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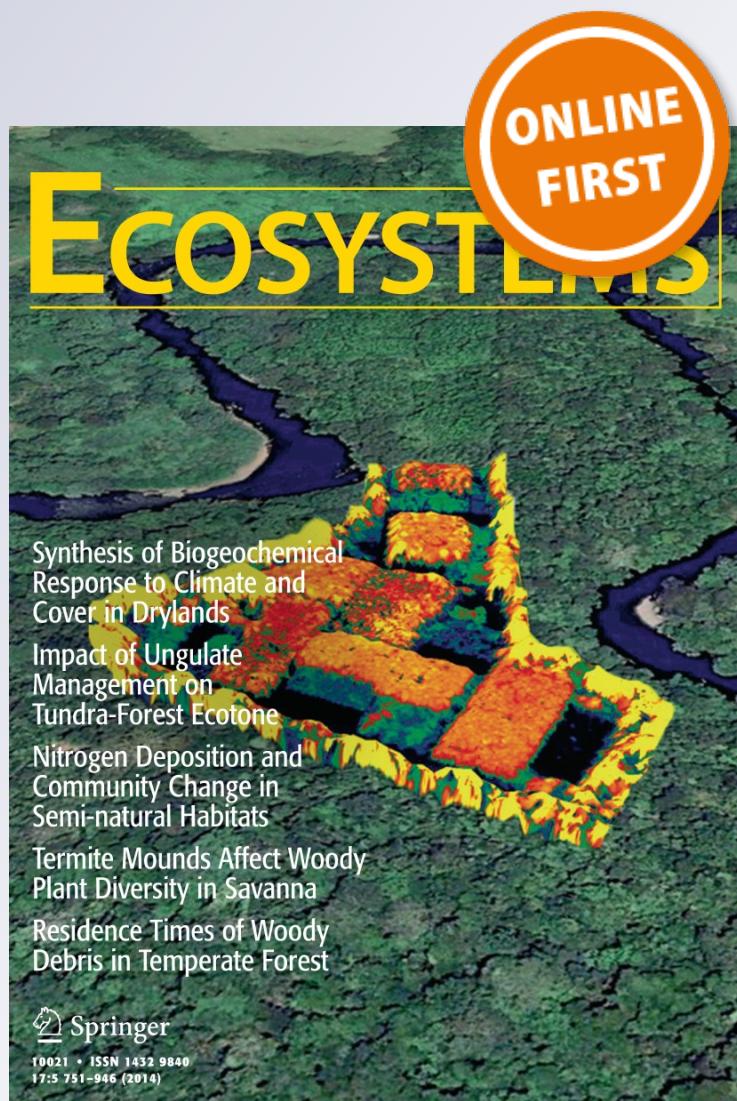
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Warming-Induced Shrub Expansion and Lichen Decline in the Western Canadian Arctic

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ABSTRACT

Strong evidence for a pan-Arctic expansion of upright shrubs comes from analysis of satellite imagery, historical photographs, vegetation plots, and growth rings. However, there are still uncertainties related to local-scale patterns of shrub growth, resulting interactions among vegetation functional groups, and the relative roles of disturbance and climate as drivers of observed change. Here, we present evidence that widespread and rapid shrub expansion and lichen declines over a 15,000 km² area of the western Canadian Arctic have been driven by regional increases in temperature. Using 30 m resolution Landsat satellite imagery and high resolution repeat color-infrared aerial photographs, we show that 85% of the land surface has a positive 1985–2011 trend ($P < 0.05$) in NDVI, making this one of the most intensely greening regions in the Arctic. Strong positive trends (>0.03 NDVI/decade) occurred consistently across all landscape

positions and most vegetation types. Comparison of 208, 1:2,000 scale vertical air photo pairs from 1980 and 2013 clearly shows that this greening was driven by increased canopy cover of erect dwarf and tall shrubs, with declines in terricolous lichen cover. Disturbances caused by wildfires, exploratory gas wells, and drained lakes all produced strong, yet localized increases in NDVI due to shrub growth. Our analysis also shows that a 4°C winter temperature increase over the past 30 years, leading to warmer soils and enhanced nutrient mineralization provides the best explanation for observed vegetation change. These observations thus provide early corroboration for modeling studies predicting large-scale vegetation shifts in low-Arctic ecosystems from climate change.

Key words: climate change; landsat; lichen; remote sensing; satellite; air photos; shrubs.

INTRODUCTION

Recent climate warming has been pronounced in the Arctic, with average annual temperature increases between 2 and 3°C since the 1950s (ACIA 2004). Accelerated temperature increases have driven declines in Arctic sea ice extent, snow cover duration, and glacier mass, and increases in permafrost temperatures (ACIA 2004). The terrestrial

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Arctic has also undergone important temperature-driven changes in the form of increased thermokarst (Jorgenson and others 2006; Lantz and Kokelj 2008), larger tundra fires (Rocha and others 2012), and enhanced vegetation productivity (Epstein and others 2012a).

Compelling evidence for pan-Arctic productivity increases comes from time-series analysis of coarse (1–8 km) resolution AVHRR satellite imagery collected since the early 1980s (Beck and Goetz 2011; Epstein and others 2012b; Xu and others 2013). In these studies, the normalized difference vegetation index (NDVI), based on the normalized difference between near-infrared and red reflectance (Tucker 1979), serves as a measure of vegetation productivity. NDVI is strongly related to shrub cover, leaf area, and biomass in tundra vegetation (Hope and others 1993; Riedel and others 2005; Reynolds and others 2012). AVHRR data show that broad areas of tundra are greening and experiencing longer growing seasons, but their large heterogeneous pixels make it difficult to determine the exact nature of the changes, including which vegetation communities, plant species, and terrain are being most affected. More recently, finer resolution Landsat and other satellite imagery have been used to map patterns of tundra greening over smaller regions to bridge the gap between plot and AVHRR image scales (Olthof and Pouliot 2008; Fraser and others 2011; McManus and others 2012; Tape and others 2012; Reynolds and others 2013).

Vegetation greening detected using coarse-resolution sensors is being increasingly corroborated at finer scales. Natural and experimentally warmed plots both show increased growth of shrub and herbaceous vegetation (Elmendorf and others 2012a, b). Recent growth ring analysis of willow and alder shrubs indicates that growth responses closely track inter-annual variation in growing season temperatures and NDVI (Forbes and others 2010; Macias-Fauria and others 2012; Tape and others 2012). Decadal-scale expansion of shrub cover has also been documented at several locations by recapturing historical oblique, vertical, and ground photos (Tape and others 2006; Myers-Smith and others 2011a; Lantz and others 2013; Ropars and Boudreau 2012; Tremblay and others 2012).

Overall, these finer-scale studies indicate that the greatest vegetation changes are in the low Arctic and involve larger deciduous shrub species (Epstein and others 2013), including alder (*Alnus* spp.), dwarf birch (*Betula* spp.), and willow (*Salix* spp.). Plot-scale warming experiments also show that shrub expansion often occurs to the detriment of

lichens and mosses, which are competitively excluded by shading and litter accumulation (Chapin and others 1995; Walker and others 2006; Elmendorf and others 2012a). However, lichen declines have not been consistently observed in plot-scale studies tracking vegetation responses to natural warming trends (Elmendorf and others 2012b).

In most cases, recent shrub expansion has been attributed to climate warming that acts directly by removing limitations to reproduction and growth (Walker 1987; Lantz and others 2010) or indirectly by stimulating soil microbial activity and mobilizing limiting nutrients (Sturm and others 2005). Others have shown that the rate of regional shrub expansion can be modified by landscape position and its influence on soil moisture and snow accumulation (Tape and others 2012; Naito and Cairns 2011; Ropars and Boudreau 2012). Disturbances acting at local scales, including fire (Lantz and others 2010), thaw slumps (Lantz and others 2009), cryoturbation (Frost and others 2013), seismic exploration (Kemper and Macdonald 2009), and exploratory hydrocarbon drilling (Johnstone and Kokelj 2008) also promote shrub growth by exposing and warming mineral soils. By contrast, grazing by herbivores, including caribou and lemmings, can exert a top-down influence on shrub abundance that may counteract a temperature-driven expansion (Manseau and others 1996; Olofsson and others 2009; Zamin and Grogan 2013).

An increase in Arctic shrub abundance is predicted to alter ecological processes in several ways. The reduction in land surface albedo and increase in evapotranspiration caused by an increase in shrub cover is likely to amplify Arctic warming (Chapin and others 2005; Pearson and others 2013). Taller shrubs efficiently trap snow, causing increases in winter ground temperatures, microbial activity, and nutrient mineralization, thus creating a positive feedback to additional shrub growth (Sturm and others 2005). Changes in vegetation composition and lichen decline resulting from shading by shrubs could also negatively affect herbivore populations (Joly and others 2007a, b).

One hotspot of Arctic greening identified in studies using coarse-resolution AVHRR NDVI is the tundra plains and foothills lying along the Beaufort Sea in Alaska and Western Canada (Goetz and others 2005; Pouliot and others 2009). In Alaska, this change coincides with increasing shrub cover (primarily alder) observed in repeat oblique air photos from 1948 and 2001 (Tape and others 2006). In the Northwest Territories, the southerly portion of the NDVI change hotspot is within the

treeline transition zone and also appears to be related to growth of shrub vegetation (Olthof and Pouliot 2008; Lantz and others 2013).

In this paper, we investigate the detailed nature of and specific causes for the recent coarse-scale NDVI increases observed over the Tuktoyaktuk Coastal Plain. A near-annual collection of 30 m resolution Landsat satellite imagery (image stack) from 1985 to 2011 is used to study NDVI greening changes across vegetation cover types, topographic gradients, disturbances, and other environmental characteristics within the study region. Regional changes to vegetation abundance are also examined in unprecedented detail using very large scale (1:2,000) vertical air photos taken in 1980 and recaptured in 2013. The simplest hypothesis to explain the satellite-detected greening is that it resulted from a warming-induced expansion of shrub cover and leaf area as a result of spreading, infilling, and growth of individual shrubs (Myers-Smith and others 2011b). We also expected that the greatest shrub expansion should occur in high-resource environments providing relatively warm, mesic soil conditions (Walker and others 2006; Tape and others 2012), and in areas impacted by various forms of disturbance (Lantz and others 2009; Frost and others 2013). A corollary hypothesis is that increased shrub cover should result in lichen decline from competitive pressures (Cornelissen and others 2001). We tested these predictions and examined a suite of factors potentially influencing the proliferation of shrubs in this region (Table 1).

METHODS

Study Area

The Tuktoyaktuk Coastal Plain (TCP) is a large ecoregion (14,816 km²) in the Low Arctic (Figure 1) characterized by rolling till deposits interspersed by widespread lacustrine deposits (Rampton 1988; Ecosystem Classification Group 2012). The region is underlain by ice-rich permafrost, as indicated by widespread polygonal terrain, retrogressive thaw slumps, and pingos (Burn and Kokelj 2009). Small lakes are widespread, covering about 30% of the area. The TCP is almost entirely represented by the low shrub tundra (S2; >40 cm tall) vegetation unit of the Circumpolar Arctic Vegetation Map (Walker and others 2005). Low shrub and sedge tundra form an almost continuous vegetation cover in upland areas that rise to 80 m elevation. The most common vegetation units include dwarf shrub heath, cotton-grass tussock,

high-center polygons, low-center polygons, and tall riparian shrub. Pockets of stunted white spruce also occur near the southern boundary of this ecoregion. Common deciduous shrub species are *Betula glandulosa*, *Betula nana*, *Salix pulchra*, *Salix glauca*, *Vaccinium uliginosum*, and *Alnus crispa*, whereas evergreen species include *Vaccinium vitis-idaea*, *Ledum palustre*, *Empetrum nigrum*, *Arctostaphylos rubra*, and *Cassiope tetragona* (Corns 1974). The most abundant lichen species, providing forage for the overwintering Cape Bathurst and Tuktoyaktuk Peninsula caribou herds are the reindeer lichens *Cladina rangiferina* and *Cladina stellaris*.

The regional climate is cold and dry. The mean annual air temperature from 1971 to 2000 at Tuktoyaktuk was -10.2°C . Mean annual precipitation averages 150 mm, with 32 cm falling as snow (Environment Canada 2012). Mean annual permafrost temperatures near the Beaufort Sea coast can be below -6°C , but south of the treeline ground temperatures range between -1 and -3°C . The contrast in ground temperatures between the tundra and upright shrub transition zone to the south is driven primarily by differences in snow depth across the tree line (Burn and Kokelj 2009; Palmer and others 2012). The ability of tall shrubs to trap snow can slow ground heat loss in winter, resulting in higher ground temperatures in areas where shrubs have proliferated, such as thaw slumps (Lantz and others 2009) or historical drilling-mud sumps (Kokelj and others 2010). Mean annual air temperature in the central Mackenzie Delta region has increased by an average of 2.2°C since 1926 (Lantz and Kokelj 2008), but the majority of this warming has occurred since 1970 (Burn and Kokelj 2009). Over the last three decades, mean annual ground temperatures in the region have increased by 1 – 3°C (Smith and others 2005; Burn and Kokelj 2009).

Trend Analysis of Landsat Image Stacks

Landsat TM and ETM + satellite images from 1985 to 2011 were acquired from the US Geological Survey's Global Visualization Server (<http://glovis.usgs.gov/>, accessed 16 June 2014). Sixty mostly cloud-free, 30 m resolution images were selected from six, highly overlapping World Referencing System-2 frames representing near-peak growing season conditions defined by a July 8–August 18 window (Table S1). To ensure that these images represented peak phenology conditions, we plotted average 1 km resolution, 10-day MODIS NDVI values against Inuvik growing degree days for the 2000–2006 growing seasons and compared this to

Table 1. Factors Thought to Influence the Expansion of Arctic Shrubs and How They were Investigated in This Study

Influencing factor	Biological significance	How measured within TCP study region	Influence on shrub growth in study region
<i>Large-scale drivers</i>			
Temperature	Increased nutrient mineralization and recruitment success	Monthly average Inuvik temperature	Likely major driver for regional NDVI and shrub increase
Sea ice extent	Temperature amplification	Minimum annual Beaufort sea ice extent	Likely major driver for temperature increase
<i>Topographic drivers</i>			
Elevation	Temperature, moisture	DEM from stereo orthophotos, relative terrain position from normalized local elevation	Each variable explains less than 1% of spatial variation in NDVI trend
Soil moisture	Nutrient flux	Topographic moisture index from DEM	
Solar insolation	Local temperature and metabolic rate	Beers transformation of aspect (SW = 0 and NE = 200)	
<i>Disturbance drivers</i>			
Wildfires	Soil warming, exposing of mineral soils increased nutrient availability	NWT fire surveys + visual GIS line database	Locally highly significant but minor in extent
Gas drilling		GIS point database	Contain high shrub growth, but mostly present at start of 1985–2011 analysis period
Seismic exploration		GIS polygon database	Locally highly significant but minor in extent
Thaw slumping			
Thermokarst lake drainage	High productivity from lake bed nutrients	Digitized lakes drained after 1985, calculated proximity to lakes	
<i>Biological drivers</i>			
Herbivory	Lichen removal, disturbance	Location of overwintering caribou herd	Likely had an impact but difficult to quantify
Plant biomass	Growing space for colonization	1985 baseline NDVI and land-cover type	Lower NDVI increase in high biomass areas
Land-cover type	Variable response among vegetation communities	1985 Landsat land cover, digitized pingos and ice-wedge polygons	All types similarly increasing (including ice-wedge polygons and pingos)

Inuvik monthly temperatures were obtained from Environment Canada (Vincent and others 2012); sea ice extent from the Canadian Ice Service of Environment Canada; 40 m digital elevation and fire history from Government of NWT; disturbances and landscape features from manual digitizing of 1:34,000 color orthophotos captured in 2004; and land cover from classification of 1985–1986 Landsat imagery (Oltmans and Pouliot 2008).

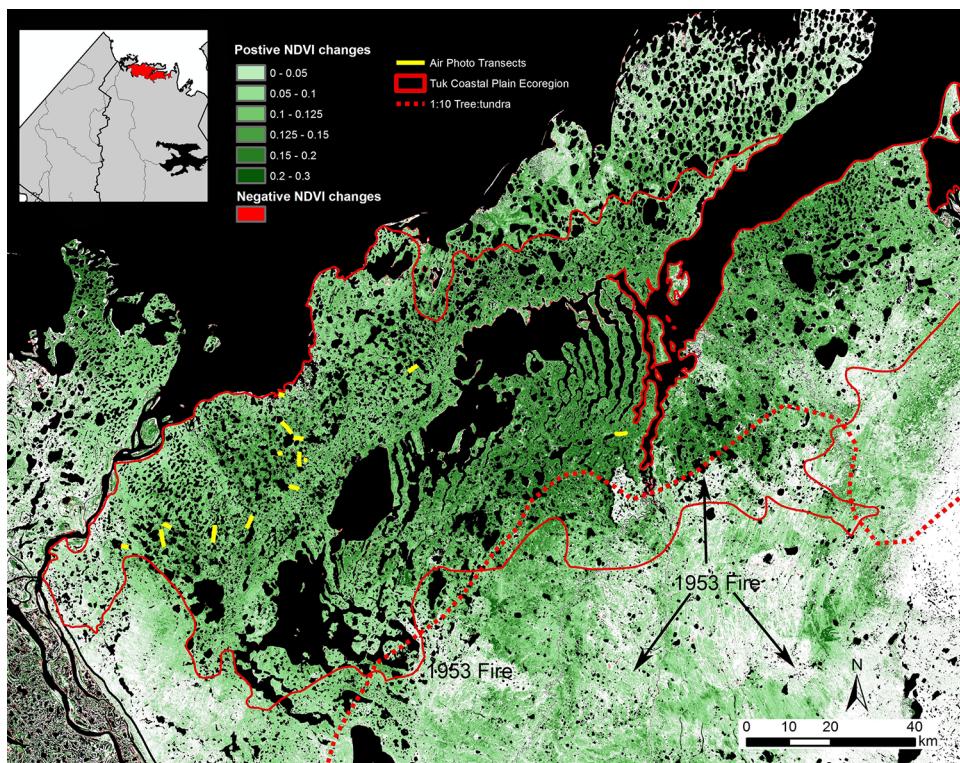


Figure 1. Tuktoyaktuk Coastal Plain (TCP) study region showing Landsat NDVI changes occurring between 1985 and 2011 that were calculated from per-pixel regression model coefficients. The treeline (1:10 isoline of tree:upland tundra cover) was digitized from Timoney and others (1992).

growing degree days for the Landsat acquisition dates (Figure S1). All 60 Landsat images fell within a growing degree window representing near-peak phenology. Deviation of Landsat sampling dates from peak phenology was also calculated by subtracting average, sampling-date NDVI from peak annual NDVI derived from 10-day AVHRR composite images (Fraser and others 2011). No temporal trend ($P > 0.05$) in NDVI deviation was observed for the Landsat dates.

Landsat images were calibrated using USGS coefficients, converted to top-of-atmosphere reflectance, masked for cloud and shadows using FMask (Zhu and Woodcock 2012) with manual editing if necessary, and processed to NDVI and tasseled cap (TC) brightness, greenness, and wetness indices as in Fraser and others (2011). This produced an image stack database where a unique time-series of clear-sky reflectance values and vegetation indices could be analyzed for each 30 m pixel for the 1985–2011 period. The NDVI, TC, and reflectance trends for each pixel were quantified using TheilSen robust regression and slope significance determined using the non-parametric, rank-based Mann–Kendall test (Kendall 1975).

NDVI trends were summarized by general vegetation units (GNWT 2011) that were mapped over the TCP using 1985–1986 Landsat scenes and 1980 1:34,000 CIR photos for cluster labeling using the methods in Olthof and Pouliot (2008). To investi-

gate factors influencing spatial variation in NDVI trends we made use of several existing datasets available over the western part of the study area (Table 1). Landscape terrain characteristics were based on a 40 m digital elevation model derived from 1:34,000 stereo color orthophotos acquired in 2004 (<http://www.geomatics.gov.nt.ca/>, accessed 16 June 2014). These variables included elevation, relative elevation normalized within a 1 km² window, distance to a water body, slope gradient, topographic moisture index (Beven and Kirkby 1979), and a transformation of aspect representing solar insolation (Beers and others 1966). We also examined NDVI trends in the context of datasets identifying high- and low-centered ice-wedge polygons, pingos, historical seismic lines, exploratory gas well sites, 1965–2012 NWT fire history, retrogressive thaw slump scars, and recently drained lake basins (Marsh and others 2009). Terrain variables were compared to spatial variation in NDVI trends using simple linear regression and a random 5% sample of 30 m pixels ($n = 105,359$). To assess differences in NDVI trends among land-cover types, we used a Kruskal–Wallis one-way ANOVA on the ranks of the non-normal data and Dunn's pairwise multiple comparison test. Terrain and land-cover variables were also combined into regression tree models using Cubist 2.05 software by Rulequest Research to reveal nonlinear interactions influencing NDVI trends.

Temperature and Sea Ice

To examine the relationship between vegetation change and regional climate, we compared NDVI change with broad-scale climate datasets. Monthly mean temperatures were obtained from the Second Generation of Homogenized Temperature dataset from Environment Canada (Vincent and others 2012). This dataset identifies and adjusts for variation in station data associated with relocations of stations or changes in observing practices. Monthly data are available since 1957 for the town of Tuktoyatuk located on the northern coastline of the Tuktoyaktuk Peninsula. However, we chose to analyze temperature trends using the more complete records available for Inuvik 50 km to the south of the TCP. Inuvik annual mean temperatures are highly correlated ($r^2 = 0.90$) with those of Tuktoyaktuk (Burn and Kokelj 2009) with summers that are about 3°C warmer. Minimum annual sea ice coverage in the Beaufort Sea since 1968 was obtained from the Canadian Ice Service of Environment Canada (<http://ec.gc.ca/glaces-ice/>, accessed 16 June 2014). The temperature and sea ice data were regressed against spatially averaged annual NDVI over the study region.

Repeat Large-Scale Aerial Photography

To determine changes in plant functional group dominance associated with NDVI changes we used fine-scale (1:2,000) vertical air photos from 1980 and 2013. From August 6–8, 1980, a total of 1,469 color-infrared (CIR) stereo photo pairs were acquired to study reindeer winter rangeland over the Tuktoyaktuk region (Sims 1983; Figure 1). Transects were defined by analyzing 1:34,000 scale CIR air photos to capture regional variability in vegetation and terrain, and several flight lines were randomly located within each transect. CIR film was used in combination with plot measurements to quantify fruticose lichen (*Cladina* spp.) cover, the major winter food source of the domestic reindeer resident at the time. The resultant images are also particularly effective at highlighting shrubs, owing to strong scattering by leaf tissue in near-infrared wavelengths.

In 2013, we obtained a complete set of the 1980 film positives. A subset of 761 images covering the TCP and with an average extent of 1 ha (100 × 100 m) was scanned at 2,400 dpi. This produced a ground sample distance of 2 cm, or an estimated effective resolution of 3–4 cm based on the smallest features (power lines, leaves, defoliated branches) resolvable in the scanned film. The spatial resolution of these images is approximately

an order of magnitude finer than aerial photos used in previous Arctic shrub change studies. The center of each scanned photo was located and georeferenced using the 2004 NWT digital orthophotos and 1:34,000 1980 CIR photos taken over the flight lines.

From August 7–8, 2013, we recaptured a selection of the 1980 photos within the TCP using cameras vertically mounted to a Bell 206 Long Ranger helicopter. Photos were taken at approximately 200 m elevation over 14 flight lines within 4 of the original 11 transects (Figure 1), yielding digital photos with a resolution similar to the 1980 images (~2 cm). Vertical photos were acquired both in color using a 16 megapixel Nikon D7000 with 35 mm lens and in color-infrared using a 16 megapixel Canon EOS with 50 mm lens. The Canon was modified by LDP-LCC (<http://www.MaxMax.com>, accessed 16 June 2014) by replacing the internal NIR blocking filter with one designed to pass NIR wavelengths in the 670–770 nm range. This approximated the response of the Kodak Aerochrome CIR film used in 1980, which is no longer in production. To characterize regional vegetation within major terrain types, nine 20-m belt transects were established under two of the flight lines.

To document fine-scale changes in shrub and lichen cover and interpret NDVI trends, we assembled 208 matching 1980–2013 photo pairs using common landmarks (for example, alders, polygon troughs). Photo pairs, which included color and NIR images from 2013, were rotated and cropped to a common ground extent. All pairs were visually assessed for directional changes in shrub and lichen cover (that is, no change, <10% increase/decrease, or >10% increase/decrease), and in alder density and crown size. Shrubs in the study area consisted of relatively pure, closed-canopy patches of dwarf and tall shrub that could be readily separated based on reflectance, leaf texture, and shadows. We found that the 2013 CIR and color photographs were both effective for identifying shrub and lichen, whereas the CIR photographs provided better discrimination of small, residual patches of lichen.

Quantitative analysis of vascular vegetation (shrub and graminoid) and lichen cover changes was also conducted for 32 photo pairs over ice-wedge polygon terrain where mapping confidence was highest. These areas had lower cover of sedge (graminoid) tussock that, when flowering or containing dead biomass, can present a bright target that may be confused with lichen (Sims 1983). In 1980, polygon terrain covered about 23% of the region and contained some of the highest cover of

reindeer lichen (Sims 1983). Vascular and lichen cover were classified for each image date using the ImageJ scientific image analysis program (Schneider and others 2012) by interactive thresholding in intensity-hue-saturation (IHS) or RGB color space (Figure 2). Ground-level and oblique low-altitude aerial photos from 1980 and 2013 served as a reference for photo-interpretation, as did interpretation notes in Sims (1983).

RESULTS

Landsat NDVI shows that vegetation greening in the TCP has been rapid and widespread (Figure 1). The NDVI trends indicated that 85% of the study area had significant ($P < 0.05$) increases in NDVI, 1% had significant decreases, and 14% had no trend ($P > 0.05$). Average terrestrial NDVI across the trend surface increased from 0.49 in 1985 to 0.59 in 2011, representing a 21% relative increase. The NDVI increase followed a nonlinear, saturating trajectory (Figure 3A). NDVI computed from the linear trends may therefore over-predict 2011 values and under-predict 1985 values to a lesser degree. The median NDVI trend varied by land-cover type ($P < 0.001$) and Dunn's multiple comparison test showed that the trend in all but five land-cover type pairs were significantly different ($P < 0.05$), with riparian tall shrub showing the largest pairwise differences (Table 2). Terrain variables, including slope, terrain position, aspect, and topographic moisture index, were significant ($P < 0.05$) predictors of spatial variation in NDVI trend due to large sample size ($n = 105,359$), but each explained less than 1% of its variation. The only variable explaining more than 1% was baseline NDVI ($r^2 = 0.06$, $P < 0.05$), indicating that areas with higher vegetation density in 1985 showed smaller NDVI increases. Regression tree modeling combining the terrain variables and land-cover types accounted for 31% of the spatial variation in NDVI trend. The four most important variables in the model were 1985 baseline NDVI, land-cover type, slope gradient, and elevation. Comparisons of average NDVI trend among disturbance types and landscape features showed that polygonal terrain, seismic lines, and pingos were all similar to the average regional trend (Table 3). Recently drained lakes, the footprint of exploratory gas wells, and recent wildfires all showed NDVI increases greater than the regional average (Table 3).

Regression analysis revealed associations between annual NDVI and climate variables. Average annual NDVI computed from Landsat trend analysis was significantly correlated to autumn ($r^2 = 0.40$,

$P < 0.05$) and winter temperature ($r^2 = 0.21$, $P < 0.05$), but not to July, spring, or summer temperature ($P > 0.05$). The largest seasonal changes in temperatures since 1980 occurred during winter (Figure 3C). Temporal variation in NDVI showed the strongest relationship to minimum annual Beaufort Sea ice extent ($r^2 = 0.51$, $P < 0.05$; Figure 3H), which has decreased since 1990.

The results of the visual comparisons of matched 1980–2013 air photo pairs are shown in Table 4. An increase in shrub cover could be detected in 97% of photo pairs, whereas a decrease in lichen cover could be detected in 94% of pairs. Figure 4 shows a portion of a CIR photo pair covering a high centered ice-wedge polygon where shrub increases and lichen reductions were both greater than 10%. In 61% of photos pairs, alder shrubs were present in 1980 and showed an increase in crown size or in size and number of individuals, whereas only 4% of photos contained alders in 1980 and had no changes.

Digital classification of 32 photo pairs using ImageJ within high centered ice-wedge polygons indicated that the average cover of vascular plants has increased by 20% and average lichen cover has decreased by 24% (Figure 5). All photo pairs except one showed changes in vascular and lichen cover that exceeded 10%. The example shown in Figure 2 lies in the upper range of changes mapped among the pairs (that is, +37–39% shrub and –33–35% lichen). Relative to 1980 levels, lichen cover decreased by 67% and the cover of vascular plants increased by 40%. Although changes were documented by separately classifying each photo, areas of expanding shrub cover in 2013 were usually observed in areas that contained lichen in 1980. Shrubs accounted for most of the vascular cover mapped, but were combined with spectrally similar graminoid vegetation (~5–10%) where fewer changes were observed.

DISCUSSION

Extent and Magnitude of Shrub Changes

Ecological modeling predicts widespread shifts in Arctic vegetation under future climates (Euskirchen and others 2009; Pearson and others 2013). For example, more than half of Arctic vegetation is expected to change to a different physiognomic class, with woody vegetation cover increasing by 52% based on climate scenarios for the 2050s (Pearson and others 2013). Some of the most rapid responses are expected to occur in the low-Arctic transition between sedge tussock tundra and shrub

tundra, because within this zone: (i) vegetation transitions are strongly related to climate; (ii) the dominant species (shrubs) show gradual changes in frequency and are already widely distributed across the transition; and (iii) dominant species have a demonstrated capacity to respond quickly to warming (Epstein and others 2004a).

Landsat NDVI trends show that widespread and rapid greening of the TCP landscape has occurred since 1985. This result corroborates model predictions and provides evidence that significant tundra greening can occur in several decades (Epstein and others 2004b; Lantz and others 2013). Most of the observed increase in NDVI occurred between 1992 and 2000 (Figure 5A), demonstrating that landscape-scale shrub cover can respond rapidly to temperature changes—something previously shown in plot-scale experimental warming studies (Chapin and others 1995; Bret-Harte and others 2001; Walker and others 2006). Analysis of fine-scale repeat photos provided clear evidence that shrub expansion is driving observed changes in NDVI, as 97% of photo pairs showed an increase in shrub cover. The magnitude of NDVI increases was similar among all vegetation types showing that shrub proliferation has occurred across the entire TCP. The average NDVI trend for pixels under the 2013 flight lines (0.0406/decade) was very similar to the average regional trend (0.0410/decade), indicating that our repeat photos areas are representative of the magnitude of changes across the larger region.

The greening observed in the TCP is amongst the largest and most rapid documented in the Arctic. Table 5 compares results from low-Arctic change studies based on observational data ranging in scale from field transects to 12.5 km resolution satellite imagery. In most regions, annual rates of change in shrub cover, NDVI, and leaf area fall under 1% but it is likely that rates calculated over longer time periods when shrub expansion is not continuous are an underestimate. By contrast, in the TCP we observed a 0.8% annual NDVI increase averaged over the 26-year study period or 2.5% averaged over the 1992–2000 period of rapid change. Note that any comparison of the magnitude and rate of change across studies is complicated by variation in NDVI or shrub cover due to sensor spectral differences, spatial resolution aggregation effects (for example, inclusion of water bodies in coarser imagery), sampling dates, and image compositing methods.

An advantage of using 30 m Landsat imagery over coarse (≥ 1 km) resolution AVHRR imagery is the ability to examine greening trends in relation to

topographic gradients, local disturbances, and other features of interest. For example, we were able to determine that unique landforms such as pingos in the region demonstrated greening that is comparable to the surrounding landscape. This extends the photographic evidence of rapid willow growth since 1996 on an eroding pingo located 150 km southeast of our study area (Mackay and Burn 2011). Similarly, the high resolution repeat air photos provided a means to detect more subtle forms of Arctic shrub growth that have not been well documented to date. For example, increasing shrub cover in sedge tussock was frequently observed where erect dwarf shrubs have expanded over tussocks (Figure S2). Tape and others (2006) proposed that such extensive shrub growth within Alaskan tussock tundra was likely considering that expanding tall shrubs did not cover a sufficient area to account for strong NDVI increases.

Reductions in Lichen Cover

The repeat photo comparison provides clear evidence that greening in the Low Arctic can be associated with widespread reductions in lichen cover. In addition to relatively low lichen cover in the 2013 air photos, we rarely observed large, near-continuous lichen mats during our aerial and ground surveys in the region. Such conditions were common in the 1980 air and ground photos (Figure S3), when lichen cover as high as 89% was recorded in 100 m² ground plots (Sims 1983). Lichen declines were also widely evident as brightness changes when comparing Landsat visible channels from near the start and end of the analysis period (Figure S4). Photo pairs in high centered polygon terrain indicate that lichen decline was at least partially the result of competition and overtopping by expanding shrub patches consisting of both scrub birch and other smaller dwarf shrubs (Figures 2, 4; Figure S2C–D). Note that plot warming experiments have documented the near elimination of lichens under a dense, expanding birch canopy (Chapin and others 1995), although the fate of overtopped lichen cannot be determined here using the air photo pairs.

It is possible that lichen reductions were also caused by caribou grazing and trampling (Manseau and others 1996; Joly and others 2007b) during the early 1990s when the Cape Bathurst population peaked at nearly 20,000 animals—a figure that matches an estimate of winter carrying capacity for the region (Sims 1983). Caribou grazing of lichen may have also facilitated shrub expansion by increasing available ground substrate for germina-

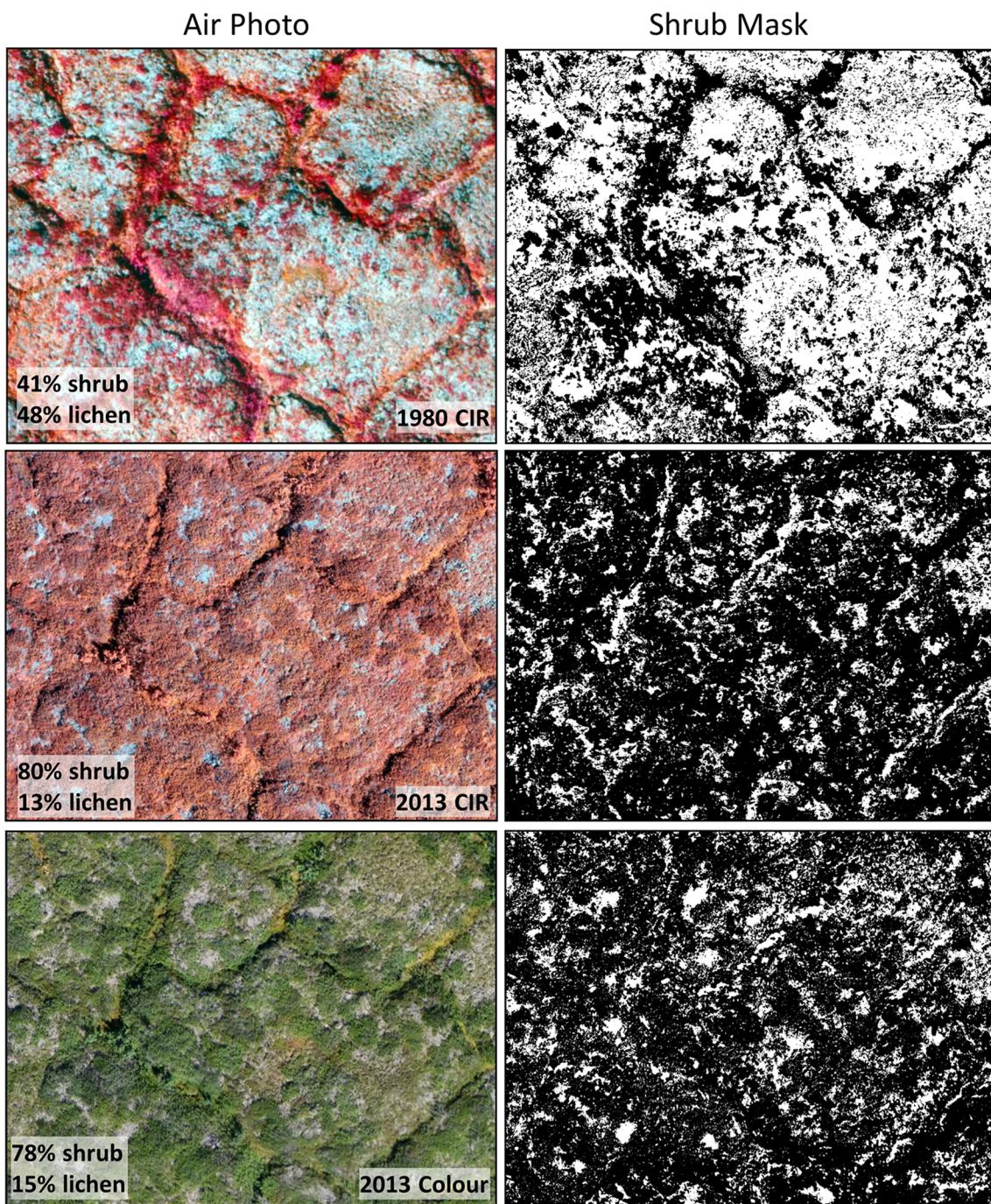
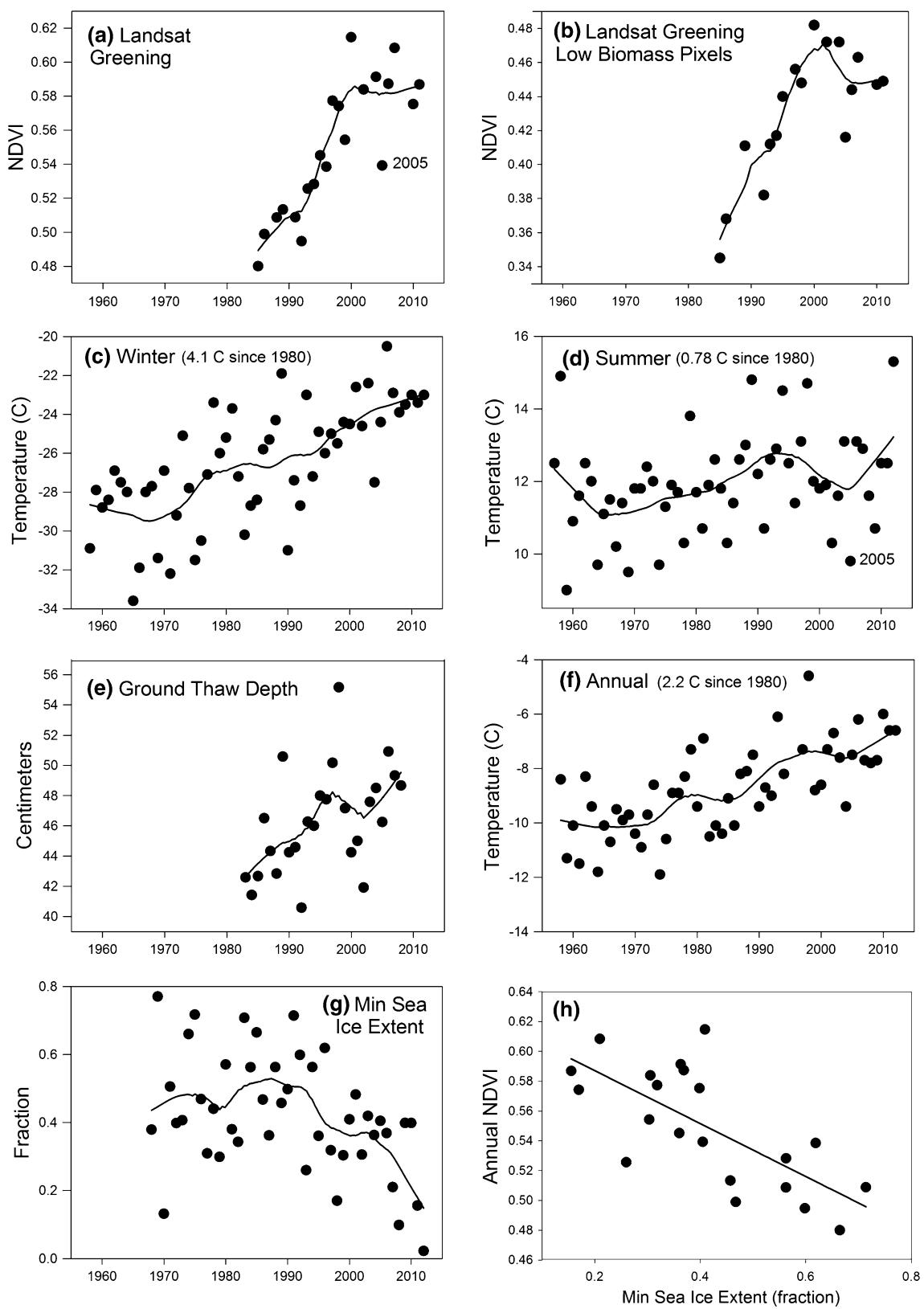


Figure 2. Sample photos over high centered polygon terrain showing shrub masks extracted using ImageJ interactive classification. The images at the left discriminate vascular vegetation (black) from non-vascular cover (white). Note that residual lichen patches are more visible in the 2013 CIR photo compared to the color photo.

tion and clonal growth, and by reducing albedo causing additional local soil warming (Manseau and others 1996). However, because shrub increases were also observed in photos containing low 1980 lichen cover, lichen removal by caribou does not provide the best explanation for shrub

expansion. Our results thus appear to be among the first to provide direct support at landscape-regional scales for the hypothesis that shrubs will outcompete lichen in a warming climate (Cornelissen and others 2001; Joly and others 2009). It is likely that the expanding shrub cover, increased leaf litter,



◀ **Figure 3.** Annual trends in NDVI (**A**, **B**), temperature (**C**, **D**, **F**) (Vincent and others 2012), thaw depth (**E**) (Burn and Kokelj 2009), and minimum Beaufort Sea ice extent (**G**) (Environment Canada). LOESS trend lines are plotted using SigmaPlot Version 12.5 (sampling proportion = 0.4, polynomial degree = 1) to highlight gradual changes. NDVI for 2008 and 2009 is not plotted in **A** because these years include only single scenes covering a small, southerly portion of the TCP. Low biomass pixels (1985 NDVI < 0.45, $n = 12,530$) shown in **B** were selected from 9% of the westerly portion of the TCP so that NDVI would be computed over the same sample pixels each year. The relationship between annual average NDVI and minimum Beaufort Sea ice extent is shown in **H**.

and subsequent ground shading will also prevent re-establishment of lichen cover to its former levels (Klein and Shulski 2011).

Spatial Variation in Vegetation Greening

Previous research has shown that shrub expansion is often associated with certain vegetation cover types and landscape positions (Naito and Cairns 2011; Tape and others 2012). However, in our study region, terrain variables including topographic moisture index, were relatively unimportant in influencing patterns of NDVI increase. This may be due to the smaller amount of relief (0–80 m ASL, mean 25 m), fewer topographic incisions, and small catchment areas within the study region compared to areas where shrub cover is expanding in Alaska (Tape and others 2006, 2012). Land-cover type was also a poor predictor of the intensity of greening across the study region. The only vegetation type with considerably lower greening trends was tall riparian shrub (for example, Figure S5). This may be the result of NDVI saturation in this highest biomass class, or an actual growth

slowdown caused by a reduction in available growing space and/or declining soil temperatures from shading (Blok and others 2010). The regression tree model using all predictor variables only explained one-third of the spatial variation in NDVI trend across the western portion of the TCP. This indicates that differences in edaphic conditions (for example, temperature, thaw depth, nutrients) that we were not able to measure likely play an important role in determining landscape-scale greening patterns (Tape and others 2012; Raynolds and others 2013).

The Role of Disturbances

Natural and anthropogenic disturbances have been identified as a key driver of fine-scale shrub proliferation in the Mackenzie Delta region (Kemper and Macdonald 2009; Lantz and others 2009, 2010, 2013). Our data are consistent with previous observations, showing that some disturbances have locally important impacts on NDVI. However, our analysis also shows that disturbance likely accounts for less than 5% of the NDVI change throughout the TCP.

NDVI trends at the locations of historical seismic line surveys and lakeshore thaw slumps were not greater than the regional trend. Most of these sites contained relatively higher shrub cover observable in recent air photos, consistent with previous observations within the region (Kemper and Macdonald 2009; Lantz and others 2009, 2013). The likely reason for the lack of NDVI increase within these disturbances is that much of the enhanced shrub growth occurred before the first Landsat image date in 1985. Data on historical seismic lines indicates that 89% of the surveys occurred before this date, whereas the slump survey includes dis-

Table 2. Median Landsat NDVI Trend by Vegetation Unit (GNWT 2011) Mapped Over the Entire Study Region Using 1985 Landsat Imagery

Vegetation unit	Median NDVI trend ($U \text{ decade}^{-1}$)	25th percentile	75th percentile
All land areas	0.040	0.029	0.049
Sparse spruce lichen	0.044	0.030	0.056
Low-center polygons and graminoid wetland	0.043	0.034	0.053
Dry saxifrage tundra	0.042	0.033	0.052
High-center polygons	0.042	0.031	0.052
Cotton-grass Tussock	0.041	0.031	0.049
Alaska birch–spruce	0.040	0.026	0.050
Dwarf shrub heath	0.039	0.031	0.047
Dark cryptogam/barren	0.034	0.000	0.051
Bare	0.031	0.000	0.049
Upland and riparian tall shrub	0.025	0.000	0.034

Table 3. Average Landsat NDVI Trend for Different Disturbances and Landscape Features

Class or feature	Area (km ²)	Number	NDVI trend (U decade ⁻¹)	Standard deviation	Notes
All land areas	8872	N/A	0.041	0.022	Lakes masked
Drained lakes	10.1	11	0.263	0.117	Those drained after 1985
Gas wells	1.6	45	0.091	0.034	Footprint of disturbance
Fires	13.5	4	0.058	0.034	0.15% of region
Flight lines (2013)	3.7	14	0.041	0.019	Total length is 36.5 km
Seismic lines	191.7	680	0.039	0.018	2.2% of region
High polygons	170.0		0.039	0.015	16% of area where mapped
Pingos	1.5	189	0.037	0.020	Sample—not comprehensive
Low polygons	32.3		0.037	0.014	3% of area where mapped
Slumps	7.4	764	0.019	0.046	2.3% of area where mapped

All features except for fires were mapped over the westerly portion of the study region from manual digitizing of 1:34,000 color orthophotos captured in 2004.

Table 4. Summary of Vegetation Changes Visually Assessed in 208 Photo Pairs from 1980 and 2013

Change metric	Percent frequency of photos by feature type and change metric		
	Shrub cover	Lichen cover	Alder shrubs
Not present	0	2	35
Decrease > 10%	1	49	
Decrease 0–10%	1	45	
No change	1	3	4
Increase 0–10%	38	1	
Increase > 10%	59	0	
Expanding crown size			19
Expanding crowns and number			42

The average common area covered by each photo pair is 3,856 m².

turbances several decades old. NDVI trends within these features were also likely diminished due to their small footprint (~5–60 m wide) relative to the 30 m Landsat imagery and the close proximity of slumps to water bodies having negative NDVI. Disturbances associated with exploratory gas wells, fires, and lakes that drained after 1985 showed some of the strongest positive NDVI trends (Table 3), but only covered a small area within the TCP. Although gas well sites contained an altered vegetation community of larger willow and alder shrubs (Johnstone and Kokelj 2008), most of their NDVI increases appear to reflect vegetation recovery to baseline NDVI levels after disturbance. Despite vigorous post-fire shrub regeneration, historical fires overlapping the southern TCP (Cody 1963) displayed no significant greening trend (Figure 1) due to high pre-1985 leaf area causing saturation of the NDVI signal. This highlights the potential for NDVI to become a less sensitive measure of Arctic shrub growth at higher biomass levels (Blok and

others 2011b). Although disturbances appeared to play a secondary role in generating the NDVI trends, we cannot exclude a potentially important role of small-scale, extensive disturbances that were not measured, such as cryoturbation (Frost and others 2013) and trampling by caribou (Manseau and others 1996).

The Role of Climate Warming

The best explanation for the rapid and widespread change in vegetation that we observed is that shrub proliferation has been facilitated by warming air and ground temperatures. Air temperature increases likely promote the growth of Arctic shrubs indirectly by warming soils and stimulating nutrient mineralization (Chapin 1983). NDVI increases in the TCP occurred during decades characterized by mild winters (Figure 3C). This suggests that winter soil processes are likely important in our study region (Sturm and others 2005; Wahren and others 2005),

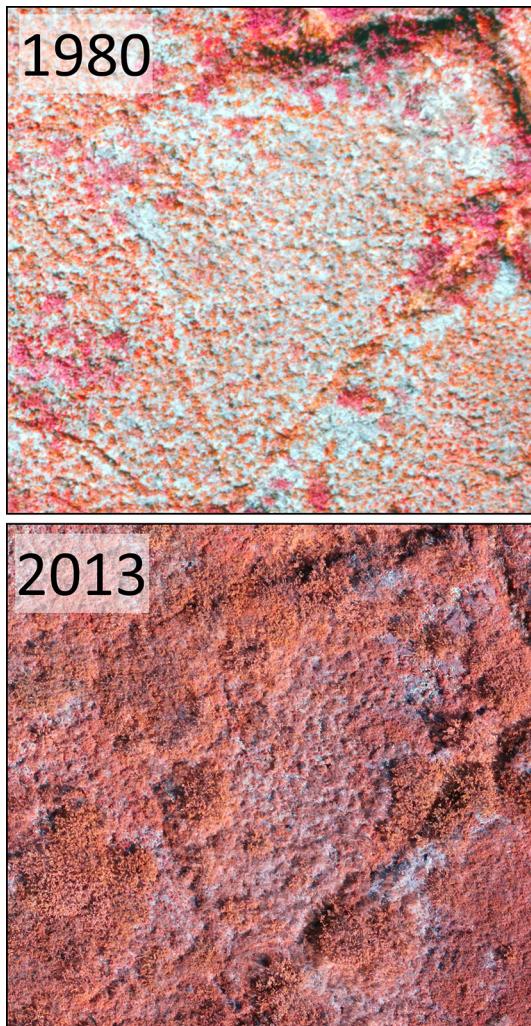


Figure 4. Close-up of 1980/2013 CIR photo pair (~25 m wide) showing expansion of shrubs with concomitant lichen declines. Deciduous dwarf shrubs (primarily birch) appear red in the 1980 photo, whereas heath shrubs (primarily Labrador tea) appear orange. Larger, deciduous shrubs show a high degree of texture in the 2013 photo due to internal shadowing.

including the potential for a positive feedback as larger shrubs trap more insulating snow cover. The primary influence of warming winter air temperatures, or increasing winter snow cover, is to slow ground heat loss and increase the duration of winter active layer freeze back (Kokelj and others 2010). This means that a portion of the active layer will be above 0°C for a longer duration in the winter, and that winter minimum ground temperatures will also be higher as the duration of conductive ground heat loss is diminished. The warming trend has translated into near-surface ground temperature increases of about 2° between 1970 and 2007 over the western

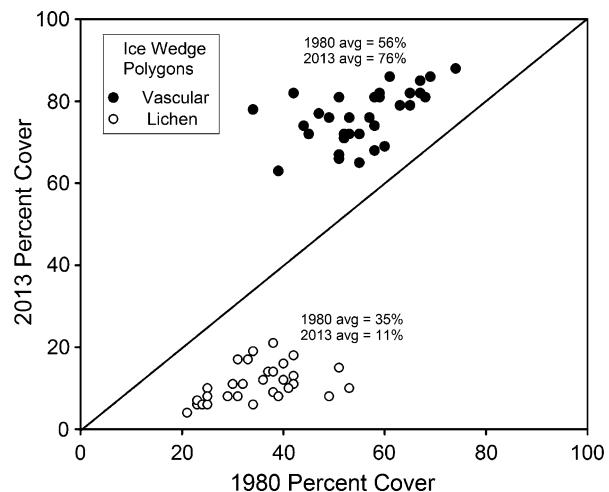


Figure 5. Percent cover of lichen and vascular vegetation within 32 photo pairs over ice-wedge polygon terrain derived using interactive photo classification in RGB or IHS color space. Average area covered by each photo is 3,162 m².

portion of the TCP (Burn and Kokelj 2009). Thaw depths to the west of the TCP show an increasing trend from 42 to 52 cm between 1983 and 2008 (Burn and Kokelj 2009) (Figure 3E).

A more ultimate cause for regional warming and shrub expansion since 1980 may be a reduction in the Beaufort summer sea ice extent. There is growing evidence that declining sea ice cover is the most important driver of Arctic amplification (Kumar and others 2010; Screen and Simmonds 2010). Reduced sea ice causes strong positive temperature trends during autumn and winter as heat is returned to the atmosphere during freezing (Screen and Simmonds 2010). In the TCP, minimum Beaufort Sea ice has declined by more than 50% since 1968, and this trend explains 54 and 51% of the variation in Inuvik winter and autumn temperatures, but only 43% of the variation in summer temperatures. Minimum annual sea ice extent was also the best predictor of 1985–2011 annual NDVI, explaining more than half of its variability (Figure 3H). Overall, these observations are consistent with a circumpolar linkage between sea ice, warming, and NDVI for Arctic tundra (Bhatt and others 2010).

A conspicuous feature of the annual NDVI trend is that it begins to flatten after the rapid 1992–2000 rise, despite a generally continued increase in ground and air temperatures (Figure 3E, F). One potential explanation for this is that NDVI is beginning to saturate at higher shrub biomass and leaf area (Riedel and others 2005; Blok and others 2011a, b), similar to areas of dense fire regenera-

Table 5. Changes in Shrub Cover and NDVI Greenness Measured in Low-Arctic Vegetation Studies

Location	Magnitude of shrub change	shrub or NDVI	Rate of change (y^{-1})	Data source and time period	References
Tuktoyaktuk Peninsula, NWT (15,000 km^2)	Positive NDVI trend in 85% of land areas; 20% abs increase in vascular cover	2.5% (1992–2000) 0.8% (1985–2011) NDVI	1985–2011 Landsat satellite imagery and 1980 and 2013 1:2,000 vertical air photos	This study	
NWT treeline transition zone	28–36% change in NDVI for lichen to vascular dominated land cover	1.4–1.8% abs NDVI	1986–2006 Landsat 30 m satellite imagery	Olthof and Pouliot (2008)	
Northern Quebec	Positive NDVI trend in 48% of area north of treeline; 20–60% increase in LAI within shrub tundra	0.83–2.5% LAI	1986–2010 Landsat satellite imagery	McManus and others (2012)	
Circumpolar Arctic tundra	17% and 25% biomass increase for erect shrub tundra vegetation types (CAVM S1 and S2)	0.61–0.89%	1982–2010 NOAA AVHRR GIMMS3 g NDVI (12.5 km resolution)	Epstein and others (2012a, b)	
Mackenzie Delta Uplands, NWT	Increase in alder density by 68% and in tall shrub tundra by 16% abs (38.5% rel)	0.5% abs shrub	1972 and 2004 air photos	Lantz and others (2013)	
North America forests and tundra	33.9% of tundra showing positive NDVI trends	~0.48% NDVI	1981–2003 NOAA AVHRR NDVI (8 km resolution)	Goetz and others (2005)	
Northwestern Quebec (672 ha)	12% abs increase on hilltops and 22% increase on terraces	0.24–0.43% abs shrub	1957 air photos and 2008 0.5 m Worldview satellite	Ropars and Boudreau (2012)	
Seward Peninsula, Alaska	8% abs (32% relative) increase	0.33% abs shrub	1981–2005 sampling of permanent transects in caribou rangeland	Joly and others (2007a, b)	
Siberian ecotonal landscapes	–1 to 26% relative change in tall shrub cover (11.7% avg)	0.29% abs shrub	1965–1969 satellite photography and 2002–2011 high resolution satellite	Frost and others (2013)	
Northeastern Quebec (1,320 ha)	10% abs (29% rel) increase in dense shrub and tree cover	0.26% abs shrub	1964 and 2003 air photos (1:10,000–1:20,000)	Tremblay and others (2012)	
Four low-Arctic national parks in Canada	Estimated shrub increases of 14–24%	0.14–0.16% abs NDVI	1985–2009 Landsat imagery and field plots for training regression trees	Fraser and others (2011)	
Alaska's North Slope (823 km^2)	NDVI increases in 5% of areas	0.15% NDVI	1985–2007 Landsat imagery	Raynolds and others (2013)	
Alaska North Slope (220,000 km^2 region)	Abs cover increase from 15–22% to 20–30% (33–36% relative change)	~0.13% abs tall shrubs only	202 pairs of oblique air photos from 1945–1953, and 1999–2002	Tape and others (2006)	

Rates of change are approximately ordered from highest to lowest (abs refers to absolute vs. relative % change).

tion within the treeline. However, NDVI flattening was also observed in a sample of lower biomass pixels (Figure 3B) where saturation would not be expected, which suggests that shrub proliferation has slowed in the last decade. In addition, the Simple Ratio vegetation index, which remains linear at higher tundra vegetation biomass (Chen and others 2012), also shows a similar slowing trend for the full sample (plot not shown). The NDVI flattening could be caused, in part, by cooler summers occurring after 2000, when July temperatures for NDVI sampling years averaged 13.8°C ($n = 7$) compared to 14.7°C during 1985–2000 ($n = 14$). Recent summers with cooler temperatures may have suppressed growth vigor and leaf size of existing shrubs in single years (Olthof and Latifovic 2007; Blok and others 2011a), which would magnify the apparent gradual slowdown in regional shrub expansion. Another factor may be that the densifying shrub canopy is causing a negative growth feedback by shading the ground surface and decreasing local soil temperatures and nutrient cycling during summer (Blok and others 2010). Interestingly, there was no correlation between 1985–2011 July temperature and annual average NDVI ($P > 0.05$, $n = 21$), but a strong positive correlation for the 2002–2011 period ($r^2 = 0.81$, $n = 7$). It is also worth noting that anomalously low NDVI in 2005 (Figure 3A) corresponded to the coolest July in Inuvik and second coolest in Tuktoyaktuk since records began in 1957 (Figure 3D).

Implications of Findings

Vegetation change across the TCP has implications for wildlife, permafrost, hydrologic regimes, wildfire, and infrastructure in the region. The large reduction in lichen forage could require the resident Cape Bathurst and Tuktoyaktuk caribou herds to shift to a lower energy winter diet containing more shrubs (Joly and others 2007a, b), unless they have alternate ranges with more abundant lichens. This could add to the multiple stressors that are thought to have led to recent population declines in these and other NWT barren-ground caribou herds. These factors include severe weather events (icing), changes in the timing of spring green-up, high predator densities, and proportionally high harvest at low populations (Circum-Arctic Rangifer Monitoring and Assessment Network; <http://carma.caff.is/>, accessed 16 June 2014).

Another impact of the regional shrub growth is increased availability of fuels to support fire spread, as has been inferred from paleorecords in Alaska (Higuera and others 2008). This, along with war-

mer and drier summers, could cause the periodic, large wildfires that have burned forest-tundra in the southerly portion of the TCP to extend northward toward the Beaufort coastline. Increased fire frequency would further promote shrub growth (Racine and others 2004; Lantz and others 2013), while limiting availability of winter lichen forage for several decades (Racine and others 2004; Jandt and others 2008).

The patterns of greening are consistent with the notion that anthropogenic disturbance can be a catalyst for local shrub proliferation (Johnstone and Kokelj 2008). Proliferation of shrubs is of particular relevance to permafrost conditions because preferential snow capture on sites where surface organic cover is disturbed can lead to rapid ground warming and potentially to permafrost thaw (Kokelj and others 2010). The role of human disturbance in stimulating the “shrub-snow cover-ground warming feedback” can no longer be ignored as a factor impacting the stability of infrastructure in low-Arctic permafrost terrain.

CONCLUSIONS

This study documented spatial and temporal changes in fine resolution NDVI and vegetation cover within a large region of the low-Arctic where coarse-resolution AVHRR-NDVI increases were previously recorded. Our major findings and conclusions are as follows.

1. Low-Arctic NDVI (measuring phytomass) can increase rapidly (<10 years) and extensively (85% of land areas over 15,000 km²) in response to warming air and ground temperatures.
2. NDVI increases are mostly attributable to expansion of erect dwarf and tall shrubs—the functional vegetation group best positioned to exploit improved growing conditions.
3. Regional cover of reindeer lichen can decline at decadal scales from shrub expansion and a potential top-down impact from winter foraging by caribou herds at historically high population levels.

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