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Source: Arctic, Antarctic, and Alpine Research, 45(4) : 515-525

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-45.4.515

Arctic, Antarctic, and Alpine Research, Vol. 45, No. 4, 2013, pp. 515–525

Shrub Expansion in SW Greenland under Modest Regional Warming: Disentangling Effects of Human Disturbance and Grazing

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Abstract

Shrub expansion has been observed widely in tundra areas across the Arctic. This phenomenon has been partially attributed to increasing temperatures over the past century. However, relationships among shrub expansion, grazing, and human disturbance have been studied little. SW Greenland is a subarctic to low-arctic region with a long and complex land-use history and only modest temperature increases over the past 50 years (0.2 °C decade^{-1}), but changes in shrub cover have not previously been studied in this region. We compiled historical photographs of vegetation in SW Greenland (1898–1974) and repeated the photos in 2010 and 2011. Sixty-four photo pairs were cropped into 133 smaller units and classified by aspect, substrate stability, muskoxen grazing, and human disturbance. The photo material was evaluated by 22 experts with respect to changes in shrub cover, revealing a general increase across the whole data set, and in a subset including only undisturbed sites. Shrub cover increased most on E and SE slopes, in sites with stable substrate, and in areas characterized by human disturbance and without muskoxen grazing. The general shrub cover increase could be caused mainly by changed land-use intensity, but effects of the moderately increased temperatures cannot be ruled out.

DOI: http://dx.doi.org/10.1657/1938-4246-45.4.515

Introduction

In subarctic, arctic, and alpine regions across the northern hemisphere, a marked increase in shrub and tree cover has been reported over the past 50 years based on historical photographs (Kullman, 2006; Tape et al., 2006; Dial et al., 2007). Shrub expansion is important since it causes a wide range of ecosystem effects. Several feedback mechanisms have been proposed including feedback between shrub expansion and reduced albedo, regional warming, higher fire frequency, increased water and nutrient availability, carbon fixation, higher species diversity, and additional shrub invasion (e.g. Chapin et al., 2005; Cornelissen et al., 2007; Myers-Smith et al., 2011). Experimental and descriptive studies have confirmed that survival, growth, and recruitment of alpine and tundra shrubs are positively related to higher temperatures (Dullinger et al., 2003; Walker et al., 2006; Hallinger et al., 2010; Blok et al., 2011). However, recent publications have indicated that also herbivory (Post and Pedersen, 2008), human impact (Kemper and Macdonald, 2009), and permafrost thawing (Lantz et al., 2009) can influence growth of arctic shrubs, thus obscuring the direct effect of warming. To achieve a more complete understanding of the mechanisms involved in shrub expansion, we need information from all parts of the Arctic (Myers-Smith et al., 2011), including areas with less pronounced warming and contrasting land-use histories.

In SW Greenland, trends of increasing temperatures are moderate during the last decades compared with most other polar regions. Actually, in the period 1961–2001 a negative trend of −0.2 °C was recorded for a composite of weather stations in S Greenland (Hanna and Cappelen, 2003). In contrast, the decade 2000–2010 was characterized by a series of warm years resulting in a slight increase in annual average temperatures (0.2 °C decade^{-1}) for the period 1961–2010, while Hansen et al. (2010) reported that average annual surface temperatures increased by 0.2–0.6 °C in the period 1900–2009. This modest warming trend is in contrast with increases of up to 4.2 °C observed for certain areas in arctic North America, arctic Russia, and N Greenland for the same period (Hansen et al., 2010). Some of the most prominent examples of shrub expansion were reported from areas with strong trends in warming of 2 °C decade^{-1} (e.g. Sturm et al., 2001; Tape et al., 2006), while no studies have investigated the long-term trends in landscape-scale shrub cover in SW Greenland.

Arctic areas are characterized by low human population density, difficult access, and large areas of limited economic interest. As a consequence, data from long-term monitoring or quantification of vegetation history are often lacking. Here the use of repeated photographs has become a useful method for detecting vegetation change over long time periods (Tape et al., 2006; Dial et al., 2007; Mackay and Burn, 2011). Some studies had access to orthophotos or oblique aerial photos and used these for the determination of shrub expansion in Alaska (Sturm et al., 2001; Tape et al., 2006; Dial et al., 2007). We found only a few aerial photos of acceptable quality from SW Greenland and, moreover, it would be very costly to take new photos from the same areas. Thus, we used historical (private) photographs taken from the ground, albeit not originally with a particular focus on shrub vegetation. The photographs were subdivided according to a set of rules that allowed us to disentangle the main drivers of vegetation change even in areas with complex and fragmented land-use histories. Due to the irregular nature of photographs taken from the ground, the pictures were evaluated by experts rather than using automated techniques. This allowed evaluation of shrub cover across different types of photos in a landscape characterized by large topographic variation.

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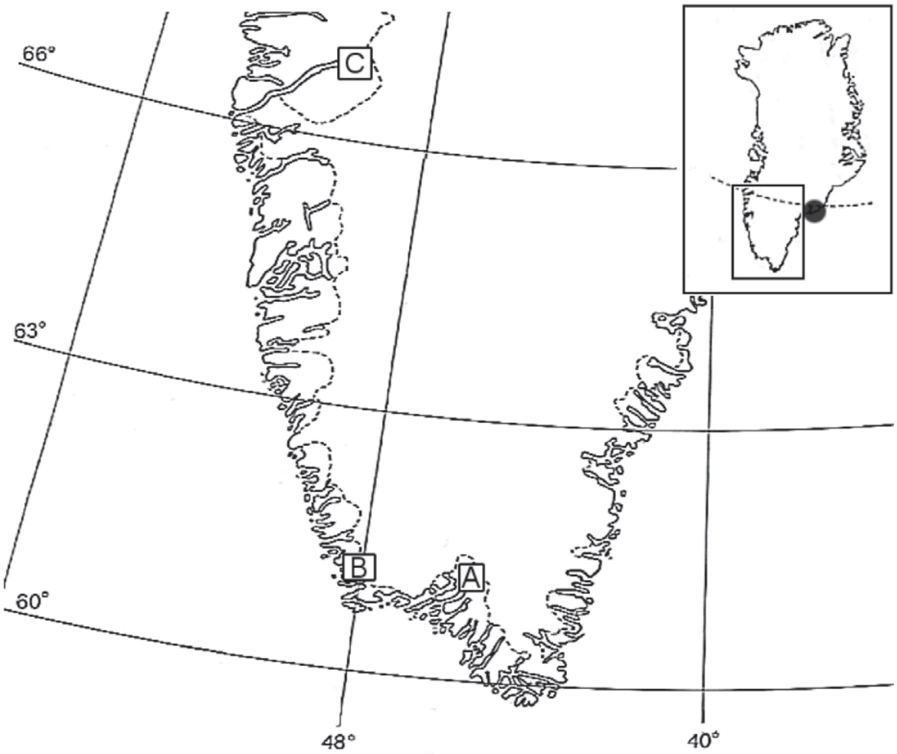

FIGURE 1. Location of the three study areas in SW Greenland: (A) Narsarsuaq, (B) Arsuk Fjord, and (C) Kangerlussuaq. The dashed line represents the limit of the ice cap. In the overview map, the dashed line represents the Arctic Circle, and the dot represents the location of the study by Daniels et al. (2011).

The overall objectives of our study were to analyze shrub dynamics in SW Greenland and to detect correlation to the main drivers over the past 50 years. We investigated five research questions: (1) Has shrub cover changed in SW Greenland despite only moderate temperature increase? (2) Has shrub cover developed differently on different slope aspects? (3) Does unstable substrate (prone to erosion) affect shrub expansion dynamics? (4) How does shrub vegetation respond to human disturbance? (5) Has the introduction of muskoxen influenced shrub dynamics after only two decades of grazing?

Materials and Methods

STUDY AREAS

Three study areas in SW Greenland were chosen according to accessibility (Fig. 1) and are characterized by Low Arctic climate (''Kangerlussuaq'' and ''Arsuk Fjord'') or subarctic climate (''Narsarsuaq''; Table 1). In these areas the ice retreated about 9500 years B.P. (Funder and Hansen, 1996), and the topography is highly varied, with lowland vegetation of vascular plants close to the fjords and in the valleys. The current vegetation is a mosaic of dwarf heath, mires, meadows, deciduous shrubs, and some evergreen (*Juniperus communis* L.). In the continental study areas (Narsarsuaq and Kangerlussuaq), *Salix glauca* L. and *Betula* sp. constitute approximately 60–80% and 20–40% of the shrub vegetation, respectively, while *Alnus viridis* (Chaix) subsp. *crispa (*Aiton) Turril is only present in the Arsuk Fjord area, where it constitutes a considerable part of the shrub vegetation (*S. glauca* 40–60%, *A. viridis* 30–50%, and *Betula* sp. 10%; R. H. Jørgensen, 2011, personal observation).

SW Greenland is dominated by south–north and continental–oceanic climatic gradients (Table 1). Average annual temperatures are higher in the southern study areas, while May–August temperatures are higher in the continental study areas (Narsarsuaq and Kangerlussuaq) compared to the oceanic study area (Arsuk Fjord). Precipitation is generally highest during the summer

TABLE 1

Climate data (Boas and Riddersholm Wang, 2011) and vegetation zones (Nørrevang and Meyer, 1971; Feilberg, 1984) from SW Greenland. Due to incomplete data for precipitation, different time periods were included. — = no data.

Study area (station number)	Vegetation zones	1981–1996 Mean temperature (whole year/Jun–Aug [°C])	1961–1973 Mean monthly precipitation (whole year/Jun–Aug [mm])	1981–1996 Mean monthly precipitation (whole year/ Jun–Aug [mm])
Kangerlussuaq (04231)	Continental, low arctic zone	− 5.5/10.3	—	12/24
Narsarsuaq (04270)	Subcontinental, subarctic zone	0.6/10.2	51/58	54/66
Arsuk Fjord (04261)	(Sub)oceanic, low- or subarctic zone	1.0/8.5	85/80	—

months, and oceanic areas receive considerably higher amounts of precipitation than continental ones (Table 1). Following a model of permafrost distribution for the period 1960–2000 (Daanen et al., 2011), the study areas Narsarsuaq and Arsuk Fjord do not appear to have permafrost, whereas the Kangerlussuaq area had an active layer depth of >3 m in 1960, but with no change during the modeled period. Therefore, large-scale impacts of permafrost thawing on the ground vegetation are unlikely in the study areas.

Under the harsher climate of SE Greenland (Fig. 1), Daniels et al. (2011) suggested a link between relatively modest warming and stable vegetation patterns, but without including effects of land-use history. Our study focuses on SW Greenland because this region shows similar climatic trends but larger human populations, which might be reflected by shrub dynamics. Most studies of large-scale shrub expansion have taken place in areas where direct human influence was low enough to be neglected as a plausible driver of vegetation change (Tape et al., 2006; Dial et al., 2007). However, direct anthropogenic drivers of arctic shrub dynamics are interesting because they may also occur in other arctic regions and will increasingly affect arctic ecosystems.

Despite low human population density and large near natural areas, the land use history of SW Greenland is complex, because A.D. 1000–1500 Norse settlers had introduced cattle, goats, and sheep to this region. The Norwegian-Danish re-colonization in 1721 resulted in some firewood collection and reintroduction of sheep to some areas, while caribou became extinct during the late 19th century. During the past 100 years, sheep grazing, introduction of muskoxen, clearing of fields, vehicle driving, and construction activities have been key factors affecting the landscape of SW Greenland. For areas grazed by sheep or used for intensive hay production, a sharp decline in shrub cover is expected, while in areas not grazed or abandoned after various types of disturbance, shrub expansion might occur. Muskoxen from NE Greenland were introduced to several parts of SW Greenland during the second half of the 20th century (Linell et al., 2000). Shrubs constitute a considerable part of the muskoxen diet (Thing et al., 1987; Larter and Nagy, 2004), and muskoxen are capable of controlling abundance of shrubs in arctic ecosystems (Post and Pedersen, 2008). The long-term effects of these types of land use changes are unknown.

COLLECTION OF PHOTO PAIRS

To obtain a sufficiently large set of suitable photos, we searched local museums and asked people interested in the history and archaeology of SW Greenland for historical photos with vegetation of shrubs, grasslands, and mountain heath, including documentation of archaeological sites. The historical photos were taken in the period 1898–1974 (Appendix Fig. A1), and the repeat photos were taken in the summers of 2010 and 2011 (Figs. 2 and 3). The variation in the duration of the period between repeated photographs (henceforth ''photo-pair period'') evened out singular short-term fluctuations, such as particularly cold summers or years of intense herbivory (e.g. by caribou, muskoxen, hare, or ptarmigan) that could potentially bias the long-term results of the study.

Often the historical photos contained objects in the foreground that were initially the main reason for taking the picture, while the background showed details of the surrounding vegetation. With assistance from local people we identified the exact spot from where the old photos were taken. We tried to make the new ones as similar as possible in terms of light conditions and season. Within the three study areas we managed to re-photograph 110 sites, of which 64 were used in the analysis. Among the selected historical photos, 34 were in black-and-white, 2 were sepia type, and 28 photos were in color.

PHOTO PREPARATION

We selected photo pairs where at least some parts of each photograph allowed a precise comparison of the vegetation. As a consequence of their unplanned nature, some photos contained landscape elements with different slopes, soil conditions, vegetation types, and land-use histories. Thus, the area shown in each photo was divided into homogeneous subareas that could be evaluated unambiguously (Figs. 2 and 3). By consulting local experts we collected information on the areas photographed, especially information on grazing, construction work, and other activities that could have affected the shrub vegetation.

Certain features of the photos would have revealed the locations and the approximate age of a particular photograph to the evaluators and possibly bias their evaluation. To avoid this problem and to present the vegetation in well-arranged units, we cropped each photo pair into one or more subareas (henceforth ''croppings'') according to the following rules: (1) all areas with distinct vegetation were generally included—by ''distinct'' we refer to vegetation sufficiently clear on both photos that a rock and a shrub could be distinguished from each other; (2) contiguous parts of the pictures composed of rock, water, or infrastructure were excluded; (3) if a given area was covered by two photo pairs, the pair with the best visual quality was chosen; (4) if vegetation occurred in different parts of a picture (foreground, middle, and background), these were separated and evaluated independently; (5) if areas of different land-use or substrate type were present in the same photo pair, these were separated and evaluated independently; and (6) if areas were subdivided for one of the reasons stated above, all contiguous areas were evaluated independently. If a cropping pair exhibited differences in color, sharpness, contrast, or light conditions, these features were adjusted to make the two photos appear similar. As a consequence, both croppings were presented in black-and-white (B/W), if the older photograph was in B/W.

The preparation of the photo pairs resulted in 133 pairs of croppings covering a wide range of sites within all three study areas (66 from color photos, 67 from B/W photos). Twenty-two croppings were from photos with only one cropping; 48 croppings were from photos with 2 croppings; 39 croppings were from photos with 3 croppings; 8 croppings were from photos with 4 croppings; 10 croppings were from photos with 5 croppings; and 6 croppings were from a photo with 6 croppings. The range of photo-pair periods was 37–113 years, with a mean of 53 years (Appendix Fig. A1). For 3 croppings we were uncertain about the year of the first photograph (although it was certainly within the age range of the other croppings), and we therefore used the average value for photo-pair period (53 years). Using Google Earth in combination with careful inspection of the croppings, we estimated the land area of each cropping.

Certain parts of SW Greenland are strongly affected by sheep grazing and fodder production. We intentionally omitted these areas

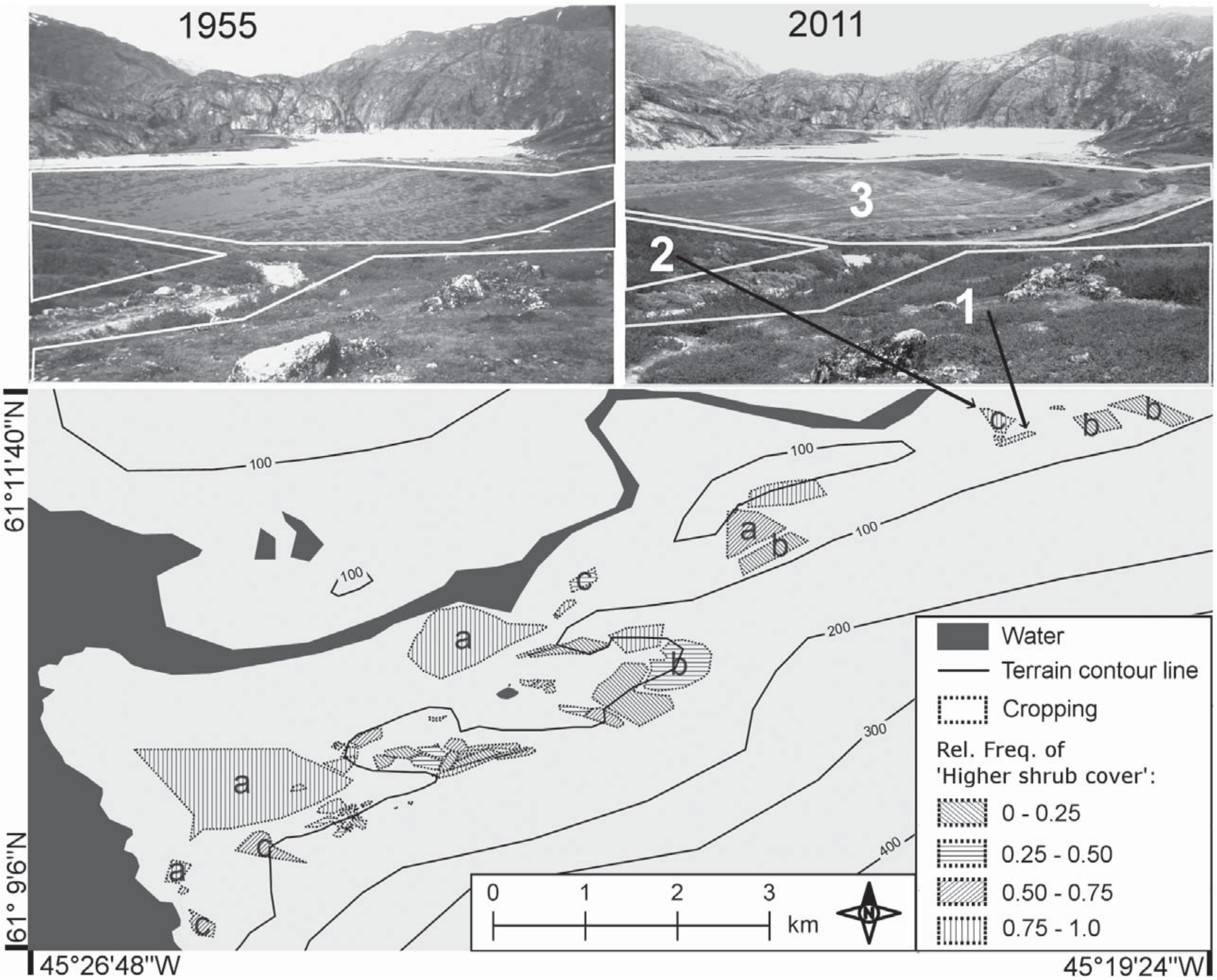

FIGURE 2. Example of a photo pair (1955, 2011) with three croppings in study area A (Narsarsuaq; cf. Fig. 1). Croppings 1 and 2 were included in the data set; 100% and 59% of evaluations indicated ''Higher shrub cover'' for these croppings, respectively. The arrows indicate the positions on the overview map. Cropping 3 was converted to a meadow during the study period and thus not included in the data set. Overview map: Location of all 61 croppings from 20 photo pairs within Narsarsuaq. Letters indicate simplified characteristics of the sites: (a) human disturbance, (b) unstable substrate sites, and (c) no disturbance. Human constructions and small water courses were not included in the map. Hatching indicates relative frequencies of higher shrub cover from evaluation of cropping pairs.

as they show a fast and predictable decline of shrub vegetation. The sample of croppings with various disturbances, location, and topography is not likely to be representative of the general situation in SW Greenland, but includes a wide range of ecological conditions. Broadly, our study can be seen as representative for areas without modern sheep farming, and ''undisturbed'' sites are representative for near-natural shrub dynamics.

EXPLANATORY FACTORS FOR PHOTO CLASSIFICATION

The landscape of SW Greenland is characterized by high topographic variation, including steep slopes and other areas with unstable substrate. In Google Earth and from topographic maps, we classified the croppings into 5 aspect categories based on the predominant slope exposition: ''North and northeast'' (10 croppings), ''East and southeast'' (17), ''South and southwest'' (48), ''West and northwest'' (47), and ''Multiple aspects and flat'' (9); each cropping was categorized as featuring ''Unstable substrate'' (28) or ''Stable substrate'' (105), based on loose substrate visible.

The study areas contained sites characterized by strong human impact, such as road construction, leveling for construction works, or excavation of archaeological sites, thus disturbing shrub vegetation. Around settlements in SW Greenland, introduced shrubs and trees (predominantly conifers) have been planted during the past 50 years. We had one series of croppings where scattered tree planting had been carried out within existing shrub vegetation. Croppings from this area were included, albeit excluding croppings where introduced species were visible. In some areas close to settlements we were suspecting that some degree of animal husbandry had taken place in 1774–1960; we regarded these activities as human disturbance. Information on human disturbance was divided into three categories, i.e. ''Yes'' (17), ''No'' (78), and ''Uncertain'' (38).

For 8 cropping pairs the new photograph was taken in the summer, whereas the old one was from winter or spring, potentially causing a false impression of shrub expansion. Some old photos had no seasonal information. Thus, croppings were categorized

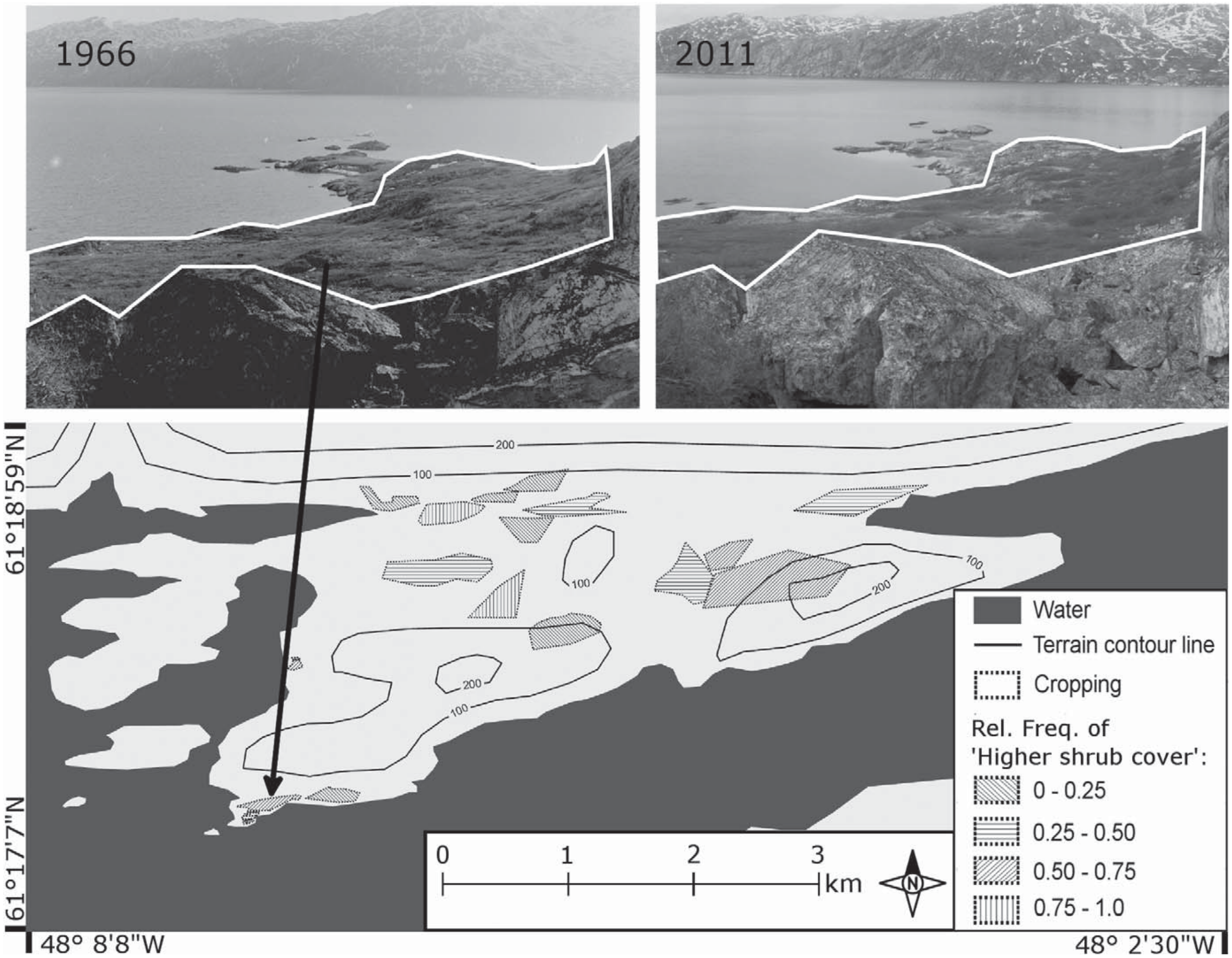

FIGURE 3. Example of a photo pair (1966, 2011) with one cropping in study area B (Arsuk Fjord; cf. Fig. 1). Sixty-eight percent of evaluations indicated ''Higher shrub cover'' for this cropping. The arrow indicates the position of the cropping on the overview map. Overview map: location of 22 croppings from eight photo pairs within a selected part of Arsuk Fjord. Human constructions and small water courses were not included in the map. Hatching indicates relative frequencies of higher shrub cover from evaluation of cropping pairs.

as ''No seasonal mismatch'' (112), ''Mismatch'' (16), or ''No information'' (5).

We used the information from Linell et al. (2000) and the local wildlife administration to classify each cropping as potentially influenced by ''Introduced muskoxen during the photo-pair period'' (49) and ''Muskoxen-free areas'' (84). Due to the limited records of exact spatial location of historic reindeer grazing and Norse settlements within the southern study areas, we did not include these factors. This implies that some ''undisturbed'' sites may have been affected by these drivers.

PHOTO EVALUATION

In order to make a reliable evaluation of the vegetation in the photos, we presented the cropping pairs to a panel of evaluators without knowledge of the particular sites and the specific land-use histories. The panel consisted of 22 academics (6 nationalities) with some experience in arctic or alpine vegetation. Eight evaluators had research experience with arctic vegetation, and 10 had visited areas with similar vegetation.

The croppings were shown in pairs of randomized order so the evaluators would not know whether the old or new cropping was shown first, although they might in some cases be able to guess it. The pairs were further randomized to mix all study areas, site conditions, land-use histories, and source photos. The cropping pairs were arranged in a slideshow so that each evaluator could flip back and forth to carefully assess possible differences in vegetation cover. The evaluators were instructed to objectively examine each pair of croppings with respect to change in shrub cover, and to choose among the following assessments: shrub cover ''Lower,'' ''Unchanged,'' ''Higher,'' or ''Undecided.'' The evaluators were informed that the croppings contained random combinations of different land-use histories and disturbances, so no general tendencies could be expected.

A total of 22 evaluations of the full set of photo material were returned. The number of (unintended) missing observations was 6

(0.21%). The evaluators stated ''Undecided'' 432 times (15%), and these observations were omitted from the analysis.

DATA ANALYSIS

We analyzed the general trend of shrub cover using a pairwise *t*-test comparing the mean proportions of statements indicating ''Higher shrub cover'' to the total mean proportions of ''Lower'' and ''Unchanged'' statements. The analysis was performed for the whole set of croppings excluding those with seasonal mismatch. We repeated this analysis on a subset where also croppings with human disturbance, introduced muskoxen, and seasonal mismatch had been removed.

We used a generalized linear model of the logit family to analyze factors influencing the change in cover. We used the statistical software R version 2.12.1 (R Core Team, 2012), and the extension packages LME4 (Bates et al., 2012) and CAR (Fox and Weisberg, 2011) for the analysis. We used ''Higher shrub cover'' statements as a response variable and included all available explanatory variables in the full model. Evaluators were included as a random factor, and evaluations of the same cropping pair were regarded as replicates. Cropping area and time period were log transformed. The basic logit model can be expressed as:

$$\begin{aligned} \ln(P_{HSC(ij)}/(1 - P_{HSC(ij)})) &= \alpha + \beta_1 \times \ln(Area_i) \\ &+ \beta_2 \times \ln(T_i) + \gamma(Study\ area_i) + \delta(Aspect_i) \\ &+ \rho\,(Season_i) + \tau\,(Human\ disturbance_i) + \eta_1 \\ &\times Substrate_i + \eta_2 \times Color_i + \eta_3 \times Muskoxen_i \\ &+ \lambda\,(Evaluator_j), \end{aligned} \tag{1}$$

where $i = 1 \ldots 133$ are the croppings; $j = 1 \ldots 22$ the evaluators; $P_{HSC(ij)}$ the probability of observing ''Higher shrub cover'' $\lambda \sim N(0,\sigma^2)$; a random evaluator effect; α, β_1, β_2, γ, δ, ρ, τ, and $\eta_1 \ldots \eta_3$ fixed parameters to be estimated for the effect of: $Area_i$ (the area of cropping i in m^2); T_i (the photo period in years); $Study\ area_i$ (''Kangerlusuaq,'' ''Narsarsuaq,'' ''Arsuk Fjord''); $Aspect_i$ (''North or northeast,'' ''East or southeast,'' ''South or southwest,'' ''West or northwest,'' or ''Flat or multiple aspects''); $Human\ disturbance_i$ (''Yes,'' ''No,'' and ''Uncertain''); $Season_i$ (''Seasonal mismatch,'' ''No mismatch,'' or ''No information''); while $Substrate_i$, $Muskoxen_i$, and $Color_i$ were dummy variables indicating whether substrate was unstable, cropping pair i was in color, or muskoxen were introduced in the period, respectively.

We considered treating croppings originating from the same photograph as a ''block,'' but this was not possible because the number of replicates per photograph was low and irregular. Moreover, croppings from the same photograph often contained contrasting area classifications, and croppings from different photographs sometimes contained areas that were geographically closer to each other than croppings from the same photograph. Finally the evaluation of the croppings was randomized, so the evaluators had no possibility to relate croppings from the same photograph to each other.

Due to the limited number of croppings it was decided to apply a 10% significance level when testing parameters. Models were reduced by type II testing, always removing the variable with highest *p*-value. As the reduction progressed, the *p*-values of the remaining variables tended to decrease. In turns we included interactions between variables in the full model (''full data set''), but they were rarely represented well enough in all of the combinations. The final models, therefore, do not include interactions.

Presence or absence of muskoxen represented a special case. We only had croppings of both presence and absence of muskoxen from the study area Arsuk Fjord, whereas croppings from Kangerlussuaq could all be influenced by muskoxen grazing, and muskoxen grazing did not occur at Narsarsuaq. Thus, the interaction between study area and muskoxen could not be modeled. To analyze the effect of muskoxen, a separate model was prepared from a subset including only croppings from Arsuk Fjord (Table 2).

Results

OVERALL TREND IN SHRUB COVER AND METHODOLOGICAL RESULTS

Evaluations of the 112 croppings without seasonal mismatch indicated that an overall increase in shrub cover occurred in the past 50 years. For all croppings without seasonal mismatch, the mean proportion of cropping pairs with higher shrub cover was greater than the mean proportions of unchanged or lower shrub cover, respectively (and the mean of the cumulated proportions of lower and unchanged, Fig. 4A). The difference was highly significant (*t*-test, $t = 3.28$, $n_{\mathrm{croppings}} = 112$, $p < 0.0014$) when comparing mean proportions of higher shrub cover to the mean of the cumulated proportions of lower and unchanged. Evaluating a subset including only croppings with no human disturbance, no introduced muskoxen, and no seasonal mismatch (Fig. 4B) also yielded significant results ($t = 2.24$, $n_{\mathrm{croppings}} = 50$, $p < 0.0298$). This suggests that shrub cover in the study areas had generally increased, even in sites with no registered disturbance.

Individual variables affecting the likelihood of respondents observing shrub expansion were analyzed with the binary logit-model. We present the reduced models in Table 2, which also contains the *p*-values of the contrasts. Cropping area was weakly significant in the model for the full data set. The negative sign of the estimate indicates that larger cropping areas were less likely to show a shrub cover increase than small cropping areas. Photo-pair period was non-significant even when the 3 croppings with lacking information about photo-pair period were excluded from the analysis.

The positive estimate of seasonal mismatch was only significant in the reduced model for the Arsuk Fjord area, which is due to the fact that croppings with seasonal mismatch were almost solely present in this study area. As expected, the sign of the estimate was positive for croppings with seasonal mismatch, indicating that evaluators were more likely to report an increasing shrub cover if the older of the two croppings was taken without leaves and the new one with leaves. In a similar way, and for the same reason, the type of photos (color, B/W) was only significant in the reduced model for the Arsuk Fjord area. The sign of the estimate was positive for color croppings, indicating that evaluators were more likely to see increases in shrub cover if the pair of croppings was in color than if it was in B/W.

EFFECTS OF SLOPE ASPECT AND SUBSTRATE STABILITY

Parameter estimates for the full data set showed somewhat lower values of shrub expansion for ''North and northeast'' facing slopes (compared to Fig. 5). Model estimates showed highest prob-

TABLE 2

Summary statistics for the reduced logit models for the full data set and for the Arsuk Fjord subset of the data. Binary logit models express the probability of increased shrub cover and test results of the effects of individual variable classes. Significant contrasts of variable classes are indicated by capital letters: A = significantly different from ''south and southwest''. B = significantly different from ''flat or multiple''. C = significantly different from ''east or southeast''. D = significantly different from ''west or northwest''. E = significantly different from ''no info.''.

		Test of variable classes			
		Reduced model, full data set		Reduced model, Arsuk Fjord croppings	
Variable	Variable class	Estimate (std. error)	Pr(>|z|)	Estimate (std. error)	Pr(>|z|)
Intercept		1.180 (0.846)	0.163	−1.2089 (0.5479)	0.027
Cropping area	Log (m^2) (continuous)	−0.134 (0.078)	0.088	NS, omitted	
Substrate ♣	Unstable	−1.006 (0.506)	0.047	NS, omitted	
Aspect ♦	W or NW	0.738 (0.487)	0.130	2.810 (0.651)	0,000 A
	N or NE	0.940 (0.836)	0.261	−3.014 (2.320)	0.193 CD
	E or SE	2.018 (0.624)	0.001 ABD	3.440 (0.966)	0.000 AB
	Flat/multiple	−0.474 (0.828)	0.567	0.332 (0.935)	0.723 D
Study area ♥	Kangerlussuaq	NS, omitted		NA due to the reduced dataset	
	Narsarsuaq	NS, omitted		NA due to the reduced dataset	
Photo-pair period	Log(years) (continuous)	NS, omitted		NS, omitted	
Seasonal mismatch ♠	Yes	NS, omitted		2.515 (0.778)	0.001
	No info.	NS, omitted		1.577 (1.208)	0.192
Human disturbance ℵ	Uncertain	−0.017 (0.475)	0.970	0.257 (0.693)	0.711
	Yes	2.454 (0.634)	0.000 E	5.614 (1.606)	0.000 E
Muskoxen introduced ℑ	Yes	NS, omitted		−1.874 (0.662)	0.005
Colour photos ℜ	Yes	NS, omitted		2.555 (1.139)	0.025

Reference variable classes: ♣: Stable, ♦: S or SW, ♥: Arsuk Fjord, ♠:No, ℵ:No, ℑ:No, ℜ: No.

abilities for shrub expansion for croppings facing ''East or southeast.'' Only ''East or Southeast'' was significantly different from other aspect classes, and only from the classes ''Multiple aspects or flat,'' ''South or southwest,'' and ''North or northwest.'' Slope exposition ''East and southeast'' was thus responsible for the significant effect of the variable. With 19 croppings in the full data set, ''East and southeast'' was fairly well represented.

Results for the full model showed significantly more often increased shrub cover on stable sites compared to those characterized by unstable substrate (Fig. 6); the two variable classes were both well represented.

EFFECTS OF HUMAN DISTURBANCE

We found significant positive effects of human disturbance on shrub expansion. Areas with uncertain information about human disturbance had lower estimates, were significantly different from areas with disturbance, and showed more variation (Fig. 7).

As an example of the position of the croppings within the study area Narsarsuaq, some croppings and their relative frequencies of higher shrub cover are shown in Figure 2, and for the study area Arsuk Fjord, Figure 3. Croppings with human disturbance were generally characterized by high frequencies of shrub expansion, whereas sites with unstable substrate had low frequencies.

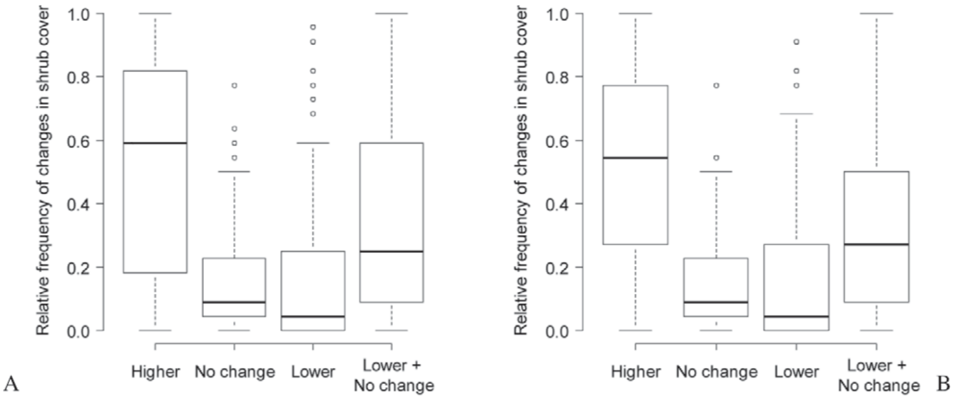

FIGURE 4. Relative frequency of three categories of shrub development, and the sum of lower and no change; each pair of croppings assessed by 22 evaluators. (A) The full data set excluding croppings with seasonal mismatch (112 croppings). (B) Undisturbed sites, including only croppings with no human disturbance, no introduced muskoxen, and no seasonal mismatch (50 croppings). In both (A) and (B) the difference between observing higher shrub cover and lower + no change was highly significant when compared with *T*-tests.

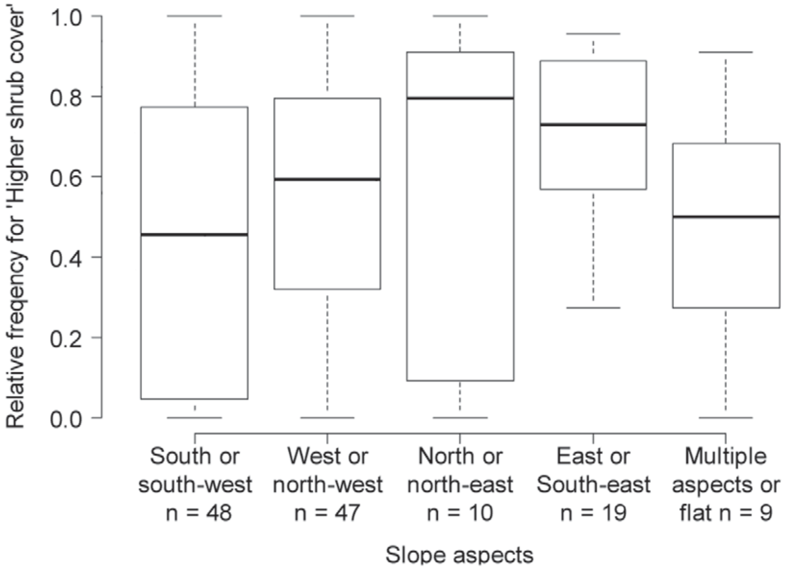

FIGURE 5. Relative frequency of ''Higher shrub cover'' at different aspects for the full data set (133 croppings, each assessed by 22 evaluators). Model results indicated that only ''East or Southeast'' was significantly different from other aspect classes, and only from the classes ''Multiple aspects or flat,'' ''South or southwest,'' and ''North or northwest.''

EFFECT OF MUSKOXEN GRAZING

In the study area Arsuk Fjord there were significantly lower frequencies of apparent shrub expansion in sites where muskoxen had been introduced compared to sites without muskoxen grazing (23 croppings without muskoxen, 38 with muskoxen; Table 2).

Discussion

OVERALL CHANGES IN SHRUB COVER

The study areas in SW Greenland showed consistent shrub expansion over the past 50 years, even when sites characterized by disturbance were excluded from the analysis. This shrub cover increase is in contrast to observations by Daniels et al. (2011) in undisturbed Low Arctic tundra in the Tasiilaq area in SE Greenland. Tasiilaq differs from our study areas by having a harsher climate and no previous Norse settlements. Moreover, it is unclear whether a caribou population has ever existed in the Tasiilaq area (Meldgaard, 1986). The Tasiilaq area experienced a stronger annual average warming in the period 1961–2010 than SW Greenland (Tasiilaq, +0.40 °C decade^{-1}; Narsarsuaq, +0.15 °C decade^{-1}; Cappelen, 2011), but the vegetation in Tasiilaq was still characterized as ''stable.'' This suggests that the different land-use histories could be responsible for the marked shrub increase observed in SW Greenland.

The Little Ice Age was particularly strong in the Atlantic parts of the Arctic, and ended around late 19th century (Miller et al., 2010). A delayed reaction to the ending of the Little Ice Age can still not be excluded but is rather unlikely to be the main reason for the shrub expansion, considering the results of the small-scale study by Daniels et al. (2011).

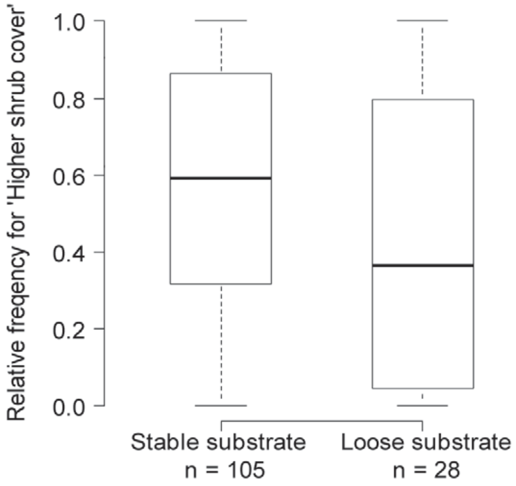

FIGURE 6. Relative frequencies of the category ''Higher shrub cover'' at sites with stable vs. unstable substrate (133 photos, each assessed by 22 evaluators). Model results indicated that stable sites had significantly increased shrub cover compared to sites with unstable substrate.

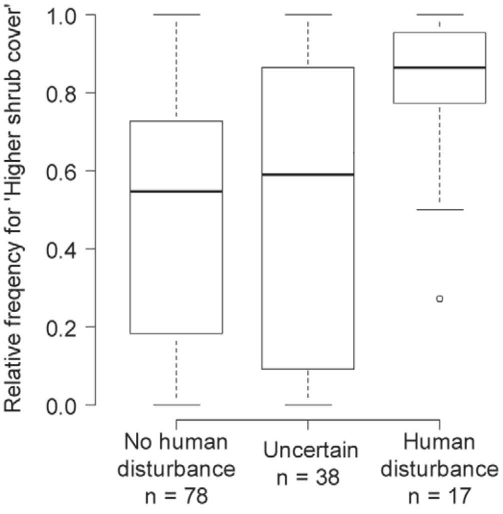

FIGURE 7. Relative frequencies of the category ''Higher shrub cover,'' with and without influence of human disturbance (112 photos, each assessed by 22 evaluators). Model results indicated significant positive effects of human disturbance on shrub cover compared to areas with no info and areas with uncertainty.

Thus, the shrub increase in the current study is most probably due to improved growth conditions caused by a combination of release from Norse settlement activities, reduced firewood collection, and lack of caribou grazing. However, an effect of improved climatic conditions on shrub cover cannot be completely ruled out based on the results of the current study. More knowledge is needed on the effects of various climatic factors in SW Greenland and their past development over time (but see Jørgensen et al., in prep.).

METHODOLOGICAL CONSIDERATIONS

A negative effect of cropping area on shrub cover statements implies that evaluators are less likely to detect increasing shrub cover for large-area croppings than for smaller ones. This indicates that evaluations of larger croppings have been more conservative, which makes sense since larger cropping area also means longer distance *per se* from the photographer to the area shown in the cropping. Long distance, and thus less clear details, would generally limit clear statements. Larger croppings are also more likely to contain contradicting developments leading to less extreme average outcomes and possibly confusing the evaluators, which would also explain the pattern observed.

When using the method of cropping of historical photos taken from the ground, where a completely homogeneous cropping material can never be ensured, the significant effect of cropping area shows the importance of including this variable in the analysis, despite the fact that it is not of particular interest for the results of the study. Inclusion of this variable is a prerequisite for using this type of photos, where high-resolution aerial photo pairs are not available.

The documented positive bias on shrub cover statements caused by seasonal mismatch was expected, since the first photo was in these cases taken without leaves, and the second with leaves. Thus, as a conservative estimate was desired, it was deemed appropriate to exclude croppings with this feature from the analysis of the overall trend in shrub cover. Given that more details are visible in color croppings, we expected the evaluation of croppings in color to be more accurate. The estimated positive effect of color croppings compared to croppings in B/W implies that the detected positive trend in the analysis of the overall shrub cover (Fig. 4), including about 50% B/W croppings, was conservative.

SLOPE EXPOSITION, SUBSTRATE TYPE, AND SHRUB EXPANSION

We observed higher probabilities of increased shrub cover on east- and southeast-facing slopes, whereas the other aspect categories did not differ significantly from each other. Dial et al. (2007) reported that areas covered by trees expanded most on northern slopes, and explained this tendency by drought stress caused by increasing temperatures being less pronounced on the northern slopes, thus allowing trees to benefit from the warming. A similar tendency was not evident for our data set. The lower frequency of shrub expansion at sites with unstable substrate is most likely a result of repeated disturbance not allowing shrub expansion over a long time period.

HUMAN DISTURBANCE AND SHRUB EXPANSION

The response of shrubs to human disturbance depends on the timing of the disturbance. Our study contains mostly cases where the disturbance occurred before the photo-pair period. In these cases shrub cover was reduced or damaged by human activities before the study period, thus restarting succession, and the growth continued at least until the vegetation had reached the state of development that it had before the disturbance.

A study conducted by Kemper and Macdonald (2009) in Low Arctic Canada showed increased cover of deciduous shrubs 18–33 years after disturbance from heavy machinery compared to undisturbed ambient tundra. By contrast a study from western Russia reported higher proportion of graminoids at the expense of deciduous shrubs on 15- to 20-year-old vehicle tracks (Kumpula et al., 2011). While our study did not permit determination of increases compared to pre-disturbance conditions, we can report a strong positive reaction of deciduous shrubs to early human disturbances at the time scale of the study. As a consequence of the strong reaction, it would in most cases be difficult to readily detect a previous disturbance solely based on the visual impression of the vegetation.

Forbes et al. (2001) described examples where graminoids invaded areas after disturbance, and in combination with grazing form self-perpetuating mats in High Arctic and Low Arctic regions. In the current study, although some graminoids were often visible on old and recent croppings, the strong reaction of shrubs after disturbance indicated that a long graminoid-dominated stage is less pronounced. This could be an effect of low grazing pressure or the generally higher succession speed characterizing Low Arctic and subarctic conditions.

MUSKOXEN GRAZING CONTROLLING SHRUB EXPANSION

The significant negative effect on the probability of observing higher shrub cover in areas grazed by muskoxen shows the potential of this animal to control shrub abundance. Muskoxen were introduced in 1962 and 1987 to the study areas Kangerlussuaq and Arsuk Fjord, respectively, and since then the populations have multiplied several times. While the capability of muskoxen to control shrub growth has also been documented with exclosure experiments (Post and Pedersen, 2008), this study to our knowledge is the first to show it on a landscape scale.

Conclusion

This study demonstrates the successful use of repeated photographs taken from the ground as a means of assessing vegetation changes over time, and the results document the effects of several drivers of shrub dynamics The temporal scale of our study with a mean period of 53 years between the paired photos was sufficient to capture vegetation change. Caribou became extinct in the two southernmost study areas in the 19th century, Norse settlers disappeared from Greenland in the 15th century, and glaciers retreated 9500 years B.P., each of which has presumably affected shrub vegetation. From dendrochronological analyses of stems of *A. viridis* subsp. *crispa* from Arsuk Fjord, we know that stem ages of 60–70 years are not uncommon in that species (R. H. Jørgensen, unpublished data), but individuals can persist for hundreds and possibly even thousands of years due to resprouting (Wilson et al., 1985). This underlines the fact that the documented part of the history of the SW Greenlandic landscape is rather short given the long persistence of clonal shrubs. Contrastingly, the populations of arctic animals including muskoxen and caribou are highly variable (Forchhammer and Boertmann, 1993; Vors and Boyce, 2009), making stable vegetation equilibriums unlikely to exist. In contrast to the report by Daniels et al. (2011), who observed stable vegetation in E Greenland under similar climatic trends, we did observe increasing shrub cover in this study. We conclude that although the modest warming in the last two decades may have contributed to shrub expansion, part of the change could be caused by changes in intensity of land use.

Acknowledgments

We thank Arktisk Institut, Narsarsuaq Museum, Ivittuut Mine- and Mineral-museum, Kangerlussuaq Museum, and their employees for providing historical photos. We are grateful to all photographers who initially took the historical photos and made them available through the aforementioned museums. We thank Per Lotz for his extensive work on Norse settlements including well-documented landscape photographs from the Arsuk Fjord area. We are indebted to the Danish Greenland Command for logistic support, and the employees for sharing their knowledge of the Arsuk Fjord area. Ole Guldager, Per Nukaaraq Hansen, John Arsuk, and Erling Dahl Jensen contributed with their invaluable knowledge about the study areas. Also, thanks are due to field assistants Jørgen Jørgensen and Ole Guldager for taking photographs. We are most obliged to the 22 evaluators for their reliable comparisons of the croppings. Finally, we acknowledge helpful comments and suggestions by two referees and the editor of the journal.

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MS accepted June 2013

APPENDIX

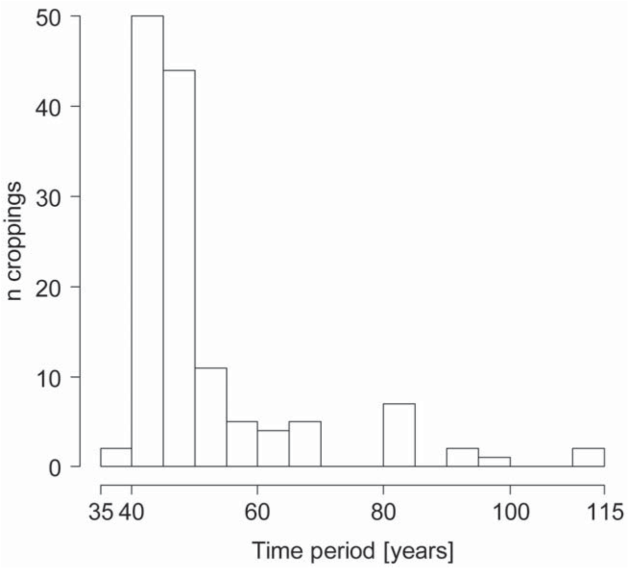

FIGURE A1. Distribution of time (photo-pair period) between repeated photos for all 133 photo croppings analyzed.