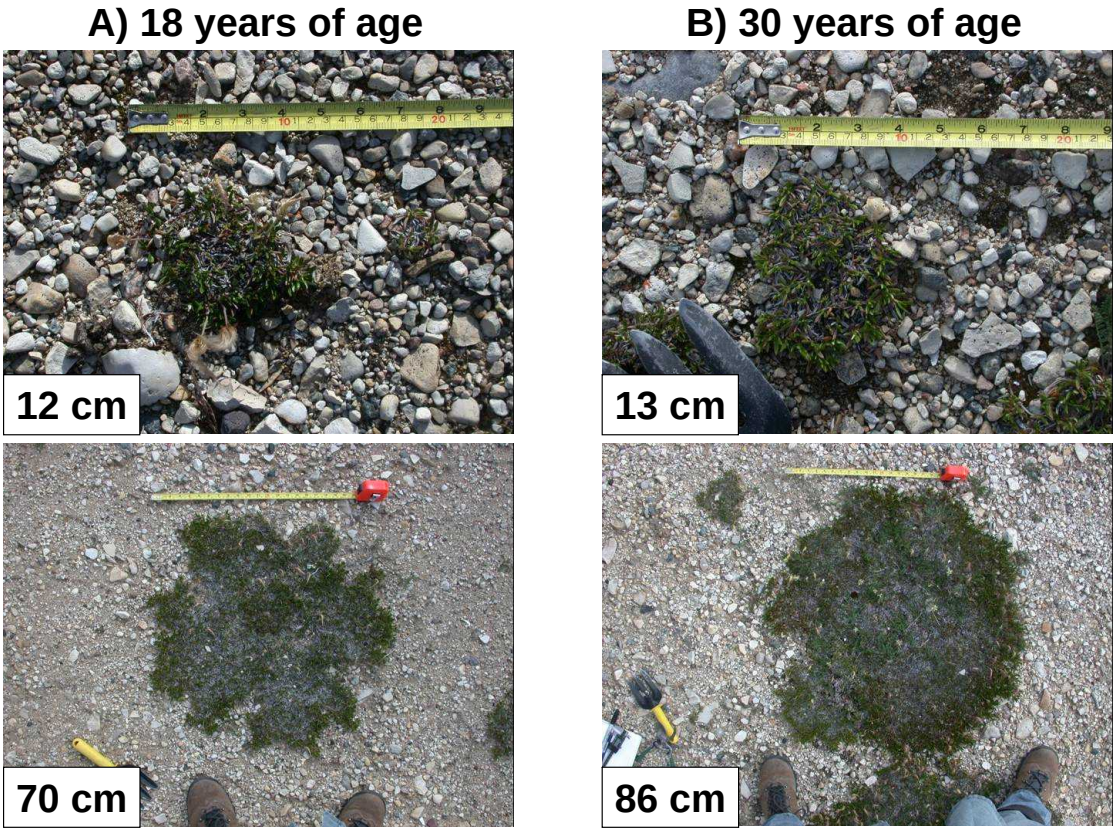

Figure 6. A comparison of *Dryas integrifolia* with different MD1s in centimeters at site-D that were 18 years of age (A) and 30 years of age (B).

dieback values for *D. integrifolia* at undisturbed sites were relatively lower for any given age than for those at disturbed sites.

3.5 *Dryas integrifolia* chronology and its association with climate

The Pearson correlation analysis from 1978 to 2004 indicated that residual growth indices of *D. integrifolia* were strongly and positively correlated with October $_{t-1}$ minimum temperature and negatively with October $_{t-1}$ snowfall. During the year of ring formation, May $_{t}$ minimum temperature, June snowfall $_{t}$ and September $_{t}$ snowfall were significantly and negatively correlated with radial growth. In contrast, radial growth was positively correlated with August $_{t}$ total precipitation (Figure 7ab).

The residual chronology developed covers the period from 1962 to 2004 and was well replicated from 1978 to 2004 (Figure 7c). The reconstructed tree-ring index from 1978 to 1999 (not estimated from 2000-2004 due to missing climate data) following a stepwise multiple regression analysis accounted for much of the variability in the residual tree-ring indices with an adjusted r-squared of 0.685 (Figure 7c). The regression model included four statistically significant ($p < 0.05$) monthly weather variables and followed the equation: radial growth = 1.852 + (0.051 $\times$ October minimum temperature $_{t-1}$) + (-0.004 $\times$ May precipitation $_{t}$) + (-0.032 $\times$ August maximum temperature $_{t}$) + (0.008 $\times$ June snowfall $_{t-1}$). These predictor variables explained the residual chronology (dependent variable) with a significance of $p < 0.001$, $F_{4,17} = 12.43$. Both the reconstructed tree-ring index and the residual chronology showed favorable periods of radial growth in 1983 and 1995 with poor growth in 1980 and 1998 (Figure 7c).

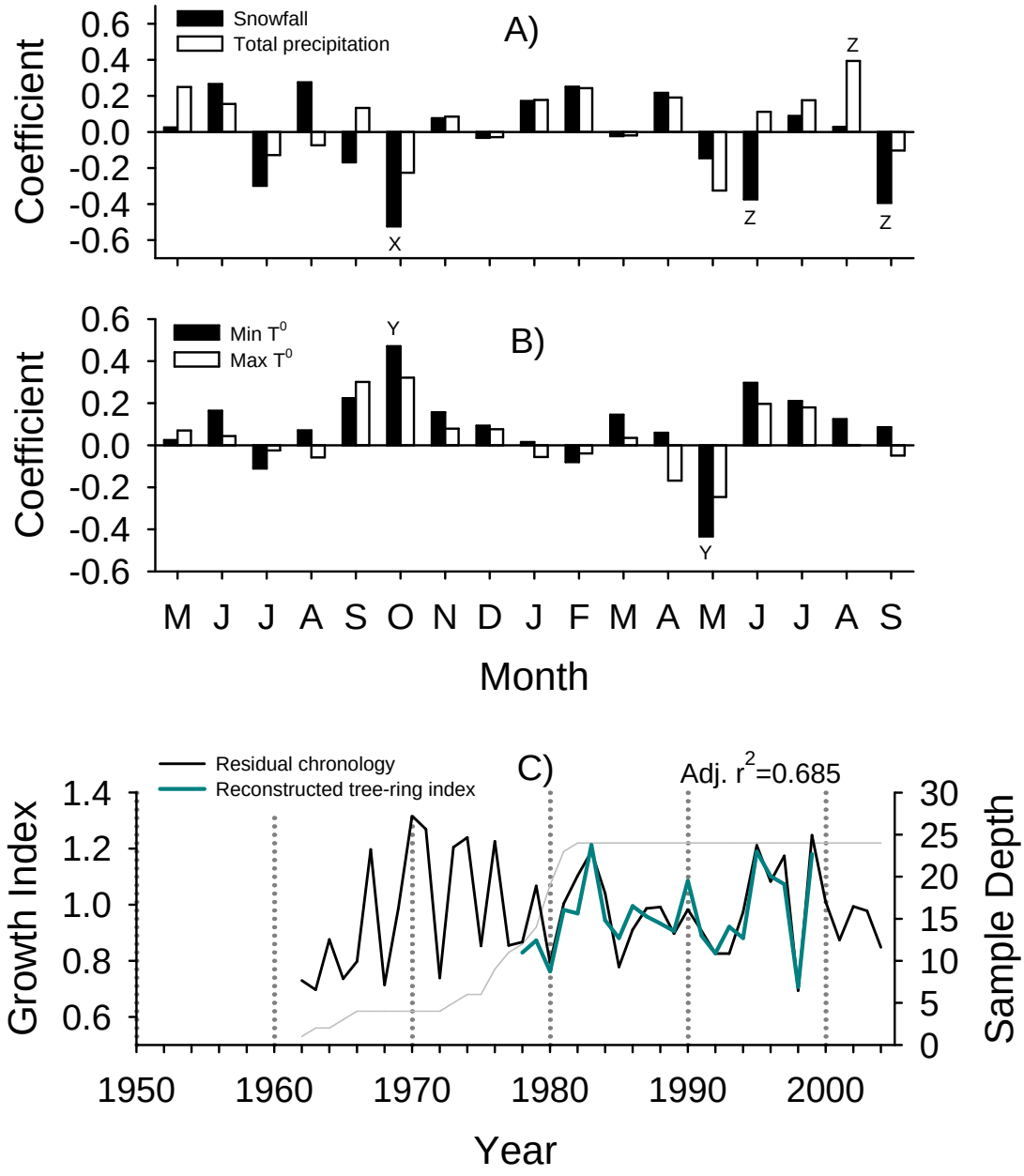

Figure 7. Pearson correlation coefficients between the *Dryas integrifolia* residual chronology and climate variables for the period 1978-2004 (A-B). The residual chronology and reconstructed tree-ring index are also compared (C). Correlation coefficients with monthly snowfall and total precipitation (A), and monthly minimum and maximum temperatures (B) are indicated. Probability values are indicated by the letters (X: $p \leq 0.01$; Y: $p \leq 0.05$ and Z: $p \leq 0.1$. The residual chronology (black line) and the reconstructed tree-ring indices (green line) using October minimum temperature, May precipitation, August maximum temperature and June snowfall are indicated (C). The gray line shows the number of samples in the residual chronology.

4.0 Discussion

4.1 Allometric relationships

The first objective of this study was to compare allometric relationships among shrub dimensions and to compare shrub dimensions with age in four populations of *D. integrifolia*. The results have shown that allometric relationships were maintained across sites except when regarding roots. The association among descriptors of mat dimension (MD1 and MA and MD1 and MP) was maintained as a consequence of having selected symmetrical mats. Furthermore, the relationship between MD1 and MSD was consistent among sites and followed an asymptotic curve. Hence, for a given increase in MD1, MSD must increase proportionally at first but then more gradually afterwards to supply nutrients and water to the expanding canopy. A similar non-linear relationship was found by Turner *et al.* (2000) who have described the allometric relationship between sapwood area and total leaf area in Douglas-fir. However, residuals from the predicted curve become increasingly important among *D. integrifolia* with MD1s greater than 50 centimeters. A possible explanation could be that *D. integrifolia* produce more rooting branches with greater mat diameters. This may indicate that these individuals would increasingly utilize adventitious roots for resource acquisition instead of through the taproot thereby reducing the demand for greater stem girth. In these shrubs, the taproot may no longer be able to entirely support the water and nutrient requirements of larger mat sizes therefore, effectively inhibiting further growth.

Another contributing factor to the weaker allometric relationship between mat and stem diameter observed in shrubs with mat diameters greater than 50 centimeters could include

dieback within mats. Larger Mean dieback values generally accompanied *D. integrifolia* of greater ages and whose presence within mats would be included in the MD1 measurement. Therefore, there would be less selective pressure for the increase in stem girth because the stems of these individuals would not be providing water and nutrients for the entire mat area but rather, only for the functional mat area. In support of this idea, Svoboda (1974) observed that there was a potential for vegetative reproduction in those *D. integrifolia* whose mats had begun to degrade at their centers.

Allometric relationships among the four sites were less consistent when TRL was compared to MD1 and MSD. Although Schenk and Jackson (2002) have documented strong allometric relationships between above-ground shrub size and root system dimensions in water-limited environments, *D. integrifolia* at sites -B and -C have invested more in TRL to maintain similar above-ground dimensions (MD1, MSD) than those in site-A. Given that individuals at sites -B and -C were generally more than three-quarters older than those at site-A, a question is raised whether sites -B and -C have lower mat and stem diameter growth rates than site-A because they must allocate more resources toward their taproots. Ruark *et al.* (1982) have shown that tree roots extended to greater depths through sands with high infiltration capacities and were less likely to spread laterally. A more thorough characterization of the substrates at study sites should be done in future studies. Firlotte (1998) indicated that the compaction of gravel pads in the Churchill region would have created conditions unsuitable for root penetration into the substrate. It was therefore speculated that the substrate at the more recently disturbed site-A may not have been compacted as greatly as those of other sites. They would have

exhibited greater aeration and water infiltration capacity, and thus resulted in faster growth of root lengths at this site. However, data on the spread of lateral roots and belowground biomass were not collected. This prevented valuable discussion on the effects of rooting depths.

4.2 Shrub dimensions and age

Shrub dimensions among and within sites -B, -C and -D and undisturbed sites generally increased irregularly with age and thus were poor indicators of age. In contrast, a linear relationship was observed between shrub dimension and age at site-A. This indicated a generally constant increase in dimensions over time. Moreover, the accumulation of detrimental effects over time was shown by the strong, positive non-linear relationship between Mean dieback and age at disturbed sites. This would imply that regardless of the unequivocal relationship between MD1 and age among disturbed sites, Mean dieback may be a better indicator of age. However, some *D. integrifolia* at undisturbed sites were shown to have low dieback values across various ages which may reflect the theoretically low level of impact received by these sites.

The age of every shrub at disturbed sites was no greater than 47 years. For the most part, aerial surveys that exceeded the maximum age among all shrubs at each disturbed site have shown undisturbed conditions in these areas. The maximum age of a shrub among all sites in Churchill, Manitoba was determined to be 68 years recorded at an undisturbed site and comparable to that of *D. octopetala* in alpine conditions which have been recorded to 80 years of age (Schweingruber and Dietz 2001b).

The results showed that MSD increased consistently with age among all sites although those at site-A increased at a faster rate and consequently diverged from the other sites. Studies in southern Manitoba, South Africa and southwestern Spain have reported that shrub basal diameters were significantly correlated to age (Ottenbreit and Staniforth 1992; Milton *et al.* 1997; Patón *et al.* 1998). Woodcock and Bradley (1994) indicated that shrub age was not a good predictor of mean stem growth rate for *S. arctica* in the high arctic. This may have been attributable to genetic variability among samples and/or high sensitivity of shrubs to differences in microsite conditions. Moreover, Corbet (1972) found that microclimates were of high ecological importance to plants growing in the arctic. Inconsistencies in the increase in stem diameter with age among *D. integrifolia* may therefore be linked to microhabitat variations that had not been considered in this study.

Dryas integrifolia at site-A were younger and required less time to develop similar dimensions compared to other sites indicating that perhaps this site contained more favorable microsite conditions. A potential argument against the younger ages of shrubs at site-A is that annual growth rings could have been miscounted thereby giving an underestimation of the real age. This argument is refuted if one considers that the site was disturbed by the construction of a road in 1994 (C. Paddack, personal communication, 2004) and that *D. integrifolia* had a mean age of five years here. An outlier that was 20 years old probably had been collected at the roadside adjacent to the scattered network of trees nearby and therefore may not have been representative of the population that had begun to colonize the site after disturbance.

Another criticism for the discrepancy in growth rates between sites was that MD1 measurements may have been underestimated due to mat dieback. This would have the effect of reducing the original mat diameters and resulted for the seemingly lower growth rates at sites -B, -C and -D. For example, the prostrate branches of *S. arctica* shed from the central burl over time and resulted in the production of new branches (Beschel and Webb 1963). However, the underestimation of MD1 in this study due to mat dieback is discredited by the strong non-linear relationship between MD1 and MSD. This association demonstrates that a given extent of mat diameter is accounted for by a proportional growth of stem diameter.

4.3 *Dryas integrifolia* chronology and its association with climate

A secondary objective of the study was to evaluate whether *D. integrifolia* could be cross-dated and therefore have a potential use in dendroclimatology. This was accomplished, however, not without difficulties. Discontinuous and missing rings were common, boundaries between rings were occasionally difficult to recognize and recent annual increments were often present only at certain locations along the stem transverse section in older individuals. Thus, many stem sections had to be rejected and only a select number were successfully cross-dated.

Chronology development with cross-datable *D. integrifolia* was limited by the relatively short lifespan of this early-colonizing species. But the chronology was significantly and positively correlated with October $_{t-1}$ minimum temperature and negatively with October

$_{t-1}$ snowfall both of the year prior to ring formation. Elevated temperature for October $_{t-1}$ in the Churchill region has also been shown to be positively associated to white spruce, black spruce and tamarack tree-ring indices (Jacoby and Ulan 1982; Girardin *et al.* 2005). October is usually the time when snowfall begins in Churchill. The positive effect of October $_{t-1}$ minimum (nighttime) temperature on growth could be related to low snowfall during this month. It is speculated that warm October temperatures and low snow accumulation in the autumn would delay the onset of ground snow cover. This would lessen the period required to melt the snow in spring and presumably favor an earlier resumption of growth and an extended length of the growing season during ring formation of the following year.

The results also indicated that warmer than average May $_{t}$ temperatures were important because they had a negative association with growth during the year of ring formation. The inhibition of growth as a result of high May $_{t}$ temperatures was also observed in black spruce and tamarack by Girardin *et al.* (2005). These authors indicated that the negative relationship may have been associated with an early snowmelt at a time when the ground has not yet thawed. This may later reduce the infiltration of water into the substrate by increasing evaporation and/or runoff (Scott *et al.* 1993). Conversely, a late snowmelt was reported to delay the onset of mat growth in *D. integrifolia* at one site and lower fruiting success as a result of the short growing season (Hart and Svoboda 1994). Likewise, Beck *et al.* (2005) have shown from their predictive habitat distribution model around the fjord Kongsfjorden, Svalbard, that the occurrence of *D. octopetala* was inversely related to snow and water cover as well as exposure toward the north aspect.

This was illustrated in our results by the negative correlation between radial growth and June $_{t}$ snowfall. An exceptionally early or late snowmelt may therefore have negative consequences to the growth of *D. integrifolia*.

Our results showed that the reconstructed tree-ring index from 1978 to 1999 using the monthly weather variables: October $_{t-1}$ minimum temperature, May $_{t}$ precipitation, August $_{t}$ maximum temperature and June $_{t-1}$ snowfall, showed that *D. integrifolia* readily respond to climatic signals in the Churchill region. The similarity of the reconstructed tree-ring index to that of the residual chronology demonstrates that dendroclimatological techniques can be applied to *D. integrifolia* with success and builds greater confidence for the use of shrubs in this field.

5.0 Conclusion

A strong and consistent allometric relationship between mat and stem diameter was observed among sites but the relationships between both mat and stem diameter and root length were found more variable except at site-A, which developed on a recent road. In addition, the Mean dieback of *D. integrifolia* was found to be a better indicator of age than MD1. Growth rates were shown to be variable within and between sites with the much younger *D. integrifolia* at site-A exhibiting markedly higher growth rates. *Dryas integrifolia* required less time to develop comparable dimensions at site-A and it was speculated that the more recently disturbed substrate at this site was an influencing factor. More studies are needed, however, to assess the influence of microsite conditions on growth. These might include more complete measurements of belowground biomass in addition to the collection of data on substrate quality.

It was found that *D. integrifolia* near Churchill, Manitoba could be cross-dated and that their annual growth increments displayed a similar correlation to climate to that of white spruce, black spruce and tamarack in the area, especially regarding the impact of October climatic conditions on growth. In addition, a reconstructed tree-ring index was created using four monthly climatic variables, which had accounted for much of the variability in the residual chronology. These findings add to the growing literature regarding the use of shrubs in dendroclimatology demonstrating that past climatic information can be obtained from the dwarf shrub, *D. integrifolia*, in sub-arctic Manitoba and may be applied to higher latitudes where no weather stations exist.

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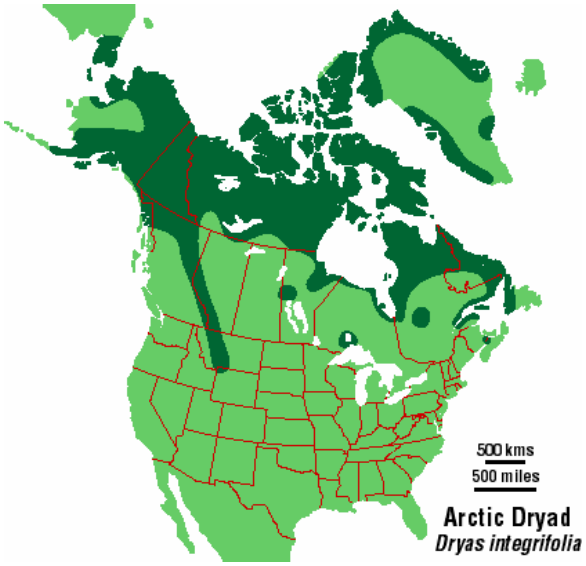
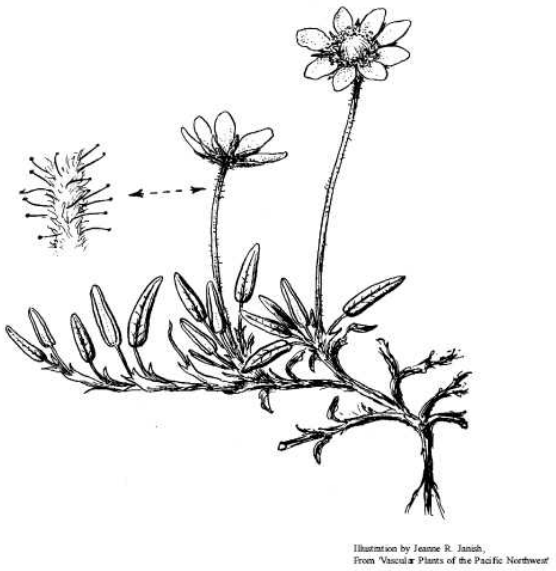
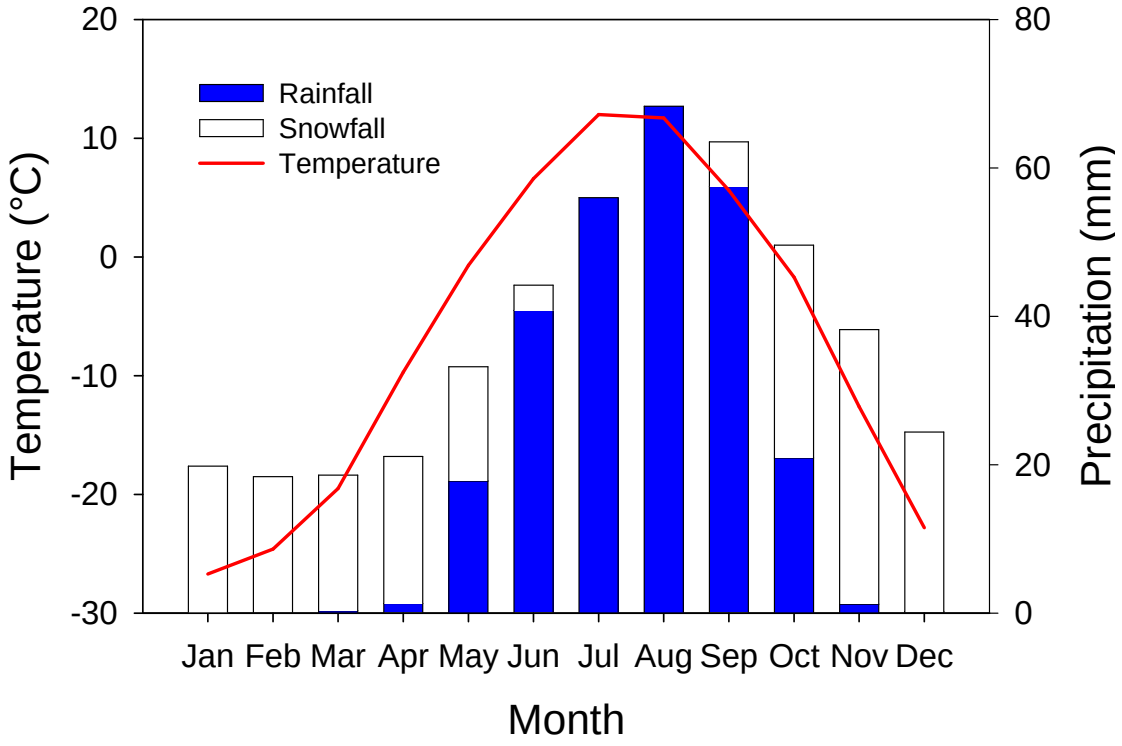
Appendices



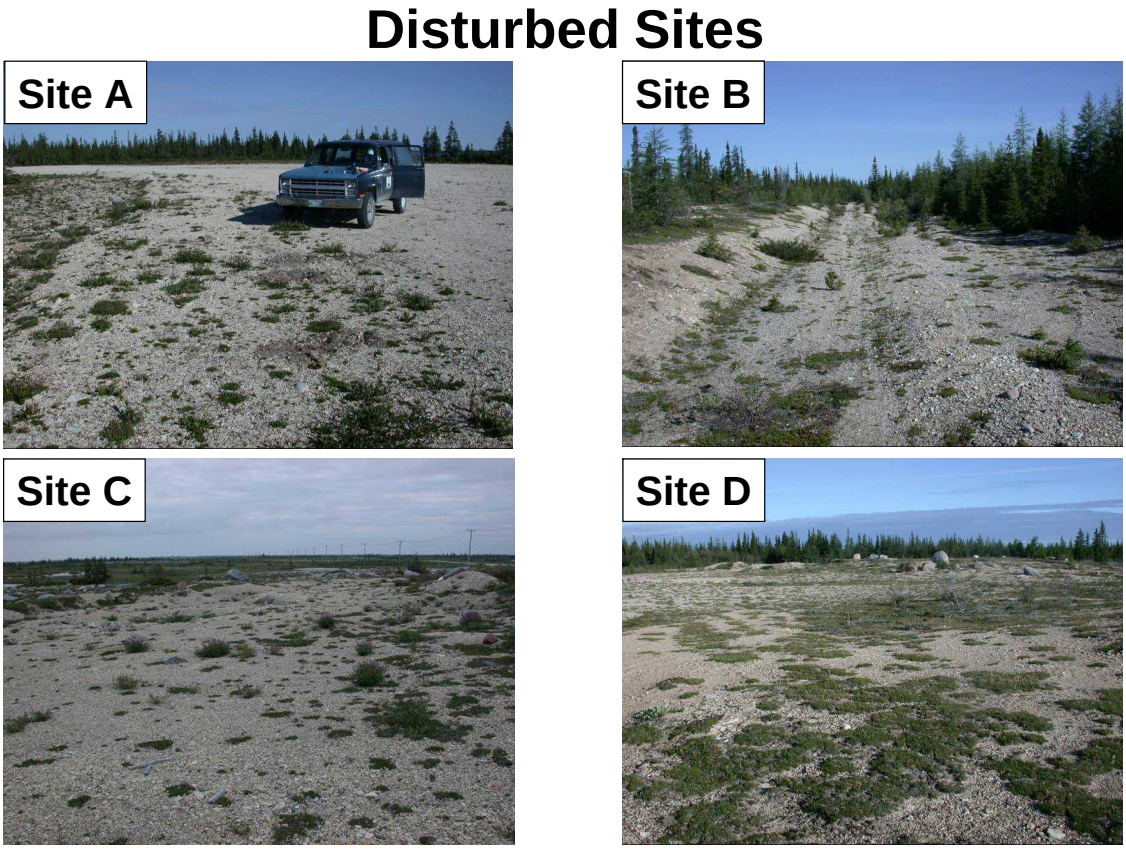
Appendix A. The distribution of the dwarf shrub, *Dryas integrifolia* in North America and Greenland. Source: http://plantwatch.sunsite.ualberta.ca/plants/images/ whi_dry_ disa.gif



Appendix B. A sketch of *Dryas integrifolia*
Source: http://nhp.nris.state.mt.us/plants/illust/sid873i.pdf



Appendix C. Mean monthly total snowfall, total rainfall and daily temperature in Churchill, Manitoba from 1971 to 2000.



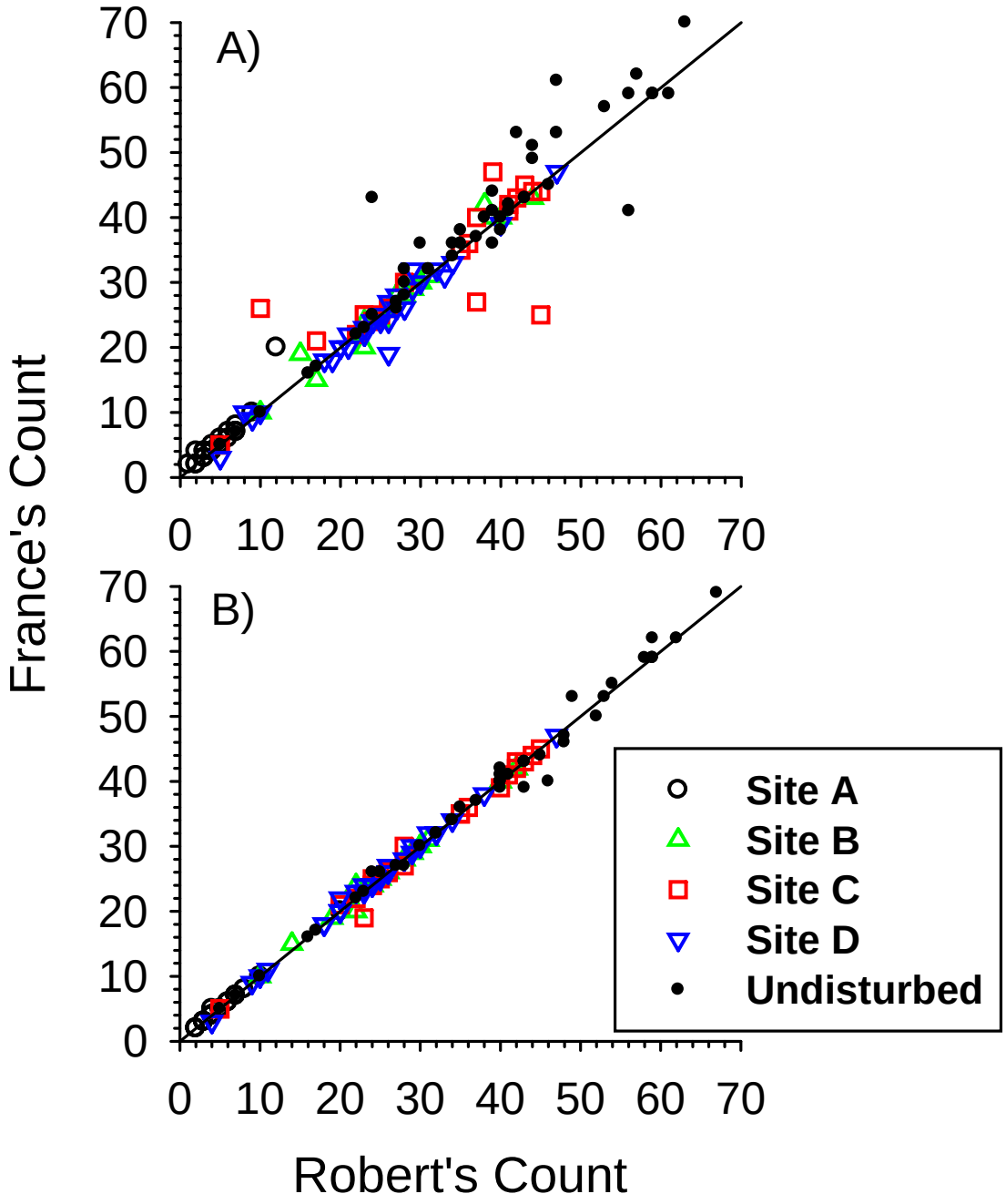
Appendix D. The four disturbed sites where *Dryas integrifolia* were sampled.

Appendix E. Number of *Dryas integrifolia* sampled at sites -A, -B, -C and -D according to diameter class (Total=98). Plants appearing in parenthesis were discovered growing together in the same mat and classified as separate individuals according to their MD1. Shrubs possessing as least one flower were distinguished from those that had none.

	Site A		**Site B**		**Site C**		**Site D**	
Diameter classes (cm)	Flower	No flower	Flower	No flower	Flower	No flower	Flower	No flower
0-5	0	4 (1)	0	2	0	2	0	4
5-10	0	2 (2)	1	1	2	1	2	2
10-15	2	2 (1)	1	1	1	1	2	2
15-20	2	2	1	1	1	1	2	2
20-30	2	0	2	1	2	1	6	0
30-40	1	0	2	0	4	2	4	0
40-50	3	0	2	0	3	0	2	0
50-100	1	0	2	0	2	0	2	0
>100	0	0	2	0	0	0	1	0
Total:	**11**	**14**	**13**	**6**	**15**	**8**	**21**	**10**
Grand Total:	**25**		**19**		**23**		**31**	

Appendix F. Ecological variables measured for each *Dryas integrifolia*. Information regarding which measurements were derived in the field, in the laboratory or from image analysis is specified with an "X".

Variable	**Place of Measurement**		
	Field	**Lab**	**Image analysis**
Longest mat diameter (MD1) (cm)	X		
Mat diameter perpendicular to MD1 (MD2) (cm)	X		
Mat dieback (%)	X		
Flower abundance	X		
Presence of lateral rooting branches (LRB)	X		
Richness of vascular and non-vascular plants	X		
Taproot diameter (TRD) (mm)	X		
Taproot length (cm)	X		
Longest mat diameter (D1) (cm)			X
Mat diameter perpendicular to D1 (D2) (cm)			X
Mat area (MA) (cm^2)			X
Mat perimeter (MP) (cm)			X
Mat dieback (%)			X
Longest stem diameter (SD1) (mm)		X	
Short stem diameter (SD2) (mm)		X	
Age		X	



Appendix G. Comparison of age determination of *Dryas integrifolia* by two people for the first (A) and second (B) trials. The black line indicates a perfect relationship between age counts.

Appendix H. Pearson correlations among mat diameter measurements (A), stem diameter measurements (B) and dieback measurements (C) in *Dryas integrifolia* near Churchill, Manitoba. Correlation coefficient and number of observations (below) are indicated for each analysis.

A (Mat diameter)						
	MD1	MD2	Mean field diameter	D1 (WinFolia)	D2 (WinFolia)	Mean diameter (WinFolia)
MD1	1.000 101	0.989* 101	0.998* 101	0.988* 97	0.991* 97	0.996* 97
MD2	0.989* 101	1.000 101	0.997* 101	0.987* 97	0.984* 97	0.993* 97
Mean field diameter	0.998* 101	0.997* 101	1.000 101	0.990* 97	0.991* 97	0.997* 97
D1 (WinFolia)	0.988* 97	0.987* 97	0.990* 97	1.000 97	0.973* 97	0.994* 97
D2 (WinFolia)	0.991* 97	0.984* 97	0.991* 97	0.973* 97	1.000 97	0.993* 97
Mean diameter (WinFolia)	0.996* 97	0.993* 97	0.997* 97	0.994* 97	0.993* 97	1.000 97
B (Stem diameter)						
	SD1	SD2	MSD	TRD		
SD1	1.000 122	0.979* 122	0.996* 122	0.950* 99		
SD2	0.979* 122	1.000 122	0.994* 122	0.942* 99		
MSD	0.996* 122	0.994* 122	1.000 122	0.952* 99		
TRD	0.950* 99	0.942* 99	0.952* 99	1.000 99		
C (Dieback estimation)						
	WinFolia dieback	Field dieback	Mean dieback			
WinFolia dieback	1.000 102	0.849* 99	0.961* 102			
Field dieback	0.849* 99	1.000 99	0.962* 99			
Mean dieback	0.961* 102	0.962* 99	1.000 102			

*. p-value < 0.001 (2-tailed)

MD1: Longest mat diameter measured in the field; MD2: a second diameter taken perpendicular to MD1; D1: longest mat diameter calculated in WinFolia; D2: length of the perpendicular diameter to D1 in WinFolia; SD1: longest stem diameter; SD2: stem diameter taken perpendicular to SD1; TRD: taproot diameter (field).
Mean field diameter was produced by the mean of MD1 and MD2; Mean diameter (WinFolia) was produced by the mean of WinFolia (D1) and WinFolia (D2); MSD: Mean stem diameter was produced by the mean of both long and short stem diameters; Mean dieback was generated by the mean of dieback estimation from both WinFolia and in the field.