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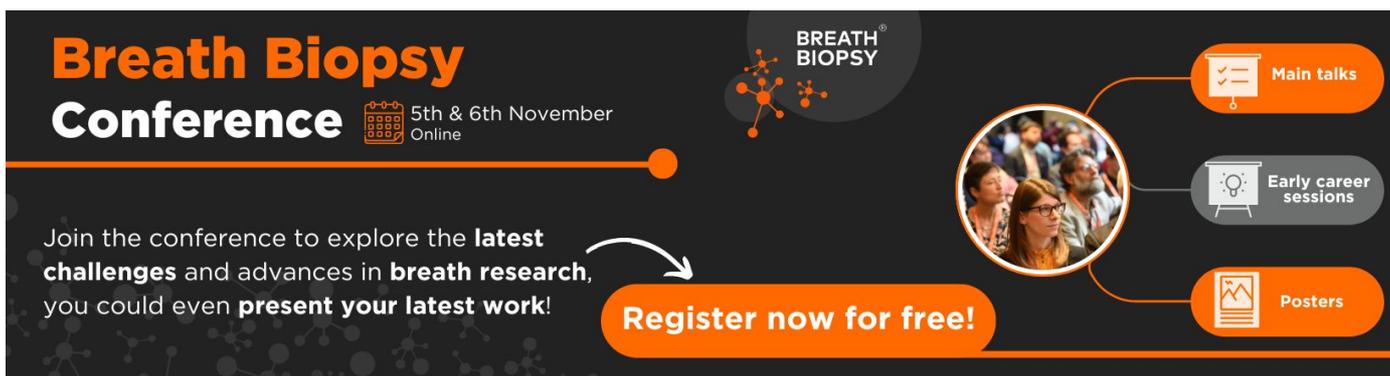
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Patterned-ground facilitates shrub expansion in Low Arctic tundra

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Abstract

Recent expansion of tall shrubs in Low Arctic tundra is widely seen as a response to climate warming, but shrubification is not occurring as a simple function of regional climate trends. We show that establishment of tall alder (*Alnus*) is strongly facilitated by small, widely distributed cryogenic disturbances associated with patterned-ground landscapes. We identified expanding and newly established shrub stands at two northwest Siberian sites and observed that virtually all new shrubs occurred on bare microsites ('circles') that were disturbed by frost-heave. Frost-heave associated with circles is a widespread, annual phenomenon that maintains mosaics of mineral seedbeds with warm soils and few competitors that are immediately available to shrubs during favorable climatic periods. Circle facilitation of alder recruitment also plausibly explains the development of shrublands in which alders are regularly spaced. We conclude that alder abundance and extent have increased rapidly in the northwest Siberian Low Arctic since at least the mid-20th century, despite a lack of summer warming in recent decades. Our results are consistent with findings in the North American Arctic which emphasize that the responsiveness of Low Arctic landscapes to climate change is largely determined by the frequency and extent of disturbance processes that create mineral-rich seedbeds favorable for tall shrub recruitment. Northwest Siberia has high potential for continued expansion of tall shrubs and concomitant changes to ecosystem function, due to the widespread distribution of patterned-ground landscapes.

Keywords: shrubification, patterned-ground, tundra, alder, facilitation, Siberia, vegetation patterns, permafrost, frost heave, *Alnus*, alder-savanna

 Online supplementary data available from stacks.iop.org/ERL/8/015035/mmedia



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1. Introduction

The expansion of deciduous shrubs is one of the primary land-cover changes that is being observed and projected to accelerate with climate warming in Arctic terrestrial

ecosystems. Observations of this phenomenon have been reported, mostly in North America (Sturm *et al* 2001, Tape *et al* 2006, Myers-Smith *et al* 2011, Lantz *et al* 2012, Ropars and Boudreau 2012, Tremblay *et al* 2012), and are corroborated by experimental field studies (Chapin *et al* 1995, Walker *et al* 2006). Shrub expansion is thought to be a major driver of widespread increases in the productivity of Arctic vegetation observed from space since the early 1980s (Jia *et al* 2003, Bhatt *et al* 2010), and future projections of shrub increase are supported by simulation modeling (Epstein *et al* 2007, Yu *et al* 2011). Shrubland expansion fundamentally changes biophysical properties of tundra ecosystems, affecting surface energy balance (Chapin *et al* 2005, Marsh *et al* 2010), hydrology (Sturm *et al* 2005), nutrient cycling (Buckeridge *et al* 2010, Kaarlejärvi *et al* 2012) biodiversity (Pajunen *et al* 2011) and permafrost temperature (Blok *et al* 2010), as well as wildlife and human land-use (Forbes *et al* 2009, Ehrich *et al* 2012). In warmer parts of the Low Arctic, expansion of tall shrubs (>1.5 m height), chiefly alders, birches (*Betula*), and willows (*Salix*), represents a biome shift from tundra to tall shrubland.

At large spatial and temporal scales, summer temperature is the primary factor controlling the extent of the Arctic tundra biome, and the zonation of vegetation within the biome (Walker *et al* 2005). Landscape-scale responses of tundra vegetation to changes in summer temperature near the biome's southern margin, however, can vary dramatically due to complex interactions between climate and local environmental factors, such as soil environment, hydrology, permafrost, and disturbance regime (Naito and Cairns 2011, Ropars and Boudreau 2012, Tape *et al* 2012). Recent studies have found that episodic disturbance events such as wildfire, landslides, and permafrost thaw can trigger the expansion of tall shrubs by creating mineral-rich soils that favor shrub recruitment (Racine *et al* 2004, Walker *et al* 2009, Lantz *et al* 2009, 2010), with little or no change observed in adjacent areas of undisturbed tundra. Thus, the northward expansion of tall shrubs may be greatly limited at local to regional scales by the frequency of disturbance events—on the order of many decades or centuries—that create suitable substrates for shrub recruitment (Racine *et al* 1985, Myers-Smith *et al* 2011).

One aspect of tall shrub distribution in tundra landscapes that has received relatively little study concerns the spatial distribution of individuals *within* shrubland communities. Alder-dominated shrublands in the southern Low Arctic (Bioclimate Subzone *E* of the Circumpolar Arctic Vegetation Map Walker *et al* 2005) frequently exhibit unusual spatial distributions of individual shrubs, in which alders occur as regularly spaced individuals or *clumps* of individuals, that overtop typical tundra shrubs, graminoids, and mosses (figure 1). Such shrubland communities, colloquially referred to as 'alder savannas', have been described at several locations in Low Arctic and interior montane Alaska (Racine 1976, Racine and Anderson 1979, Chapin *et al* 1989). Regular spacing of alders in 'alder savannas' has been attributed to intra-specific competition for limiting nutrients (Chapin *et al* 1989), but recent work highlighting the role of local geomorphology and disturbance in driving landscape-scale



Figure 1. Aerial view of alder shrubland or 'savanna' in which alders are regularly spaced, Selawik River area, northwest Alaska. Photo courtesy Matthew J Macander.



Figure 2. Patterned-ground with young alders growing on circles, Obskaya site, northwest Siberia.

variability in shrub recruitment suggests that regular spacing of alders could also be linked to patterns of shrub recruitment on geomorphic microsites in permafrost patterned-ground that exhibit regular spacing at similar scales.

We integrated a remote-sensing data record spanning five decades, with field-based measurements to elucidate the role of local mechanisms, related to permafrost geomorphology, soils, and disturbance processes, in promoting tall shrub expansion in the northwest Siberian Low Arctic. In the areas that we studied, alder recruitment is closely linked to small, bare microsites within extensive patterned-ground landscapes (figure 2). Here we describe a mechanism for the expansion of tall alder, whereby annual, meter-scale disturbance processes in patterned-ground maintain a mosaic of microsites that facilitate shrub recruitment across contiguous areas of tundra during periods of favorable climate. The facilitation of alder recruitment on regularly spaced microsites, in turn, promotes the development of tundra shrub communities in which alders are regularly spaced.

2. Methods

2.1. Study area

We studied changes in Siberian alder (*A. viridis* ssp. *fruticosa*) extent at two ecotonal landscapes near the towns of Kharp

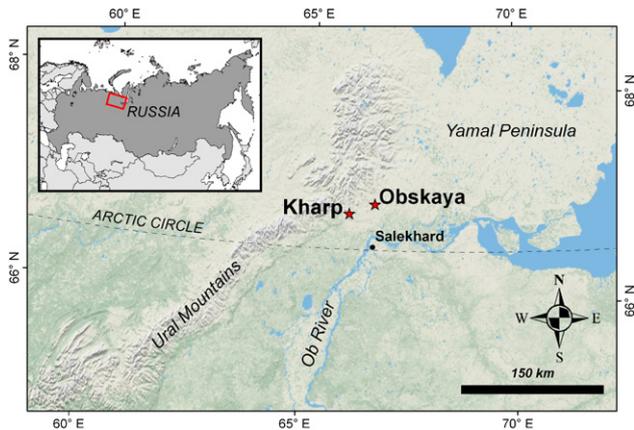


Figure 3. Map of southern Yamal Peninsula region, Russia, showing locations of Kharp and Obskaya study sites and other places mentioned in the text.

(66.83°N, 65.98°E) and Obskaya (66.92°N, 65.61°E), Russia (figure 3). The Kharp and Obskaya study landscapes are 64 km² and 59 km² in area, respectively. Both sites are located in the eastern foothills of the northern Ural Mountains near the lowermost reach of the Ob River. Terrain features in the study areas consist of low, gently sloping uplands separated by small alluvial valleys within an elevation range of ~200–300 m. Common vegetation types include dwarf-shrub tundra, low birch-ericaceous shrubland (shrubs ≤ 1 m height), and tall alder shrubland (shrubs > 1.5 m height). Sparse stands of Siberian larch (*Larix sibirica*) occur locally at lower elevations. The region experiences a continental, sub-Arctic climate; long-term meteorological records (1883–2011) at Salekhard, ~40 km southeast of the study sites, indicate a mean annual temperature of -6.3 °C, mean summer (June–August) temperature of 11.2 °C, and mean annual precipitation of 464 mm. Soils and geomorphic features are similar at the sites; soils are rich in fine silts derived from mafic parent materials, permafrost is widespread, and active patterned-ground features are abundant. However, the sites have contrasting disturbance histories; the Kharp site experienced a severe wildfire sometime before 1821 (based on examination of soil pits, and annual growth rings of living larch trees), while there is no evidence of historical wildfire at Obskaya.

Patterned-ground features (PGFs) are characteristic of permafrost-dominated regions of the world and are widely distributed throughout the Pan-Arctic (Washburn 1980, Walker *et al* 2008). ‘Circles’, often termed ‘frost-boils’, are a common PGF that occur as approximately circular patches of mineral soil within a highly symmetrical mosaic of microsites, repeating at intervals of ~1–3 m. Circles develop due to meter-scale biogeophysical processes during seasonal freezing that cause differential frost-heave (DFH), with enhanced frost-heave of circles relative to adjacent areas (‘inter-circles’) (Taber 1929, Peterson and Krantz 2003). As soils freeze each winter, complex interactions occur among soil, water, ground-ice, live vegetation, organic matter, and snow cover that cause downward freezing to proceed more rapidly at exposed surfaces relative to vegetated

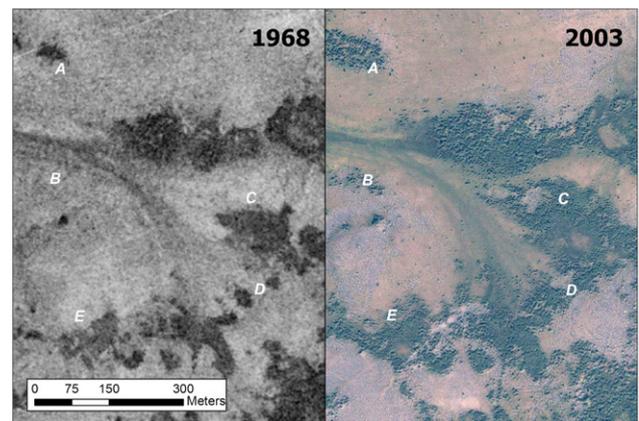


Figure 4. Comparison of 1968 (Corona) and 2003 (QuickBird) satellite images showing representative area of recent shrub expansion at Kharp site. Letters indicate alder stands that are expanding (A, C–E) or newly established (B). Alder cover increased 29% within the 0.5 km² area shown. QuickBird image copyright Digital Globe, Inc.

areas, resulting in DFH and a self-organizing pattern of bare circles surrounded by vegetation (see supplementary figure 1 available at stacks.iop.org/ERL/8/015035/mmedia). Vegetation and organic matter are key controls of DFH because they shade and insulate the subsurface; an uneven distribution of vegetation promotes sharp contrasts in microsite thermal regimes. PGFs tend to be less conspicuous in the southernmost Low Arctic and northern boreal forest, where warmer summer temperatures promote vegetation growth and DFH is inhibited by the buildup of a continuous organic mat (Walker *et al* 2004, Kade and Walker 2008).

2.2. Methods

We quantified changes in tall shrub extent at Kharp and Obskaya over the past ~40 years using high-resolution satellite imagery from 1968 and recent years: panchromatic KH-4B ‘Corona’ imagery from 19 August 1968, and multi-spectral QuickBird and IKONOS imagery and panchromatic WorldView-1 imagery from 2003 to 2010. We co-registered the imagery and overlaid a grid of sampling points spaced 30 m apart for each site using ArcMap 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA). We recorded the number of sampling points with alder shrubland cover in 1968 and 2010 by visual interpretation of the imagery; due to their dark leaves and extensive canopy shadowing, alders produce a dark photo-signature that is readily identified in high-resolution (≤2 m pixel) imagery of tundra-dominated areas (figure 4). We recorded modern shrub cover mainly from 2010 imagery, but used imagery from 2003 to 2004 for some areas that had partial snow cover in the 2010 imagery. From the sampling-point data, we calculated the total areal extent of alder shrublands in 1968 and 2010, and calculated the per cent difference in alder ‘hits’ between 1968 and 2010. We also identified expanding and stable shrub stands for field visits.

In the field, we collected soil and vegetation data at the Kharp site to test if alder recruitment was facilitated by

circles, and if shrub distribution in older stands was linked to underlying, inactive circles that were covered by vegetation. Because DFH is largely driven by uneven distribution of vegetation between circles and inter-circles, the development of a continuous vegetation mat (e.g., as with shrub expansion) attenuates DFH. Active circles are easily recognized, but over time they can become covered by vegetation and cannot be visually identified if DFH has ceased. Subsurface soils remain strongly sorted, however, and we used simple measurements of two soil variables—surface organic depth and total thickness of mineral soil—to infer the presence of inactive circles. We also established transects in older shrub stands (i.e., those that were already evident in the 1968 satellite imagery) in order to test if the spatial distribution of mature shrubs could be explained by recruitment on circles. We did not make systematic field measurements at Obskaya, but we made qualitative observations there to determine if relationships between alder expansion and PGFs were consistent with those observed at Kharp, and to assess the disturbance history of the site.

We stratified shrub stands into three categories of stand-age: colonization zone, mature, and paludified. Colonization zones lacked shrub cover in 1968 Corona imagery and are mostly dominated by small alders (≤ 1.5 m height). Mature stands were dominated by large shrubs (> 2 m height) that were already present in 1968, and most patterned-ground microsites were concealed by vegetation and organic matter. Paludified stands were also present in 1968 imagery, but were dominated by older, largely moribund shrubs and virtually all patterned-ground was concealed by a thick layer of moss and organic material. Although we did not age shrub ramets, shrubs in paludified stands have numerous characters that indicate greater age and reduced vigor relative to shrubs in mature stands, including dead ramets, reduced ramet height, short internode length, and abundant annual abscission scars. We established a total of 19 transects: 12 in colonization zones, 3 in mature stands, and 4 in paludified stands. Transect length varied from 20 to 100 m depending on the size and density of circles and alders; we established larger transects where shrubs and circles were widely spaced.

We measured surface organic depth and thaw-depth/depth-to-rock using a steel thaw-probe at 1 m intervals along the transect centerline, and at the base of the alder nearest to the transect sampling-point, regardless of size, on all transects. Due to the rocky soils, thaw-probe measurements usually hit frost-shattered rock rather than the permafrost table. We determined the total thickness of mineral-dominated soil horizons by subtracting the surface organic thickness from the thaw-depth/depth-to-rock measurement. We also recorded the age class of each alder as seedling (≤ 5 cm height), sapling (≤ 75 cm height and not reproductively active), or adult (reproductively active and usually > 75 cm height). Finally, we deployed 53 iButton thermochron dataloggers (Embedded Data Systems LLC, Lawrenceburg, USA) at 5 cm depth to obtain daily soil temperature time-series at circles (with alders) and at inter-circles (without alders) for each shrub stand-age; an additional 4 iButtons recorded air temperature at a height of 2 m. We also obtained soil temperature time-series

Table 1. Total alder cover in 1968 and 2010, and areal and relative changes in alder cover (1968–2010), at Kharp and Obskaya study sites.

Site	Total alder cover (ha)			Relative change (%)
	1968	2010	Δ	
Kharp	721	779	58	8.0
Obskaya	482	583	101	21.0

at circles and inter-circles in alder-free tundra adjacent to colonization zones. All iButtons recorded temperature simultaneously at 4 h intervals. We then calculated the mean temperature for each 4 h time-step, for each category of microsite and stand-age.

In colonization zone transects, circle microsites were easily recognized (i.e., not covered in vegetation), so we recorded the microsite from which alders emerged according to three categories: circle center, circle margin, and inter-circle. At three of these transects, we mapped the locations of alders and circles using X/Y coordinates and recorded organic depth and thaw-depth/depth-to-rock at every alder in the transect area, in addition to the transect centerline measurements.

We conducted statistical analyses of soil physical attributes and temperature using SAS 9.2 (SAS Institute Inc., Cary, USA). After testing variables for normality, we employed two-tailed t -tests and non-parametric Kruskal–Wallis tests for comparisons as appropriate. We also calculated the nearest-neighbor distance ratio (NNDR), a spatial statistic that identifies spatial distribution patterns (e.g., random, uniform, clumped), for the transect maps of alder and circle location.

In order to characterize the recent climate history of the study sites, we derived a time-series of mean growing-season temperature (June–August; hereafter, ‘JJA’) from ground station data recorded ~ 40 km southeast at Salekhard. We calculated JJA temperature from mean monthly temperature datasets downloaded from the National Climatic Data Center (NCDC, www.ncdc.noaa.gov/land-based-station-data) and evaluated linear trends in JJA temperature for the entire period-of-record (1883–2011). We also evaluated linear trends for 1965–2011, which encompasses the time interval examined in the satellite imagery comparisons; we included three preceding years to account for short-term effects of preceding summer temperatures on viable seed production by pre-existing, mature shrubs. Due to the difference in elevation between the study sites (~ 250 m) and Salekhard (66 m), we adjusted the mean monthly temperature values using a temperature lapse rate of $-6.2^\circ\text{C km}^{-1}$ generated for a sub-Arctic region of Alaska (Haugen *et al* 1971).

3. Results

Comparisons of high-resolution satellite imagery from 1968 to 2010 indicate extensive areal expansion of tall alder at both sites. The total cover of alders increased 8.0% at Kharp and 21.0% at Obskaya (table 1). Although many individual shrub stands did not expand, we detected no areal loss of shrub cover at either site.

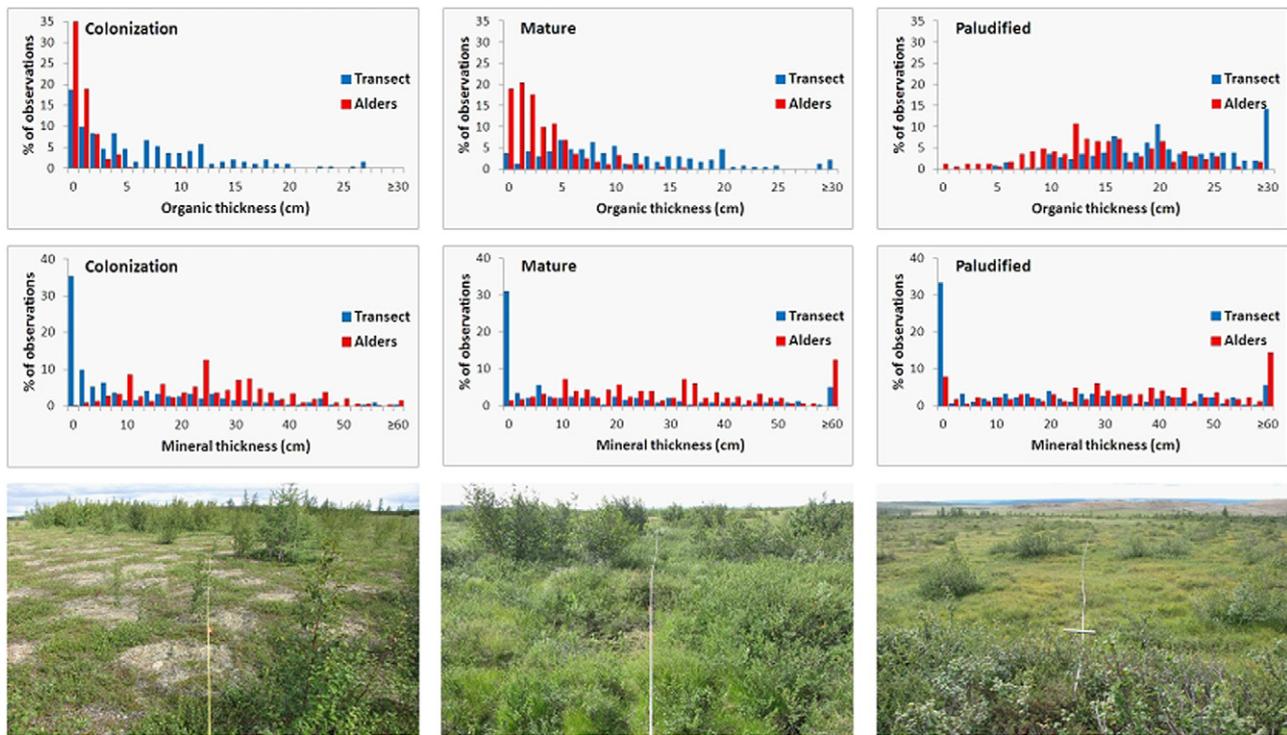


Figure 5. Soil characteristics in alder stands of varying age, shown as frequency distributions of organic thickness (top row) and total mineral horizon thickness (middle row) along transects and at alders in colonization zones (left column), mature stands (center column), and paludified stands (right column). Mineral horizon thickness is binned in 2 cm increments. Photos of each stand-age are also shown (bottom row).

Table 2. Median values of soil organic depth, mineral soil thickness, and sample sizes measured along transects and at adjacent alders at Kharp. Organic depth is significantly less, and mineral thickness significantly greater, at alders compared to transects for all stand-ages ($p < 0.001$).

Stage	Organic depth (cm)		Mineral thickness (cm)		Number of observations	
	Transect	Alders	Transect	Alders	Transect	Alders
Colonization	4.5	0.	4.0	24.0	252	630
Mature	9.0	1.0	6.0	33.0	235	279
Paludified	20.0	14.0	15.5	33.0	254	166

In the field, we observed at both sites that nearly all shrub expansion occurred in patterned-ground, and that shrub recruitment had occurred almost exclusively on active circles that lack vegetation and organic material; mean surface organic depth is significantly lower, and mineral thickness greater, at alders compared to the uniform transect measurements for all three shrub stand-ages (Kruskal–Wallis test; $p < 0.001$ for all transects) (table 2). In colonization zones, virtually all alders occur where surface organic material is thin or lacking altogether; >85% of alders occurred at sites with <3 cm of surface organic material; sites with <3 cm of organic matter comprised <30% of available sites (figure 5). In older shrub stands, contrasts in soil properties between alders and uniform transect measurements were qualitatively similar to those found in colonization zones; alders tended to occur where there was less surface organic matter and mineral soil thickness was high. Organic depth increases throughout stand development, indicating the accumulation of an organic mat on the circles and the cessation of DFH.

The spatial distribution of shrubs within transects in colonization zones shows that shrub recruitment is tightly linked to active circles in patterned-ground (figure 6). Shrub recruitment declines as stands mature and essentially ceases in paludified stands (table 3). Spatial statistics of shrub distribution using the NNDR indicate that young alders are found in evenly spaced clumps that co-occur with circles. The NNDR at 3 transects in colonization zones indicates that young alders are highly clumped (mean Z-score = -16.1; $p < 0.001$ for all transects), while circles are evenly spaced (mean Z-score = 6.9; $p < 0.001$ for all transects). Although we only mapped the locations of alders and circles along three 80 m² transects at Kharp, we repeatedly observed that alders were concentrated at circles in areas of recent shrub expansion throughout both study areas.

In tundra and colonization zones, mean near-surface soil temperatures at circles are warmer than at inter-circles (t -test; $p < 0.05$) (figure 7). This microsite pattern is reversed in paludified stands (t -test; $p < 0.05$), and soil temperatures do not differ significantly between microsites in mature stands.

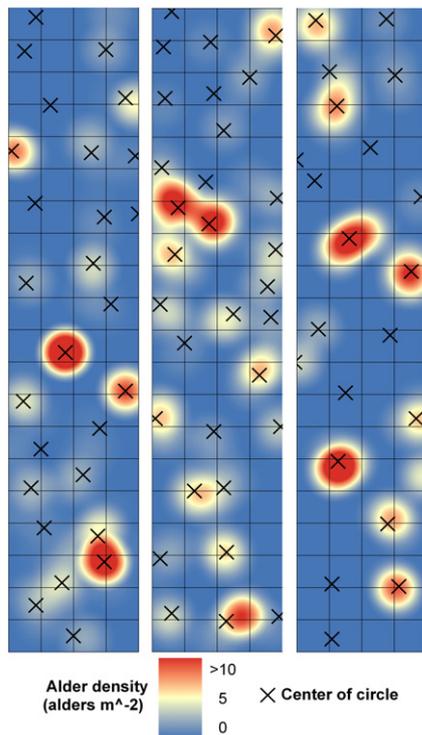


Figure 6. Maps of circle distribution and alder density for three 4 × 20 m transects, showing locations of circle centers and density of alders. Each square is 1 m².

Table 3. Relative abundance of shrub age classes, by shrub stand-age, at the Kharp site.

Stage	Age class		
	Seedling (%)	Sapling (%)	Adult (%)
Colonization	43.7	39.7	16.7
Mature	30.1	22.3	47.6
Paludified	0	7.9	92.1

Across stand-ages, mean soil temperature at circles declines from one category of stand-age to the next (*t*-test; *p* < 0.05).

4. Discussion

Our field observations, coupled with satellite observations dating to 1968, demonstrate direct linkages between disturbance processes in patterned-ground and the recruitment of individual alders and increases in the abundance and areal extent of tall shrub patches in the southern Yamal region. This finding is consistent with other studies that have linked tundra shrub increase to biotic and abiotic disturbance mechanisms that remove or suppress competing vegetation and promote mineral-rich substrates, such as wildfire, landslides, permafrost thaw, fluvial processes, and animals (e.g., Racine *et al* 2004, Tape *et al* 2006, Lantz *et al* 2009, Tremblay *et al* 2012). One implication of these studies is that the susceptibility of tundra landscapes to climate-induced vegetation changes in general, and to shrubification in particular, largely hinges on the frequency of disturbances and the spatial scale at which they operate.

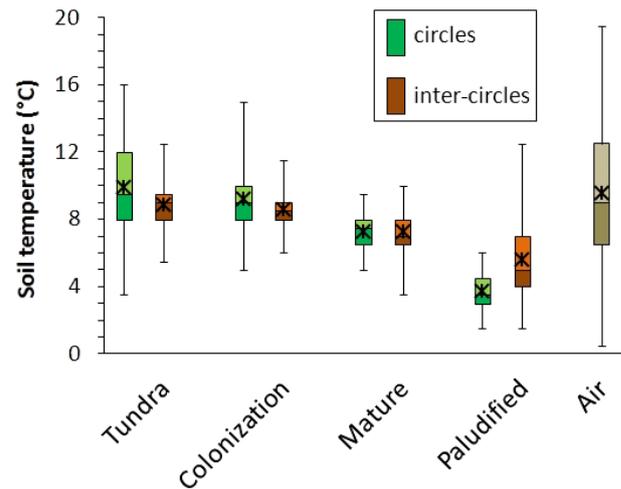


Figure 7. Mid-summer 5 cm soil temperatures. Measurements were taken at Kharp at 4 h intervals from 24 July to 1 August 2011, at circles and inter-circles, by stand-age; box-and-whisker plots indicate range, 1st and 3rd quartiles, median, and mean values (black markers).

As a disturbance mechanism, DFH in patterned-ground is unusual because of its temporal and spatial attributes. First, unlike ‘pulse’ disturbances that occur episodically on multi-decadal or centennial timescales, DFH occurs annually and thereby maintains mineral-rich microsites that are continually available for shrub recruitment. Second, although individual microsites are no more than a few meters in size, DFH is linked to large, contiguous areas where soils and topography are favorable, such as in gently sloping terrain with unsaturated, silt-rich soils. These spatio-temporal attributes promote the development of extensive mosaics of mineral substrates that not only favor shrub recruitment, but are also immediately available to shrubs during periods of favorable climate.

The close correspondence between alder and evenly spaced patterned-ground microsites plausibly explains the development of alder shrublands with evenly spaced shrubs (or evenly spaced *clumps* of shrubs), commonly termed ‘alder savannas’, in disparate parts of the Low Arctic. Nutrient limitation has been identified as a mechanism for regular spacing of alders in interior Alaska (Chapin *et al* 1989), but we find that in the areas that we studied, such communities are strongly predisposed to regular spacing of shrubs at the recruitment stage. The development of these shrublands, in turn, initiates a cascade of powerful feedbacks in patterned-ground landscapes, beginning with the attenuation of DFH, followed by the establishment of continuous vegetation cover, a decline in summer soil temperatures, and the accumulation of organic matter, with implications for permafrost thermal regime, soil hydrology, and carbon balance. These feedbacks warrant further study, particularly in view of the large areal extent and abundance of patterned-ground landscapes in northwest Siberia and elsewhere in the circumpolar Arctic.

Virtually all of the tall shrub expansion that we observed at Kharp and Obskaya since 1968 is due to expansion of

alder. We find that circles are ‘hotspots’ for alder expansion for several reasons. Alder is minerotrophic (Zasada *et al* 1986) and has higher potential growth-rates than do typical arctic species; these high growth-rates, coupled with the lack of established competitors on circles, likely enable alder to successfully colonize cryoturbated soils despite seasonal DFH. Alder also hosts symbiotic nitrogen-fixing bacteria, which likely enhance growth on mineral-dominated substrates that might be low in N (Kaiser *et al* 2005). Finally, alders strongly modify the surrounding microenvironment due to their tall stature. By shading the ground surface, and by trapping insulating snow, the developing alder canopies quickly begin to suppress the microsite thermal gradients that drive DFH. In other words, alders only experience strong DFH during the initial stages of shrubland development. These species traits—coupled with the warm summer soil temperatures on exposed circles—explain why alder successfully colonizes bare, cryoturbated microsites, where annual disturbance is too severe for slow-growing Arctic species. As DFH begins to decline, the establishment of understory vegetation—particularly mosses—promotes the accumulation of a continuous organic mat that further suppresses DFH. This feedback explains the lack of exposed circles in older stands. In paludified stands, DFH and shrub recruitment essentially cease: our satellite photo-comparisons revealed virtually no change in shrub distribution in paludified stands, despite conspicuous expansion in adjacent areas with active PGFs. The capacity of vegetation in paludified areas to respond to climate warming is probably very limited due to the cold soils and associated limitations on microbial decomposition and nutrient mineralization.

Meteorological records from Salekhard indicate that a warming summer climate has probably played a major role in shrub expansion observed since 1968 in this region. Growing-season temperature is the chief limitation on the growth of boreal trees and shrubs in tundra ecotones, with sharp increases in shrub abundance, growth, and reproduction evident above a threshold mean summer temperature of 10 °C (Alexandrova 1974, Lantz *et al* 2010). Mean summer temperature at Salekhard has warmed about 1 °C per century since 1883 ($p < 0.001$) (figure 8), a trend corroborated by growth-ring chronologies of tundra shrubs elsewhere in northwest Siberia (Forbes *et al* 2010). Strong warming occurred from the late 1960s to 2010—the satellite period-of-record examined here—with virtually all of the warming occurring from 1968 to 1980 ($p < 0.001$). Although summer temperatures have been highly variable and no trend is evident since 1980, mean summer temperatures have usually exceeded the 10 °C threshold (21 of 31 years); expansion of tall shrubs appears likely to continue in the areas we studied, even without additional increases in summer temperature.

The ecotonal landscapes we studied share very similar climate, soils, and geomorphology, but have different centennial-scale disturbance histories. Field observations indicated that virtually all of the Kharp site experienced severe wildfire at least 191 years ago, while there was no evidence of historical wildfire at the Obskaya site. These contrasting disturbance histories raise the question of

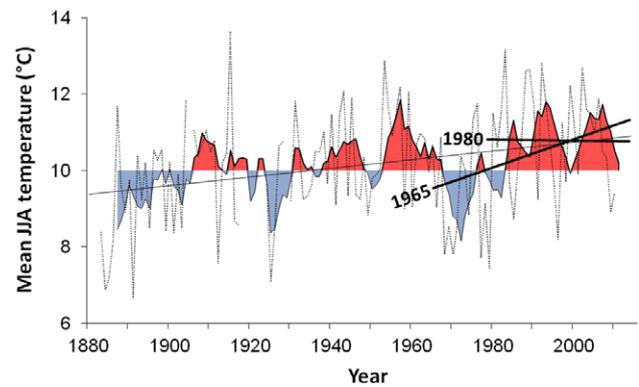


Figure 8. Time-series of mean June–August (JJA) temperature for Kharp and Obskaya. The dotted line indicates the raw values, the solid line indicates the 5 yr moving average, and linear trendlines are shown for 1883–2011, 1965–2011, and 1980–2011. Warm periods, in which the 5 yr moving average exceeds 10 °C, are colored red; periods below this threshold are colored blue.

whether the recent shrub expansion we observed at Kharp can be explained simply by alder colonization of burned substrates and successional processes after fire. We argue that neither the meter-scale patterns of shrub recruitment on circles, nor the landscape-scale patterns of shrub expansion in patterned-ground, can be readily explained by successional processes after historical fire. First, we recorded the largest increases in alder cover at the unburned Obskaya site, where microsite patterns of alder recruitment were identical to those observed at Kharp. Additionally, the increases in tall shrub abundance that we observed at Kharp occurred after at least 150 years of tundra vegetation development post-fire. Alder recruitment is rapid in early succession after fire in the boreal forest (Matthews 1992), and available information indicates that alder responds similarly following tundra fire (Lantz *et al* 2010). We suggest that a lag in the recruitment of alder exceeding 150 years is longer than would be expected at the Kharp site if other factors, such as patterned-ground processes or changes in climate, were not also involved. We conclude that the shrub expansion observed at Kharp probably occurred due to the interaction of climate effects on alder reproduction and growth, coupled with the wide availability of favorable seedbeds in active patterned-ground landscapes; however, historical wildfire probably played an important role in restoring DFH across much of the Kharp site, by removing vegetation and organic material from underlying patterned-ground.

PGFs are widespread in the northwest Siberian region and elsewhere in the Low Arctic, particularly where soils are silt-rich and prone to DFH (Walker *et al* 2008). Although the regional and circumpolar extent of active circles is difficult to quantify from space due to the small size of individual microsites, we conservatively estimate that active features cover ~35% of the landscapes that we studied. The distribution of active PGFs appears to be comparable in many other areas with high-resolution imagery across a ~1200 km belt of the northwest Siberian Low Arctic (supplementary figures 2 and 3 available at stacks.iop.org/ERL/8/015035/mmedia). Active patterned-ground is at least

locally common in many other areas of the Low Arctic, including the Brooks Range foothills of arctic Alaska (Walker *et al* 2008). Additionally, relic areas of patterned-ground, where DFH has been suppressed by the development of continuous vegetation and organic matter, are common and widespread in warmer parts of the Low Arctic; tundra fire in these areas could restore DFH and result in microsite recruitment patterns similar to those we have described here. Given alder's widespread distribution in the circumpolar Low Arctic, microsite facilitation of alder expansion in patterned-ground could account for the occurrence and spatial characteristics of shrublands in many other areas of the Low Arctic.

5. Conclusions

PGFs such as circles are widespread throughout the Arctic tundra biome. Our space- and field-based observations indicate that these features strongly facilitate tall shrubland development, and promote the development of shrubland communities in which alders are regularly spaced. We conclude that warmer parts of the Low Arctic that are rich in active PGFs are highly susceptible to shrub-induced biome shifts, because of the unusual spatio-temporal attributes of cryogenic disturbance in patterned-ground. DFH occurs annually, rather than episodically, and thereby maintains a mosaic of mineral substrates at the meter scale that are immediately available for shrub recruitment during periods of favorable climate. These mosaics can extend across large parts of the landscape where soils and topography are favorable, such as in gently sloping uplands with unsaturated, silt-rich soils. The northwest Siberian Low Arctic in particular appears highly susceptible to rapid, widespread, and persistent changes in ecological regime due to the ready availability of mineral-rich seedbeds in the extensive patterned-ground ecosystems of the region.

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