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Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades

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Abstract

Numerous studies have evaluated the dynamics of Arctic tundra vegetation throughout the past few decades, using remotely sensed proxies of vegetation, such as the normalized difference vegetation index (NDVI). While extremely useful, these coarse-scale satellite-derived measurements give us minimal information with regard to how these changes are being expressed on the ground, in terms of tundra structure and function. In this analysis, we used a strong regression model between NDVI and aboveground tundra phytomass, developed from extensive field-harvested measurements of vegetation biomass, to estimate the biomass dynamics of the circumpolar Arctic tundra over the period of continuous satellite records (1982–2010). We found that the southernmost tundra subzones (C-E) dominate the increases in biomass, ranging from 20 to 26%, although there was a high degree of heterogeneity across regions, floristic provinces, and vegetation types. The estimated increase in carbon of the aboveground live vegetation of 0.40 Pg C over the past three decades is substantial, although quite small relative to anthropogenic C emissions. However, a 19.8% average increase in aboveground biomass has major implications for nearly all aspects of tundra ecosystems including hydrology, active layer depths, permafrost regimes, wildlife and human use of Arctic landscapes. While spatially extensive on-the-ground measurements of tundra biomass were conducted in the development of this analysis, validation is still impossible without more repeated, long-term monitoring of Arctic tundra biomass in the field.

Keywords: Arctic tundra, circumpolar, NDVI, remote sensing, spatial and temporal dynamics, vegetation biomass

1. Introduction

Numerous observations of the Arctic tundra over time, using both field and remotely sensed methodologies, have indicated that the aboveground component of tundra vegetation has been increasing since at least the middle of the 20th century. An extensive set of repeat photographs of areas throughout the North Slope of Alaska indicated an expansion of several

types of shrubs, including alder, willow and birch, largely on hillslopes and in valley bottoms over the past 50 or so years (Tape *et al* 2006, Sturm *et al* 2001). Multi-spectral remote sensing from Earth-orbiting satellites corroborated and added to this finding for northern Alaska (Jia *et al* 2003), detecting a 16.9% increase in the peak normalized difference vegetation index (NDVI—an index of green vegetation) over the period from 1981 to 2001, from Advanced Very High

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Resolution Radiometer (AVHRR) sensors with 8 km \times 8 km pixel resolution (and from 1990 to 2000 with 1 km resolution). In a broader study of Alaska, Verbyla (2008) confirmed these findings of increased annual maximum NDVI for the Alaskan tundra from 1982 to 2003, with the greatest changes occurring within the Alaska Coastal Plain, also noting rapid increases in NDVI during the early part of the growing season (first half of June).

For the high latitudes of continental North America (Alaska and Canada), numerous studies have examined these greening trends, also using coarse-resolution, multispectral remote sensors. Goetz et al (2005) found increased photosynthetic activity (i.e. NDVI), using the 8 km AVHRR data for North American tundra over the period 1981–2003, including an earlier onset to the tundra growing season. Bunn et al (2005) analyzed the same dataset from 1981 to 2000, and found that tundra photosynthetic activity responded largely to maximum summer temperatures, which increased over this time period. For Canada specifically, Jia et al (2009) found that greening has occurred in all five Arctic tundra bioclimate subzones (Walker et al 2005 subzones A-E ranging from north to south), with increases in peak NDVI of 0.49-0.79% yr⁻¹ for the High Arctic (subzones A-C) and increases of 0.46–0.67% yr⁻¹ for the Low Arctic (subzones D–E) over the period 1982-2006. Arctic subzones A-C exhibited a trend of earlier peak NDVI over time, whereas subzones D-E had earlier onsets of vegetation growth. In a finer resolution study, Pouliot et al (2009) used both 1 km AVHRR data and 30 m Landsat data to identify significant positive trends in NDVI for 22% of the Canadian land surface from 1985 to 2006, with some of the greatest increases occurring in the tundra. Olthof et al (2008) also indicated that increasing vegetation trends in Canadian tundra were greater for areas dominated by vascular plants, as opposed to those that were lichen-dominated.

Finally, at the circumpolar scale, the greening of the northern high latitudes and the Arctic tundra specifically has been observed with remotely sensed data for some time (Myneni et al 1997, Tucker et al 2001, Zhou et al 2001, Slayback et al 2003), and more recent studies have noted the continuation of this trend (Bunn and Goetz 2006, Bunn et al 2007, Neigh et al 2008, Bhatt et al 2010). Neigh et al (2008) used several higher resolution datasets (e.g. Landsat, IKONOS) to elucidate the causal mechanisms for change and found that tundra vegetation was largely responding to climatic changes. Bhatt et al (2010) examined the link between sea-ice decline and tundra vegetation increases, dividing the circumpolar Arctic into oceanic sub-regions sensu Treshnikov (1985). They found a nearly ubiquitous greening of the near-coastal tundra, in both the maximum NDVI and the seasonally integrated NDVI, with some decline in the Bering and West Chukchi regions. Interestingly, the tundra vegetation of North America appears to be greening to a greater extent than that of Eurasia (Dye and Tucker 2003, Bunn et al 2007, Bhatt et al 2010, Goetz et al 2011). Bhatt et al (2010) found a 9% increase in the maximum NDVI for North American tundra from 1982 to 2008, but only a 2% increase for Eurasian tundra.

While there are extensive studies of Arctic vegetation change over the past several decades, there are still many aspects of these dynamics that are not well understood. For one, we do not really have a good sense for what changes of NDVI actually mean on the ground. Several studies have developed and used relationships between NDVI and aboveground vegetation biomass (phytomass) for Arctic tundra (Shippert et al 1995, Boelman et al 2003, 2005, Walker et al 2003, Raynolds et al 2006, Reidel et al 2005, Jia et al 2006). Some of these studies constructed relationships between NDVI from hand-held spectrometry and aboveground phytomass for specific tundra sites (Boelman et al 2003, 2005, Reidel et al 2005), while others used a more regional scale approach with field biomass data and satellite-derived NDVI across some different locations (Shippert et al 1995, Walker et al 2003, Jia et al 2006). Raynolds et al (2006) used the NDVI-biomass relationships developed for the Alaska North Slope from Walker et al (2003), combined with published biomass data for the low and high ends of the NDVI gradient to estimate circumpolar aboveground biomass. This NDVI-biomass relationship has recently been modified with improved remote sensing information and biomass data from two extensive Arctic transects (Walker et al 2011, Raynolds et al 2012).

A second gap in our understanding of tundra phytomass dynamics is that a comprehensive spatial analysis of vegetation change within the Arctic tundra biome has not been conducted. Both Bhatt et al (2010) and Jia et al (2006) have made advances in this regard, with Bhatt et al (2010) analyzing heterogeneity across Arctic oceanic sub-regions, and Jia et al (2006) analyzing NDVI changes across Arctic tundra subzones, but only for Canada. In the present study, we attempt to fill these two gaps. First, we use a newly developed and highly robust relationship between satellite NDVI and field-sampled aboveground tundra biomass, constructed from points along North American and Eurasian Arctic transects, encompassing the full latitudinal extent of Arctic tundra (Raynolds et al 2012). Second, we examine the biomass dynamics throughout the circumpolar Arctic tundra with respect to geographic regions, tundra bioclimatic subzones, floristic provinces, and vegetation types.

2. Methods

Aboveground biomass data were collected along two transects that spanned the full climate range of the Arctic (figure 1). The North America Arctic Transect was sampled from 2002 to 2006 and included eight field locations (Walker *et al* 2012). The Eurasian Arctic Transect was sampled from 2007 to 2010 and included five field locations (Walker *et al* 2011). The field locations were chosen to represent the zonal vegetation of each of the five Arctic bioclimate subzones as displayed on the Circumpolar Arctic Vegetation Map (CAVM) (Walker *et al* 2005)—from subzone A in the north where shrubs are absent, mosses and lichens are dominant, and bare ground is common, to subzone E in the south, which is characterized by complete ground cover and abundant erect dwarf shrubs.

At each of the 13 field locations (eight in North America and five in Eurasia), several 20 cm \times 50 cm quadrats were

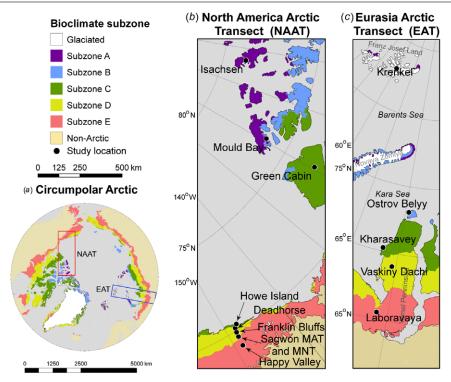


Figure 1. Locations of the North American and Eurasian Arctic Transects, 13 field sampling sites, and the five Arctic subzones (A–E).

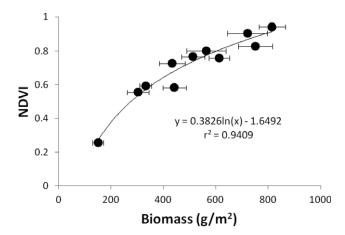


Figure 2. The relationship between aboveground tundra biomass (g m⁻²) and NDVI for 13 field sites across North America and Eurasia. Data are from Raynolds *et al* (2012). Bars are \pm one standard error for the biomass samples within each site.

harvested for aboveground biomass estimates. For the North American Arctic Transect field sites, where vegetation cover was more heterogeneous, five samples were taken from each of several microhabitats identified within a 10 m \times 10 m landscape. Landscape level phytomass was then calculated as the area-weighted average of the component vegetation types, based on the 10 m \times 10 m map. For the Eurasian Arctic Transect, five samples were harvested for each field site, distributed uniformly within a 50 m \times 50 m grid. These five values were averaged for a landscape level estimate. When sampling, the 20 cm \times 50 cm sections of tundra were removed from the field intact. Vegetation above the dead moss layer

(or above the mineral soil layer, when there was no dead moss present) was removed, dried, and weighed for estimates of aboveground biomass. Raynolds *et al* (2012) describe the biomass sampling procedures in greater detail.

The NDVI for each sampling date and location were extracted from a maximum annual NDVI dataset based on AVHRR 12.5 km pixel data extending from 1982 to 2010. This Global Inventory Modeling and Mapping Studies 3rd generation (GIMMS3g) dataset was developed specifically for polar areas, with a polar projection and revised calibration optimized for the Arctic. The new dataset addresses several issues in the previous GIMMS dataset for polar areas, including a calibration discontinuity at 72°N, and areas of the Arctic that were missing in previous versions of the GIMMS NDVI data. This new GIMMS3g dataset was first used in Bhatt et al (2010), and the methodologies describing the dataset development have yet to be published, however the data compare well to those from the Moderate Resolution Imaging Spectroradiometer (MODIS) across their years of overlap (Pinzon et al 2011). We used the single AVHRR GIMMS3g pixel that encompassed each of our field locations for developing the relationship between NDVI and aboveground phytomass.

The relationship between aboveground biomass and NDVI was calculated using the logarithmic regression (NDVI = 0.383 ln(biomass) - 1.649, r^2 = 0.94, p < 0.001, where biomass is in g m⁻²) (figure 2). This relationship was applied to the GIMMS3g maximum annual NDVI data (1982–2010) to calculate biomass. Trends in biomass were calculated by applying a linear regression to the time series for each pixel. The significance of the trends was calculated, and only pixels with significant trends (p < 0.05) are displayed on

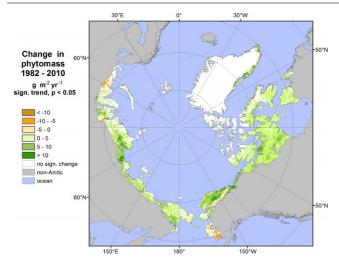


Figure 3. Significant changes (p < 0.05) in aboveground tundra phytomass from 1982 to 2010.

the trend map (figure 3). Summaries of aboveground biomass, changes in biomass, and trends in biomass were calculated for different portions of the Arctic, as defined by the CAVM.

3. Results

In all cases, the tundra phytomass (biomass) being considered here is only the aboveground fraction as calculated from the remotely sensed NDVI and the relationship between field-sampled aboveground phytomass and NDVI. The aboveground phytomass of circumpolar Arctic tundra increased from 2.02 Pg (1015 g) in 1982 to 2.41 Pg in 2010 for a total increase of 0.40 Pg, a change of \sim 19.8% over a 29 yr time period $(0.7\% \text{ y}^{-1})$ (table 1). A relatively ubiquitous increase in tundra phytomass over time is observed circumpolarly, with isolated areas of phytomass decline in Beringian Alaska and the Kanin–Pechora region of western Eurasia (figure 3). With respect to the different tundra bioclimatic subzones, the three southernmost subzones (C, D and E) exhibited extensive increases in aboveground phytomass (20.9%, 25.6% and 20.6% respectively), whereas the two northernmost subzones (A and B) showed substantially smaller increases (2.1% and 6.4% respectively) (table 1); the temporal differences in tundra biomass for subzones C, D and E are greater than the standard errors for site-level biomass samples. In addition, subzones C, D and E comprise 87.5% of the tundra landmass and 95.5% of the initial tundra biomass in 1982; therefore the dynamics of the three southern subzones dominate the circumpolar tundra phytomass change. Whereas subzone D showed the greatest relative phytomass increase of 25.6%, subzone E exhibited the greatest average absolute biomass increase of 96.1 g m $^{-2}$ (3.4 g m $^{-2}$ yr $^{-1}$).

North America (Alaska and Canada) represented approximately 43.2% of the tundra landmass and 45.4% of the tundra aboveground biomass in 1982 (table 2). Eurasian tundra was approximately 27.1% of the tundra landmass, and 44.0% of the tundra aboveground biomass. However, increases in

tundra phytomass in North America over the past 29 yr were generally greater than those in Eurasia. Alaskan tundra phytomass increased 7.8%, and Canadian tundra phytomass increased 36.5%, whereas tundra biomass in Russia increased 15.7% (9.4% in western Siberia and 23.4% in eastern Siberia). The total aboveground tundra phytomass is therefore now slightly less equally distributed between North America and Eurasia (0.91 Pg in North America and 0.89 Pg in Eurasia in 1982 compared to 1.07 Pg and 1.02 Pg respectively in 2010). On average though, aboveground phytomass in 2010 for North America was only 353 g m $^{-2}$, whereas for Eurasia the average phytomass was 494 g m $^{-2}$.

Absolute phytomass increases were substantive for several of the larger Arctic regions. Alaskan tundra phytomass increased 40.3 g m⁻² over the 29 yr period, Canadian tundra phytomass increased 83.6 g m^{-2} , and tundra phytomass in Russia increased 68.6 g m^{-2} . For floristic provinces, the greatest changes were seen in Central Canada and West Hudsonian provinces (45.3% and 41.1% increase, respectively) as well as Anabar-Olenyek and Kharaulakh provinces in eastern Siberia (44.6% and 41.7% increase respectively); the absolute phytomass increases for these provinces were extremely high at 188.3 g m⁻² and 155.6 g m⁻² respectively (table 3). Kanin-Pechora (western Siberia) and Beringian Alaska provinces showed small declines in tundra phytomass of 2.7% and 3.5% respectively. With regard to vegetation types, some of the greatest changes were seen in the moist non-acidic tundra (MNT) with a 33.4% increase and an absolute phytomass increase of 129.2 g m⁻² (table 4). Wet mires of subzone E had the smallest increases of any vegetation-dominated type at 3.9%.

4. Discussion

Based on remotely sensed vegetation indices and strong empirical relationships between tundra biomass and the NDVI, aboveground phytomass of Arctic tundra increased by 0.40 Pg or 19.8% over the past three decades. One key point of clarification for the numbers presented in this paper is that the Arctic tundra is statically defined by the CAVM (Walker et al 2005). Changes in tundra boundaries are not taken into consideration; therefore northward movement of the latitudinal treeline, which would change the designation from tundra to taiga (reducing tundra area and therefore its phytomass), is not figured into this analysis. However, northward movement of treeline is uncertain, and any potential reduction in tundra due to expansion of taiga is likely to be minimal over this time period relative to the extensive areas of tundra that are greening (Chapin et al 2010, Berner et al 2011, Lloyd et al 2011). Since Arctic tundra effectively extends to the northernmost landmasses on the planet, there are no similar issues with regard to northward expansion of tundra into areas previously defined as other vegetation types. Our analysis does however include pixels identified as either glacier or lake, which may or may not contain some areas of tundra vegetation; therefore reductions or expansions of glaciers and lakes and their effects on tundra biomass are represented in this analysis. We

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	Rate of change (% yr ⁻¹)	0.025	0.073	0.228	0.745	0.913	0.734	0.705
	% change	0.70	2.05	6.39	20.85	25.56	20.55	19.75
I	Change	0.0011	0.0004	0.0048	0.0575	0.1396	0.1948	0.3982
Fotal biomass $(Pg - 10^{15} g)$	2010	0.15	0.02	80.0	0.33	69.0	1.14	2.41
Total bi $(Pg - 1)$	1982	0.15	0.02	0.08	0.28	0.55	0.95	2.02
	Rate of change (g m ⁻² yr ⁻¹)	0.02	0.07	0.33	1.49	2.92	3.43	
ı	Change in mean biomass (g m ⁻²)	9.0	2.0	9.1	41.6	81.7	96.1	
	SD	18.0	53.4	118.4	148.7	195.2	153.1	
Mean biomass (g m ⁻²	2010	84.4	100.3	151.8	241.2	401.5	563.6	
Mean bior	SD	14.0	39.2	100.9	116.6	145.6	142.5	
	1982	83.8	98.3	142.7	199.6	319.8	467.5	
	Area (km²)	1795920	200 964	530 780	1380 760	1708430	2027 020	
	Bioclimate subzone	Greenland ice cap	А	В	C	D	ш	Total

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Table 2. Ar

			Mean bio	Mean biomass (g m ⁻²)	2)	l		Total b (Pg –	Total biomass (Pg – 10 ¹⁵ g)			
Country	Area (km2) 1982	1982	SD	2010	SD	Change in mean biomass (g m $^{-2}$)	Rate of change (g m ⁻² yr ⁻¹)	1982	2010	Change	% change	Rate of change (% yr ⁻¹)
United States (Alaska)	538 929	517.1	153.4	557.3	149.3	40.3	1.44	0.28	0.30	0.0217	7.79	0.278
Canada	2768 760	229.3	116.4	312.9	199.5	83.6	2.99	0.63	0.87	0.2315	36.46	1.302
Denmark (Greenland ^a)	2273 500	93.6	47.2	6.96	62.4	3.3	0.12	0.21	0.22	0.0074	3.50	0.125
Iceland	7 073	314.3	168.6	436.9	248.0	122.5	4.38	0.00	0.00	0.0009	38.98	1.392
Norway (mostly Svalbard)	62 809	107.2	60.5	127.3	130.2	20.1	0.72	0.01	0.01	0.0013	18.73	699.0
Russia	1999 650	438.0	155.1	9.909	188.6	9.89	2.45	0.88	1.01	0.1371	15.65	0.559
Percentages North America (%) Eurasia ^b (%)	43.2 27.1							45.4 44.0	48.4 42.5	63.3 34.8		

^a Includes ice cap.

^b Not including Greenland.

H E Epstein $et\ al$

Table 3. Arctic tundra biomass dynamics by floristic province.

Change in mean Rate of change (g m ⁻²) (g m ⁻² yr ⁻¹) 1982 2010 Change % change 1850 0.6 0.02 0.02 0.15 0.15 0.0011 0.70 0.105 0.005 30.63 0.00 0.0005 30.63 0.005 0.0005 0.0005 30.63 0.000 0.0005 0.0005 30.63 0.107 0.10 0.13 0.0005 0.10007 0.13 0.0005 0.1187 45.30 0.10 0.13 0.0187 45.30 0.10 0.13 0.0187 45.30 0.100 0.100 0.1187 45.30 0.10 0.1187 45.30 0.10 0.1187 45.30 0.10 0.000 0.000 0.0006 1.20 0.004 0.004 0.004 0.000 0.0000 0.00006 1.20 0.004 0.004 0.000 0.0000 0.00004 41.66 0.17.7 0.004 0.001 0.011 0.0011 0.13.30 0.120 0.17.7 0.005 0.000 0.000 0.00004 41.66 0.17.7 0.005 0.000 0.0000 0.00004 41.66 0.17.7 0.005 0.11 0.11 0.00011 0.13.30 0.120 0.17.7 0.000 0.000 0.00004 41.66 0.125.2 0.205 0.001 0.011 0.011 0.0011 0.18.3 0.0000 0.18.3 0.18.3 0.19 0.20 0.000 0.0000 0.0000 0.000 0.000 0.10000 0.10000 0.10000 0.100000 0.100000 0.10000 0.10000 0.10000 0.10000 0.1000000 0.100000 0.100000 0.100000 0.100000 0.100000 0.100000 0.1000000 0.100000 0.100000 0.100000 0.100000 0.100000 0.100000 0.1000000 0.100000 0.100000 0.100000 0.100000 0.100000 0.1000000 0.1000000 0.1000000 0.1000000 0.1000000 0.1000000 0.1000000 0.1000000 0.10000000 0.100000000			Mean biomass (g m ⁻²)	ıass (g m	-2)			Total l	Total biomass $(Pg - 10^{15} g)$			
0.6 0.02 0.15 0.15 0.00 0.00 96.5 3.45 0.00 0.00 0.005 30.63 -20.4 -0.73 0.19 0.19 -0.0067 -3.45 139.8 4.99 0.10 0.13 0.0326 32.19 111.5 3.98 0.26 0.38 0.1187 -3.45 102.0 3.64 0.20 0.038 0.1187 -45.30 102.0 3.64 0.26 0.38 0.1187 -45.30 1.2 0.04 0.02 0.081 1.20 1.2 0.04 0.04 0.005 1.20 1.7.4 6.34 0.00 0.00 0.001 1.23 1.7.4 6.34 0.00 0.00 0.001 1.33 1.7.4 6.34 0.00 0.00 0.001 1.33 1.7.4 0.34 0.01 0.01 0.01 1.33 2.5 0.80 0.15 0.042<	Area (km ²) 1982 SD 2010		2010		SD	Change in mean biomass (g m ⁻²)	Rate of change (g m ⁻² yr ⁻¹)	1982	2010	Change	% change	Rate of change (% yr ⁻¹)
195.7 96.5 3.45 0.00 0.0005 30.63 127.1 -20.4 -0.73 0.19 0.19 -0.0067 -3.45 172.7 139.8 -0.73 0.19 0.19 -0.0067 -3.45 206.9 111.5 3.98 0.26 0.38 0.0187 45.30 204.8 102.0 3.64 0.20 0.28 0.0816 41.13 126.9 44.5 1.59 0.14 0.16 0.0268 19.63 126.9 1.2 0.04 0.04 0.006 1.20 245.2 17.4 6.34 0.01 0.001 1.20 126.1 140.7 5.02 0.00 0.000 0.0016 1.20 126.1 140.7 5.02 0.01 0.001 1.33 0.25 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.001 0.002	83.8 14.0		84.4		18.0	9.0	0.02	0.15	0.15	0.0011	0.70	0.025
127.1 -20.4 -0.73 0.19 0.19 -0.067 -3.45 -1.5 206.9 111.5 3.98 0.10 0.13 0.0326 32.19 206.9 111.5 3.98 0.10 0.13 0.0326 32.19 206.9 102.0 3.64 0.20 0.28 0.0181 45.30 126.9 44.5 1.59 0.14 0.16 0.0268 19.63 126.9 44.5 1.59 0.14 0.06 0.0016 53.29 46.0 1.2 0.04 0.006 0.0016 53.29 120 166.1 140.7 5.02 0.00 0.0016 53.29 120 120.0 -17.7 -0.63 0.01 0.01 0.001 1.83 125.2 2.5 0.80 0.15 0.04 1.84 156.6 188.3 6.72 0.06 0.09 0.07 1.83 156.6 188.3 6.72 0.06	315.1 132.4		411.6		195.7	96.5	3.45	0.00	0.00	0.0005	30.63	1.094
172.7 139.8 4.99 0.10 0.13 0.0326 32.19 206.9 111.5 3.98 0.26 0.38 0.1187 45.30 204.8 102.0 3.64 0.20 0.28 0.0816 41.13 126.9 44.5 1.59 0.04 0.04 0.006 1.20 46.0 1.2 0.04 0.04 0.006 1.20 1.20 245.2 177.4 6.34 0.00 0.001 6.001 1.20 166.1 140.7 5.02 0.00 0.000 41.66 53.29 150.0 -17.7 -0.63 0.11 0.001 13.36 12.22 120.0 -17.7 -0.63 0.11 0.001 13.36 125.2 22.5 0.80 0.15 0.04 0.001 13.36 156.6 188.3 6.72 0.04 0.04 0.002 13.36 111.2 15.56 0.21 0.01 0.01 <td>592.6 135.7</td> <td></td> <td>572.</td> <td>2</td> <td>127.1</td> <td>-20.4</td> <td>-0.73</td> <td>0.19</td> <td>0.19</td> <td>-0.0067</td> <td>-3.45</td> <td>-0.123</td>	592.6 135.7		572.	2	127.1	-20.4	-0.73	0.19	0.19	-0.0067	-3.45	-0.123
206.9 111.5 3.98 0.26 0.38 0.1187 45.30 204.8 102.0 3.64 0.20 0.28 0.0816 41.13 126.9 44.5 1.59 0.04 0.04 0.006 120 46.0 1.2 0.04 0.04 0.000 1.20 245.2 177.4 6.34 0.00 0.000 41.66 92.4 13.0 0.46 0.01 0.001 13.36 120.0 -17.7 -0.63 0.11 0.11 -0.031 -2.72 224.2 5.6 0.20 0.04 0.004 41.66 125.2 22.5 0.80 0.15 0.16 0.001 1.33 125.2 22.5 0.80 0.15 0.16 0.001 1.83 125.2 22.5 0.80 0.15 0.16 0.001 0.001 156.6 188.3 6.72 0.06 0.00 0.002 0.003 <td< td=""><td></td><td></td><td>574.</td><td>_</td><td>172.7</td><td>139.8</td><td>4.99</td><td>0.10</td><td>0.13</td><td>0.0326</td><td>32.19</td><td>1.150</td></td<>			574.	_	172.7	139.8	4.99	0.10	0.13	0.0326	32.19	1.150
204.8 102.0 3.64 0.20 0.28 0.0816 41.13 126.9 44.5 1.59 0.14 0.16 0.0268 1963 46.0 1.2 0.04 0.04 0.00 0.0005 1.20 245.2 177.4 6.34 0.00 0.00 0.0016 53.29 166.1 140.7 5.02 0.00 0.0004 41.66 120.0 -17.7 -0.63 0.11 0.001 13.36 120.0 -17.7 -0.63 0.11 0.001 13.36 120.0 -17.7 -0.63 0.11 0.001 13.36 122.2 22.5 0.80 0.15 0.16 0.007 1.83 125.2 22.5 0.80 0.15 0.16 0.007 1.83 156.6 188.3 6.72 0.06 0.09 0.0422 21.97 111.2 155.6 5.56 0.01 0.01 0.01 0.01 0.02	246.1 112.0		357.	9	206.9	111.5	3.98	0.26	0.38	0.1187	45.30	1.618
126.9 44.5 1.59 0.14 0.16 0.0268 19.63 46.0 1.2 0.04 0.04 0.04 0.006 1.20 245.2 177.4 6.34 0.00 0.0016 53.29 166.1 140.7 5.02 0.00 0.0016 41.66 92.4 13.0 0.46 0.01 0.010 13.36 120.0 -17.7 -0.63 0.11 0.01 13.36 120.0 -17.7 -0.63 0.01 0.000 13.36 122.2 5.6 0.20 0.04 0.000 1.83 125.2 2.55 0.08 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.01 0.02 0.02 0.02 0.02	248.0 121.0		350.	0	204.8	102.0	3.64	0.20	0.28	0.0816	41.13	1.469
46.0 1.2 0.04 0.04 0.04 0.005 1.20 245.2 177.4 6.34 0.00 0.0016 53.29 166.1 140.7 5.02 0.00 0.0016 53.29 166.1 140.7 5.02 0.00 0.001 41.66 92.4 13.0 0.46 0.01 0.01 0.001 13.36 120.0 -17.7 -0.63 0.11 0.11 -0.031 -2.72 122.2 22.5 0.80 0.12 0.04 0.007 1.83 125.2 22.5 0.80 0.15 0.04 0.007 1.83 156.6 188.3 6.72 0.06 0.09 0.0422 21.97 111.2 155.6 5.56 0.01 0.01 0.022 44.64 153.5 81.6 2.92 0.12 0.14 0.002 13.11 163.1 83.0 2.95 0.02 0.002 0.002 10.01	226.8 91.8		271.3	~	126.9	44.5	1.59	0.14	0.16	0.0268	19.63	0.701
245.2 177.4 6.34 0.00 0.0016 53.29 166.1 140.7 5.02 0.00 0.0004 41.66 92.4 13.0 0.46 0.01 0.01 0.001 13.36 120.0 -17.7 -0.63 0.11 0.11 -0.031 -2.72 120.0 -17.7 -0.63 0.11 0.11 -0.0031 -2.72 122.2 22.5 0.80 0.15 0.04 0.007 1.83 125.2 22.5 0.80 0.15 0.04 0.007 1.86 196.3 84.8 3.03 0.19 0.23 0.0422 21.97 111.2 155.6 5.56 0.01 0.00 0.0026 44.64 111.2 155.6 5.56 0.01 0.01 0.01 0.01 18.14 163.1 83.0 2.92 0.12 0.14 0.016 19.61 163.1 83.0 2.94 0.05 0.05	98.1 36.9		99.	~ 1	46.0	1.2	0.04	0.04	0.04	0.0005	1.20	0.043
166.1 140.7 5.02 0.00 0.00 4.166 92.4 13.0 0.46 0.01 0.01 0.010 13.36 120.0 -17.7 -0.63 0.11 0.11 -0.031 -2.72 -2.72 120.0 -17.7 -0.63 0.11 0.11 -0.0031 -2.72 -2.72 125.2 22.5 0.80 0.04 0.04 0.007 1.83 196.3 84.8 3.03 0.15 0.16 0.0071 4.66 196.3 84.8 3.03 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.01 0.01 18.14 153.5 81.6 2.92 0.12 0.14 0.02 0.02 0.02 0.02 0.02 0.02 0.01 0.01 0.01 0.01 0.01 0.01 0.01	332.9 134.0		510.3	~	245.2	177.4	6.34	0.00	0.00	0.0016	53.29	1.903
92.4 13.0 0.46 0.01 0.01 0.010 13.36 120.0 -17.7 -0.63 0.11 0.11 -0.0031 -2.72 -2.72 224.2 5.6 0.20 0.04 0.04 0.0071 4.66 125.2 22.5 0.80 0.15 0.16 0.0071 4.66 196.3 84.8 3.03 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.002 44.64 111.2 155.6 5.56 0.01 0.002 44.64 153.5 81.6 2.92 0.12 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.01 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00	337.7 74.5		478.	4	166.1	140.7	5.02	0.00	0.00	0.0004	41.66	1.488
120.0 -17.7 -0.63 0.11 0.11 -0.0031 -2.72 224.2 5.6 0.20 0.04 0.04 0.007 1.83 125.2 22.5 0.80 0.15 0.16 0.0071 4.66 196.3 84.8 3.03 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.00 41.70 153.5 81.6 2.92 0.14 0.0212 18.14 163.1 83.0 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.00 0.00 0.0 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 <	30.4		110.	0	92.4	13.0	0.46	0.01	0.01	0.0010	13.36	0.477
224.2 5.6 0.20 0.04 0.04 0.007 1.83 125.2 22.5 0.80 0.15 0.16 0.0071 4.66 196.3 84.8 3.03 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.026 41.70 153.5 81.6 2.92 0.14 0.026 41.70 153.5 81.6 2.92 0.14 0.0212 18.14 163.1 83.0 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.002 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 17.75 125.7 24.1 0.86 0.01 0.01 0.01 0.01 0.01 0.01 127.3 10.8 0.2 0.01			633.	7	120.0	-17.7	-0.63	0.11	0.11	-0.0031	-2.72	-0.097
125.2 22.5 0.80 0.15 0.16 0.0071 4.66 196.3 84.8 3.03 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.0026 41.70 153.5 81.6 2.92 0.14 0.026 41.70 153.6 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.00 0.00 0.00 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.013 13.01 163.3 61.4 2.19 0.01 0.00 0.003 24.07 127.3 10.8 0.39 0.01 0.00 0.000 0.000 0.000 11.3 0.2 0.03 0.01 0.00	304.0 216.8		309.	2	224.2	5.6	0.20	0.04	0.04	0.0007	1.83	0.065
196.3 84.8 3.03 0.19 0.23 0.0422 21.97 156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.026 41.70 153.5 81.6 2.92 0.14 0.026 41.70 153.5 81.6 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.002 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.013 17.75 137.8 31.8 1.14 0.01 0.01 0.00 0.003 24.07 163.3 61.4 2.19 0.01 0.01 0.00 0.000 0.000 0.000 11.3 0.2 0.01 0.00 0.00 0.000 0.000 0.000 11.3	483.4 101.9		505.	6	125.2	22.5	08.0	0.15	0.16	0.0071	4.66	0.166
156.6 188.3 6.72 0.06 0.09 0.0276 44.64 111.2 155.6 5.56 0.01 0.01 0.0026 41.70 153.5 81.6 2.92 0.14 0.0212 18.14 163.1 83.0 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.0022 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.013 17.75 137.8 31.8 1.14 0.01 0.01 0.003 24.07 163.3 61.4 2.19 0.01 0.01 0.003 24.07 11.3 0.2 0.01 0.01 0.00 0.000 0.000 91.6 9.2 0.01 0.01 0.01 0.00 8.44 73.8 9.0 0.32 0.01 0.01 0.01 0.00 8.63	385.9 125.3	-	470.	∞	196.3	84.8	3.03	0.19	0.23	0.0422	21.97	0.785
111.2 155.6 5.56 0.01 0.01 0.0026 41.70 153.5 81.6 2.92 0.12 0.14 0.0212 18.14 163.1 83.0 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.005 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.00 17.75 137.8 31.8 1.14 0.01 0.01 0.00 17.75 163.3 61.4 2.19 0.01 0.01 0.00 24.07 127.3 10.8 0.39 0.01 0.00 0.000 0.00 0.00 91.6 9.2 0.03 0.01 0.01 0.00 0.00 8.44 73.8 9.0 0.32 0.01 0.01 0.01 0.00 8.63	421.8 77.3		610.	_	156.6	188.3	6.72	90.0	60.0	0.0276	44.64	1.594
153.5 81.6 2.92 0.12 0.14 0.0212 18.14 163.1 83.0 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.0072 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.003 17.75 137.8 31.8 1.14 0.01 0.01 0.01 13.01 163.3 61.4 2.19 0.01 0.01 0.003 24.07 127.3 10.8 0.39 0.01 0.01 0.000 0.000 91.6 9.2 0.33 0.01 0.01 0.000 8.44 73.8 9.0 0.32 0.01 0.01 0.000 8.44	373.1 63.5		528	7:	111.2	155.6	5.56	0.01	0.01	0.0026	41.70	1.489
163.1 83.0 2.96 0.08 0.10 0.0162 19.61 134.3 57.0 2.04 0.05 0.05 0.007 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.00 17.75 137.8 31.8 1.14 0.01 0.01 0.003 13.01 163.3 61.4 2.19 0.01 0.01 0.003 24.07 127.3 10.8 0.39 0.01 0.01 0.000 0.000 91.6 9.2 0.33 0.01 0.01 0.000 8.44 73.8 9.0 0.32 0.01 0.01 0.000 8.44	449.9 106.0		531	Z.	153.5	81.6	2.92	0.12	0.14	0.0212	18.14	0.648
134.3 57.0 2.04 0.05 0.05 0.07 15.19 126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.00 17.75 137.8 31.8 1.14 0.01 0.01 0.013 13.01 163.3 61.4 2.19 0.01 0.02 0.0030 24.07 127.3 10.8 0.39 0.01 0.01 0.00 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.00 8.44 73.8 9.0 0.32 0.01 0.01 0.00 8.44	423.1 142.4		506.	_	163.1	83.0	2.96	0.08	0.10	0.0162	19.61	0.700
126.2 114.4 4.08 0.06 0.07 0.0123 22.05 0.0 0.0 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.000 17.75 137.8 31.8 1.14 0.01 0.01 0.001 13.01 163.3 61.4 2.19 0.01 0.02 0.0030 24.07 127.3 10.8 0.39 0.01 0.01 0.003 4.69 11.3 0.2 0.01 0.00 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.00 8.44 73.8 9.0 0.32 0.01 0.01 0.00 8.63	375.2 111.0		432.	7	134.3	57.0	2.04	0.05	0.05	0.0072	15.19	0.543
0.0 0.0 0.00 0.00 0.00 0.00 0.00 125.7 24.1 0.86 0.01 0.01 0.01 0.00 17.75 137.8 31.8 1.14 0.01 0.01 0.01 0.013 13.01 163.3 61.4 2.19 0.01 0.02 0.030 24.07 127.3 10.8 0.39 0.01 0.01 0.003 4.69 11.3 0.2 0.01 0.00 0.000 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.00 8.44 73.8 9.0 0.32 0.01 0.01 0.004 8.63	518.7 108.5		633.	_	126.2	114.4	4.08	90.0	0.02	0.0123	22.05	0.787
125.7 24.1 0.86 0.01 0.01 0.009 17.75 137.8 31.8 1.14 0.01 0.01 0.013 13.01 163.3 61.4 2.19 0.01 0.02 0.0030 24.07 127.3 10.8 0.39 0.01 0.01 0.003 4.69 11.3 0.2 0.01 0.00 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.009 8.44 73.8 9.0 0.32 0.00 0.01 0.004 8.63	83.0 0.0		83	0.	0.0	0.0	0.00	0.00	0.00	0.0000	0.00	0.000
137.8 31.8 1.14 0.01 0.01 0.0013 13.01 163.3 61.4 2.19 0.01 0.02 0.0030 24.07 127.3 10.8 0.39 0.01 0.01 0.003 4.69 11.3 0.2 0.01 0.00 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.009 8.44 73.8 9.0 0.32 0.00 0.01 0.004 8.63	135.9 67.4		160.	_	125.7	24.1	98.0	0.01	0.01	0.0009	17.75	0.634
163.3 61.4 2.19 0.01 0.02 0.0030 24.07 127.3 10.8 0.39 0.01 0.01 0.003 4.69 11.3 0.2 0.01 0.00 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.009 8.44 73.8 9.0 0.32 0.00 0.01 0.004 8.63	244.5 89.8		276.3		137.8	31.8	1.14	0.01	0.01	0.0013	13.01	0.465
127.3 10.8 0.39 0.01 0.01 0.003 4.69 11.3 0.2 0.01 0.00 0.00 0.000 0.20 91.6 9.2 0.33 0.01 0.01 0.009 8.44 73.8 9.0 0.32 0.00 0.01 0.004 8.63	255.1 108.4		316.5		163.3	61.4	2.19	0.01	0.02	0.0030	24.07	0.860
11.3 0.2 0.01 0.00 0.00 0.0000 0.20 91.6 9.2 0.33 0.01 0.01 0.009 8.44 73.8 9.0 0.32 0.00 0.01 0.0004 8.63	230.8 122.6		241.	_	127.3	10.8	0.39	0.01	0.01	0.0003	4.69	0.167
91.6 9.2 0.33 0.01 0.01 0.0009 8.44 73.8 9.0 0.32 0.00 0.01 0.0004 8.63	84.7 10.9		84.	6	11.3	0.2	0.01	0.00	0.00	0.0000	0.20	0.007
73.8 9.0 0.32 0.00 0.01 0.0004 8.63	108.5 63.6		117.7	_	91.6	9.2	0.33	0.01	0.01	0.0009	8.44	0.301
	47 973 104.0 50.0 113.0		113.	$\overline{}$	73.8	0.6	0.32	0.00	0.01	0.0004	8.63	0.308

Table 4. Arctic tundra biomass dynamics by vegetation type. (Note: B1: polar desert—cryptogam, cushion-forb barren; G1: herb AB—rush/grass, cryptogam tundra; B2: shield—cryptogam barren (bedrock); P1: dry shrub BC—prostrate dwarf-shrub, herb tundra; G2: gram BC—graminoid, prostrate dwarf-shrub, forb tundra; P2: Cassiope—prostrate dwarf-shrub tundra; G3: MNT—non-tussock sedge, dwarf-shrub, moss tundra; G4: TT—tussock sedge, dwarf-shrub, moss tundra; S1: dwarf shrub—erect dwarf-shrub tundra; S2: low shrub—low-shrub tundra; W1: mire BC—sedge/grass, moss wetland; W2: mire D—sedge, moss dwarf-shrub wetland; W3: mire E—sedge, moss, low-shrub wetland; B3: acid mtns.—non-carbonate mountain complex; B4: carb. mtns.—carbonate mountain complex.)

complex, D4 : caro. muns.—caroonate mountain complex.)	mate incultar	u compres.,									
		Mean bion	Mean biomass (g m ⁻²	2)			Total (Pg –	Total biomass (Pg - 10 ¹⁵ g)			
Area (km²)	1982	SD	2010	SD	Change in mean biomass (g m $^{-2}$)	Rate of change (g m ⁻² yr ⁻¹)	1982	2010	Change	% change	Rate of change (% yr ⁻¹)
251	111.6	48.3	123.2	76.4	11.6	0.41	0.03	0.03	0.0028	10.39	0.371
1381	171.0	106.1	187.1	134.7	16.0	0.57	0.02	0.03	0.0023	9.38	0.335
5234	200.2	9.89	267.0	129.0	6.99	2.39	0.08	0.11	0.0272	33.40	1.193
8898	205.4	103.6	252.3	148.8	47.0	1.68	0.09	0.11	0.0197	22.88	0.817
868 9	281.7	127.6	347.6	158.4	65.9	2.35	0.13	0.16	0.0300	23.40	0.836
0000	185.5	83.8	237.8	134.6	52.2	1.87	0.03	9.0	0.0078	28.15	1.005
2119	377.2	121.5	506.4	176.4	129.2	4.61	0.23	0.31	0.0791	34.25	1.223
54411	500.6	105.7	580.9	126.1	80.3	2.87	0.18	0.21	0.0293	16.04	0.573
769723	399.1	125.7	500.7	157.1	101.6	3.63	0.31	0.39	0.0782	25.45	0.909
3161	521.2	136.4	610.3	141.6	89.1	3.18	0.35	0.41	0.0600	17.09	0.610
8 247	280.4	146.7	337.9	173.7	57.5	2.05	0.03	9.00	0.0062	20.51	0.733
4 688	402.9	121.7	465.5	136.2	62.6	2.23	90.0	0.07	0.0091	15.53	0.555
6824	536.3	148.0	557.1	157.9	20.8	0.74	0.00	0.10	0.0037	3.88	0.138
9068	241.6	157.7	287.4	204.3	45.8	1.64	0.14	0.17	0.0265	18.95	0.677
5463	247.9	184.2	288.4	231.0	40.5	1.45	0.03	9.00	0.0055	16.34	0.584
5331	87.9	19.0	0.06	42.5	2.1	80.0	0.01	0.01	0.0002	2.43	0.087
0909	84.8	16.8	86.2	28.2	1.4	0.05	0.18	0.18	0.0029	1.66	0.059
71498	310.1	129.7	418.1	199.9	108.0	3.86	0.02	0.03	0.0077	34.81	1.243
1378	349.0	159.7	350.5	172.7	1.5	0.05	0.00	0.00	0.0000	0.43	0.015

feel confident in our estimates of circumpolar aboveground tundra biomass; other recent estimates, generally using less comprehensive datasets of remotely sensed NDVI, maps of tundra vegetation types, and field-sampled aboveground biomass, have all yielded values in the range of 2.4-2.5 Pg (Walker et al 2003, Raynolds et al 2006, Walker et al 2008), and our estimate is 2.41 Pg. An additional clarification to make, though, is that while the information used to develop the extrapolations in this study comes from the full range of bioclimate subzones in the Arctic, the vegetation sampled was on mesic zonal landscapes. The relationship may not apply equally well for wet tundra, dry tundra or mountainous tundra landscapes, which are extensive. There also may be some uncertainties given that only the leaf fraction of increasing aboveground biomass contributes to the NDVI signal, whereas the NDVI-biomass relationship includes both foliar and woody phytomass components.

The 0.40 Pg of aboveground biomass change could represent a substantive sink of carbon by the Arctic tundra over the past three decades. If we make some basic assumptions that there is an equivalent amount of below-ground biomass increase over this time period and that 50% of vegetation biomass is carbon, the total difference in carbon in live vegetation is 0.40 Pg C. Note that this carbon difference is not equivalent to the carbon sequestered over the 29 yr time period; the amount sequestered would also be a function of the plant tissue turnover rates and the ultimate fate of this dead tissue. If we assume a linear increase in vegetation C over the 29 yr time period, then a very high-end estimate of sequestered carbon would be 5.8 Pg C or 0.20 Pg C yr⁻¹; in this estimate, all of this additional plant C (on average 0.20 Pg) turns over every year and enters a long-term storage pool.

This likely overestimated annual value represents < 10% of the annual terrestrial carbon sink; the land sink for carbon is rather variable interannually, but has been estimated at $2.3 \pm 0.4 \text{ Pg C} \text{ yr}^{-1} \text{ for } 2008 \text{ (Le Quéré } et al. 2009)}$ and $2.3 \pm 0.4 \text{ Pg C} \text{ yr}^{-1}$ for 2000 (Pan et al 2011). The northern hemisphere terrestrial carbon sink was estimated to be $\sim 1.7 \text{ Pg C yr}^{-1}$ from 2000 to 2004 (Ciais et al 2010). Our estimated tundra carbon sink is however a substantive part of the Arctic land sink, which includes boreal forest and other vegetation types in permafrost regions, and was estimated to be 0.3-0.6 Pg C yr⁻¹ during the late decades of the 20th century (McGuire et al 2009). From a broader perspective however, based on these remotely sensed observations over the past three decades, the Arctic tundra greening will likely not lead to any important reduction of atmospheric carbon dioxide, although it may offset some of the losses of soil carbon to the atmosphere that are occurring in the Arctic and expected with continued warming (McGuire et al 2010, Euskirchen et al 2009).

There was a high degree of spatial variability of change, particularly across subzones. Most of the biomass changes were seen in the three southernmost subzones (C—20.9%, D—25.6% and E—20.6%), with very little change in subzones A (2.1%) and B (6.4%) (figure 4). The greatest relative changes occurred in subzone D, which is consistent

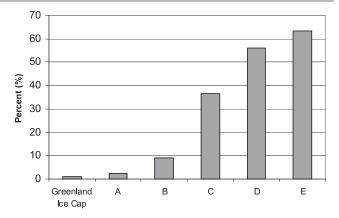


Figure 4. Per cent of subzone pixels with significant (p < 0.05) positive trend.

with a remote sensing analysis of Alaska from 1981-2001 (Jia et al 2003), whereas a remote sensing analysis of Canadian tundra showed subzone C peak NDVI increasing by 0.79% yr⁻¹and subzone D peak NDVI increasing by $0.67\% \text{ yr}^{-1}$ from 1982 to 2003 (Jia et al 2009). Phytomass increases in North America were greater than in Eurasia. Alaska and Canada aboveground biomass increased by 7.8% and 36.5% respectively, compared to 15.7% for Russia (9.4% and 23.4% for western and eastern Siberia respectively). These results are consistent with substantially greater summer warming for the North American Arctic tundra compared to the Eurasian Arctic tundra, and also for eastern Siberia compared to western Siberia (Bhatt et al 2010). Potential aboveground phytomass increases in response to warming could also be constrained by grazing of managed reindeer herds in regions throughout western Siberia (Forbes et al 2009, Yu et al 2009, 2011). The large difference in percentage increase between Alaska and Canada is also due to spatial heterogeneity of change; whereas Canada exhibited relatively consistent greening, strong increases in aboveground vegetation on the North Slope of Alaska are countered by declines in green vegetation in the Bering Region of Alaska. The vegetation type with the greatest increase in aboveground biomass (34.3%) was the moist non-acidic tundra (MNT-non-tussock sedge, dwarf-shrub, moss tundra), which is widespread in subzones C and D of northern Alaska and Canada.

While this NDVI-based analysis suggests some increases in aboveground tundra biomass of >100 g m⁻² and >40% over the past three decades, it is still extremely difficult to compare these results to changes that have been observed in the field, largely due to the paucity of studies that have repeated field biomass measurements over time (Fung 1997). Experimental studies conducted between 1981 and 2000 at the Toolik Lake Long Term Ecological Research site in subzone E of northern Alaska included biomass monitoring through field-harvests over time; while plant community composition in un-manipulated control plots changed throughout this time period, there was no indication of any directional change in total aboveground phytomass (Chapin *et al* 1995, Shaver *et al* 2001). Study sites at

Environ. Res. Lett. **7** (2012) 015506 H E Epstein *et al*

Alexandra Fiord, Ellesmere Island, Nunavut, Canada have provided the only plot-based observational data demonstrating a recent increase in aboveground tundra biomass over time. Hudson and Henry (2009) found an increase of 53.4 g m⁻² (160%) over the 27 yr period from 1981 to 2008 in a coastal lowland heath community, and Hill and Henry (2011) found a 158% increase in aboveground tundra biomass for wet sedge communities from 1981 to 2005.

Greenhouse warming studies conducted in Arctic tundra over periods of up to 13 yr essentially have not shown changes in aboveground biomass (van Wijk *et al* 2004), however warming studies using open-top chambers (OTCs) as part of the International Tundra Experiment (ITEX) have indicated common increases in vegetation height (Walker *et al* 2006), which could correspond to biomass increases. The widespread expansion of tall shrubs throughout the circumpolar Low Arctic into areas previously occupied by much shorter-stature vegetation (Tape *et al* 2006, Lantz *et al* 2009, 2010, Blok *et al* 2010, 2011, Naito and Cairns 2011) most likely leads to large increases in aboveground biomass (Bret-Harte *et al* 2001), although there have not yet been any comprehensive assessments of the potential biomass implications of this phenomenon.

Recent simulation modeling of Arctic tundra response to climate warming has projected relatively comparable biomass changes to what we are estimating here. Using a production efficiency model (PEM), based on satellite remote sensing data similar to those used in this study, Zhang et al (2008) estimated increases in tundra net primary productivity (NPP) of 0.5% yr⁻¹ compared to our 0.7% yr⁻¹ change in biomass. Using the same production efficiency model as Zhang et al (2008), Kimball et al (2007) estimated tundra NPP for Alaska and western Canada to have increased 0.8% yr⁻¹ from 1982 to 2000. Kimball et al (2007) also found for the same region and time period that the Terrestrial Ecosystem Model (TEM) and BIOME-BGC model both estimated NPP increases of 0.5% yr⁻¹. Also using the TEM model, Euskirchen et al (2009) projected NPP increases in sedge tundra ranging from 0.3 to 0.8 g C m⁻² yr⁻¹, and NPP increases in shrub tundra ranging from 0.9 to 2.7 g C m⁻² yr⁻¹, values that are comparable to our estimates of biomass increases (assuming biomass is typically 45-50% C). The ArcVeg model (Epstein et al 2000, Yu et al 2009) projects tundra biomass increases on the order of $1-10 \text{ g m}^{-2} \text{ yr}^{-1}$, projections that overlap with, yet extend to greater than, the range of estimates from this study.

Regardless of the carbon implications, an average 19.8% Arctic-wide increase in biomass throughout the past 29 yr has major implications for nearly all aspects of tundra ecosystems including hydrology, active layer depths, permafrost regimes, wildlife and human use of Arctic landscapes, especially if the trend continues as projected by most models. We still however do not know where all of this increase in biomass is occurring, both within landscapes and within the different layers of the plant canopy. Clearly, more extensive studies of NDVI-biomass relationships are needed across a greater range of tundra habitats and across additional Arctic climate gradients, with varying substrates and precipitation regimes.

Long-term studies of tundra biomass across the full range of Arctic climates are absolutely needed. In the meantime, studies with time series of high spatial resolution remote sensors, such as Landsat, and very high resolution sensors, such as Quickbird and GeoEye, will help us answer the question of where the changes are occurring, and detailed studies of how vegetation canopies are changing over time will provide much-needed information.

In summary, we used a strong regression model between NDVI and aboveground tundra phytomass, developed from extensive field-harvested measurements of vegetation biomass, to estimate the biomass dynamics of the circumpolar Arctic tundra over the period of the satellite AVHRR record (1982–2010). We found that tundra subzones C-E dominate the increases in biomass, ranging from 20 to 26%, although there was a high degree of heterogeneity across regions, floristic provinces, and vegetation types. The estimated change in carbon in live vegetation of 0.40 Pg C over the past three decades is substantive, albeit quite small relative to anthropogenic C emissions. However, a 19.8% average increase in aboveground biomass has major implications for the structure and functioning of Arctic tundra ecosystems. While spatially extensive on-the-ground measurements of tundra biomass were conducted in the development of this analysis, validation is still impossible without more repeated, long-term monitoring of Arctic tundra biomass in the field.

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