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SYNTHESIS AND REVIEW

Recent dynamics of arctic and sub-arctic vegetation

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Abstract
We present a focus issue of Environmental Research Letters on the ‘Recent dynamics of arctic and sub-arctic vegetation’. The focus issue includes three perspective articles (Verbyla 2011 Environ. Res. Lett. 6 041003, Williams et al 2011 Environ. Res. Lett. 6 041004, Loranty and Goetz 2012 Environ. Res. Lett. 7 011005) and 22 research articles. The focus issue arose as a result of heightened interest in the response of high-latitude vegetation to natural and anthropogenic changes in climate and disturbance regimes, and the consequences that these vegetation changes might have for northern ecosystems. A special session at the December 2010 American Geophysical Union Meeting on the ‘Greening of the Arctic’ spurred the call for papers. Many of the resulting articles stem from intensive research efforts stimulated by International Polar Year projects and the growing acknowledgment of ongoing climate change impacts in northern terrestrial ecosystems.

Keywords: arctic tundra, boreal forest, remote sensing, shrub expansion, vegetation dynamics

1. Introduction

Vegetation at the high northern latitudes has been rather dynamic over the past few decades (i.e. the period over which we have more comprehensive observations) and seems to be continuing to change. However, these dynamics are highly variable in space and over time, with substantive differences in magnitude and even direction of change. The research papers in this special issue collectively use remote sensing techniques, field observations and experiments, and simulation modeling to examine vegetation dynamics across arctic tundra and boreal forests in areas that span the entire circumpolar North.

Findings reported in this focus issue highlight the following.

1) There is continued evidence for a ‘greening’ of tundra ecosystems from increased NDVI (Beck and Goetz 2011, Fraser et al 2011, Epstein et al 2012, Lin et al 2012), which is likely the result of increased biomass (Epstein et al 2012), changes in plant community composition (Blok et al 2011, Boelman et al 2011, Villarreal et al 2012, Walker et al 2012), and influenced by changing plant phenology (Buizer et al 2012, Zeng et al 2011).

2) A major component of the observed greening could be due to the proliferation of tall shrub species in Low Arctic ecosystems (Beck and Goetz 2011, Fraser et al 2011, Myers-Smith et al 2011, Naito and Cairns 2011, Ropars and Boudreau 2012, Lin et al 2012, Tremblay et al 2012).
Though many tundra landscapes are greening, some boreal forest regions are ‘browning’ (Beck and Goetz 2011), and a loss of temperature-sensitivity of growth is being observed in some tree-ring studies (Andreu-Hayles et al 2011, Ohse et al 2012), perhaps indicating increased drought stress.

These vegetation changes could lead to enhanced climate and ecosystem feedbacks involving surface energy and water balances (Blok et al 2011, Lawrence and Swenson 2011, Bonfils et al 2012), carbon fluxes (Lara et al 2012), and plant–herbivore interactions (Yu et al 2011).

And, although large-scale vegetation changes are being observed in high-latitude ecosystems, landscape-scale dynamics underlie these broader-scale changes (e.g. Andreu-Hayles et al 2011, Johnson et al 2011, Naito and Cairns 2011, Gamon et al 2012, Lara et al 2012, Villarreal et al 2012, Tremblay et al 2012).

2. Remote sensing of tundra vegetation change

The treeless region of the Arctic was a major focus of the published articles with 20 papers addressing vegetation dynamics in arctic tundra and/or the tundra component of the forest–tundra transition zone; of these papers, a majority used some aspect of remote sensing. At the coarsest spatial scale, Beck and Goetz (2011) analyzed the spatio-temporal dynamics of the normalized difference vegetation index (NDVI) between 1982 and 2008, using both the Advanced Very-High Resolution Radiometer (AVHRR) sensors onboard NOAA satellites (entire record—~8 km pixel size) and the MODerate resolution Imaging Spectroradiometer (MODIS) from the Terra satellite (record from 2002–1 km pixel size). They found that during the period of overlap between AVHRR and MODIS data (2002–2008), the area of arctic tundra where vegetation productivity (in this case, NDVI) is significantly increasing expanded from approximately 15% to >30% in North America, whereas the area of tundra ‘greening’ in Eurasia remained constant at approximately 20%. Also using an AVHRR-derived dataset of NDVI (12.5 km pixel size), combined with field-sampled, aboveground tundra biomass data from 13 locations throughout North America and Eurasia, Epstein et al (2012) found an average circumpolar increase in aboveground tundra biomass of 19.8% between 1982 and 2010. This increase was accentuated in the mid- to southern tundra subzones (20–26% increase), yet was substantially less in the more northern tundra (2–7%). A third paper using coarse resolution satellite data from AVHRR and MODIS sensors examined the dynamics of tundra vegetation phenology over the past three decades (Zeng et al 2011). MODIS data indicated that from 2000 to 2010, the growing season length increased by greater than six days throughout the Arctic, with a significantly greater increase for North America (∼13.6 days) relative to Eurasia (∼6.2 days), due to a significantly earlier start of the growing season (∼11.5 days earlier). AVHRR data concurred with an increasing length of growing season (∼5.4 days), yet there were differences in the details between sensors.

Several of the papers examined high-latitude vegetation change using some finer resolution remote sensing data: Fraser et al (2011) used Landsat imagery (Landsat-5 TM and Landsat-7 ETM—30 m resolution) spanning from 1984 to 2009 to evaluate vegetation dynamics for four Canadian national parks. They found that across these national parks, the per cent area of significant NDVI increase ranged from 5.6 to 26.7%, whereas the per cent area of significant NDVI decrease ranged from 0.3 to 6.0%; greatest NDVI increases were found in the Torngat Mountains, an Arctic Cordillera site. This study also analyzed changes in three tasseled cap indices and compared the finer resolution results to those using the coarser resolution AVHRR NDVI. Lin et al (2012) used historic color-infrared photography and Corona grayscale satellite imagery compared with modern very-high-resolution Quickbird satellite imagery (spatial resolutions ranged from 1.4 to 5 m) to examine vegetation changes at seven locations in Northern Alaska, Beringian Alaska, and East Chukotka, Russia. Over time periods that ranged from 1948 to 2008, four of the five Alaskan sites exhibited an increase in drier land cover types; whereas the two Chukotka sites showed increases in wetter land cover types.

Three studies addressed, at least in part, the utility of remotely sensed vegetation indices for assessing what is actually on the ground in terms of tundra vegetation composition. From an extensive set of field observations in addition to remotely sensed data, Walker et al (2012) analyzed vegetation, soil, and climate properties along two latitudinal gradients spanning the complete arctic tundra biome from south to north. The North American Arctic Transect extended from the North Slope of Alaska to the High Arctic islands of the Canadian Archipelago. The Eurasian Arctic Transect (Russia) included the Yamal Peninsula in northwestern Siberia and the Franz Josef Land Archipelago. Walker et al (2012) quantified the linear relationships between both aboveground vegetation biomass and the 1 km AVHRR NDVI as functions of the Summer Warmth Index (sum of mean monthly temperatures > °C) for each of the transects, demonstrating a strong connection between remote sensing data and field-measured vegetation biomass. Blok et al (2011) found an increasing, but saturating, relationship between Betula nana (dwarf birch) fractional cover and MODIS-derived NDVI across 20 sites at the Kytalyk nature reserve in northeastern Siberia, Russia. Boelman et al (2011) related field-measured NDVI to structural characteristics of deciduous shrub vegetation along six transects (four in tussock tundra and two in riparian shrub tundra) in the northern foothills of the Brooks Mountain Range, Alaska, during the growing season of 2010. They found that NDVI measured prior to leaf out was strongly negatively related to maximum shrub height, per cent woody stem cover, and branch abundance (particularly from 10 to 50 cm height). Peak NDVI was strongly and positively related to per cent deciduous canopy cover.

3. Shrub expansion in arctic tundra

A majority of the papers, including many of the remote sensing studies, addressed the issue of shrub expansion in
arctic tundra ecosystems. In the Fraser et al (2011) paper mentioned above, for the two Canadian national parks with fractional shrub cover data, 23.9–24.4% of the total area exhibited significant increases in shrub cover, compared to 9.2–23.2% for herbaceous vegetation cover increases and 4.2–5.1% for bare ground cover increases. On average, shrub cover increased 3.3–3.6% over the 1984–2009 timeframe, whereas average bare ground cover decreased from −1.8% to −4.7%, with much of this potentially occurring in broad valley landscapes. Lin et al (2012) had shrub cover data for their two Chukotka sites ranging from 1963 to 2008; even though historic shrub cover percentages were low (1.58–2.88%), there were absolute increases of 0.85–0.91% over the 45 year period. Three additional studies used very-high-resolution imagery specifically to examine shrub dynamics in arctic systems. Naito and Cairns (2011) analyzed shrub expansion at five sites in the Alaskan Brooks Range and North Slope region, using a variety of images from USGS aerial photography, GeoEye-1, Quickbird-2, and IKONOS-2 satellites. They found that total shrub cover changed from −0.65 to 46.56% over the past 3–4 decades, and that shrub cover changes in floodplains ranged from 3.38 to 76.22%, suggesting that shrubs were expanding preferentially into areas with greater topographic wetness index (TWI) values. Ropers and Boudreau (2012) used aerial photography and WorldView-1 imagery to examine vegetation changes at the forest–tundra ecotone near the Boniface River research station in sub-arctic Québec, Canada. They found that from 1957 to 2008 shrub cover increased 21.6% on sandy terraces compared to 11.6% on hilltops; the dominant shrub species associated with these changes was Betula glandulosa Michx. (dwarf birch). Finally, Tremblay et al (2012) used two series of vertical aerial photographs at the forest–tundra transition near Kangiqsualujjuaq in eastern Nunavik (Québec) to examine shrub and tree expansion between 1964 and 2003. They found that the area with >90% shrub and tree cover increased from 34% in 1964 to 44% in 2003, whereas the area with <10% shrub and tree cover decreased from 45% to 29%. As in Ropers and Boudreau (2012), the dominant shrub species was Betula glandulosa Michx. While this collection of remote sensing papers generally indicates an expansion of shrub cover, the study by Beck and Goetz (2011), using coarse resolution remote sensing, suggested that the ‘greening’ that has occurred on the North Slope of Alaska was not confined solely to shrub-dominated landscapes.

A single experimental study examined the response of shrubs to warming manipulations (Buizer et al 2012). In this case, open-top chambers were used to warm air temperature at sites in the Netherlands (~52.4°N) and on Svalbard (~78.1°N), and the target species for both ecosystems was the dwarf evergreen shrub, Empetrum nigrum L. At the more southern (Netherlands) site, warming led to increases in biomass, shoot growth, and fruit production in E. nigrum, as well as earlier phenological stages and an extended growing season. There was no evidence of reduced competitiveness of E. nigrum relative to the other dominant shrub, Calluna vulgaris. In the more northern site (Svalbard), E. nigrum also showed increased biomass, shoot growth, and fruit production, and in this case indicated a competitive advantage relative to Cassiope tetragona, the other dominant shrub species. In an observational study from Barrow, Alaska, Villarreal et al (2012) revisit 330 vegetation plots across 33 sites established during the International Biological Programme in 1972. Their results showed that over the past 3–4 decades cover of the erect deciduous shrub, Salix pulchra, increased, whereas cover of the prostrate shrubs, Cassiope tetragona (evergreen) and Salix rotundifolia (deciduous), decreased, yielding no net change in overall shrub cover.

Three modeling studies addressed the issue of shrub expansion in arctic tundra and its implications for other ecosystem properties and system functioning. Yu et al (2011) used a tundra vegetation dynamics model (ArcVeg) to examine the responses of arctic tundra plant communities to climate change and reindeer grazing along a latitudinal tundra gradient in northwestern Eurasia, which includes the Yamal Peninsula and the Franz Josef Land Archipelago, Russia. On average, evergreen shrub biomass increased by 96%, and deciduous shrub biomass increased by 102% with an approximate 2 °C warming over a 50 year period. Heavy grazing by reindeer however led to a decline in deciduous shrub biomass by 93% in the absence of warming; this decline in deciduous shrub biomass was only slightly reduced (89%) with climate warming. Evergreen shrubs, which are generally less palatable than deciduous shrubs, could on the other hand benefit from reduced competition with deciduous shrubs under grazing scenarios. Lawrence and Swenson (2011) used the Community Climate System Model (CCSM4), which includes the Community Land Model (CLM4) and the Community Atmosphere Model (CAM4), to examine the effects of increasing the erect shrub component of the land surface from 20% to 40% (and decreasing the herbaceous vegetation component from 80% to 60%). Whereas shrubs can act locally to cool summer soil temperatures through shading, reducing active layer thickness, when climate feedbacks were considered, the 20% increase in shrubs led to atmospheric heating, warmer soil temperatures, and a deeper active layer. The increased atmospheric heating was largely due to reduced spring albedo, with erect shrubs extending above the snow cover. Bonfils et al (2012) used the same suite of models to more specifically examine the effects of shrub height on the climate of the northern high latitudes. They simulated three vegetation scenarios—(i) the present day vegetation distribution, (ii) an increase in the total shrub cover fraction to 51% (from the current 32%) with 0.5 m tall deciduous shrubs replacing bare ground, and (iii) again an increase in the total shrub fraction to 51% but with 2.0 m tall shrubs replacing bare ground and shorter shrubs. These model results also suggest that shrub expansion of this magnitude would increase atmospheric heating through reduced surface albedo and increased atmospheric moisture from greater evapotranspiration; these effects are accentuated by the taller shrubs (almost three times the average temperature increase relative to the shorter shrubs), which extend above the snow cover and have greater transpiration efficiency than the short shrubs. Also, the invasion of tall shrubs tended to warm the

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soils, increase the depth of the active layer, and degrade permafrost to a greater extent than an expansion of short shrubs.

The field study by Blok et al (2011) provides somewhat of a contrast to the modeling results described above. Across four arctic tundra study sites from Alaska, Canada, and western and eastern Siberia, they found that the annual maximum NDVI (which was positively logarithmically related to shrub cover) was related to the annual minimum white sky albedo at only one of the four sites (the expected negative relationship). Additionally, shrub tundra had a greater albedo than both wetland and barren tundra at all four sites, suggesting that shrub expansion may not always lead to a decrease in summer albedo. Finally, Myers-Smith et al (2011) present a synthesis of recent studies documenting shrub expansion across arctic and alpine tundra ecosystems, and their impacts on various ecosystem functions, including (but not limited to) energy exchange, carbon cycling and nitrogen cycling. Local, regional and global scale feedbacks of shrub expansion are illustrated/hypothesized in a key conceptual diagram.

4. Dynamics of boreal forest vegetation

In their circumpolar remote sensing analysis, Beck and Goetz (2011) continue to show decreasing NDVI in boreal forest ecosystems from 1982 to 2008, with a recent amplification of this trend in North America. They also demonstrated that the area of significantly decreasing NDVI in boreal forests is greater with an increasing fraction of evergreen (as opposed to deciduous) trees. Post-fire recovery of broad-leaved deciduous trees and shrubs in North America appears to occur more rapidly than that of larch forests in northern Eurasia. This study is one among several in the recent literature that demonstrates a negative response of boreal forest trees to increasing temperatures, with increasing drought stress as the suggested mechanism. Ohse et al (2011) examined the responses of white spruce at the Alaska treeline to dynamics of temperature and precipitation related to different phases of the Pacific Decadal Oscillation (PDO) between 1925 and 1998. They found markedly varied responses of tree growth (from tree-ring data) to climate both spatially and temporally. Prior to 1947 (positive PDO), they found that tree growth was positively related to summer temperatures, as might be expected. However, during the positive phase of the PDO between 1977 and 1998, there was not a very pronounced effect of annual climate on white-spruce growth, indicating that other factors, such as competition or disturbance (e.g. insect outbreaks) could be more important for treeline dynamics. Andreu-Hayles et al (2011) also analyzed white-spruce growth, in this case from the Firth River site in northeastern Alaska in a forest–tundra transition region, between 1901 and 2001. Using both tree-ring width (TRW) and maximum latewood density (MXD) data, they found positive relationships between TRW and summer temperatures from 1901 to 1950, but no significant relationships between 1951 and 2001 (similar to Ohse et al 2011), whereas MXD had essentially consistent positive relationships with summer temperatures throughout the entire time period.

5. Other dynamics of plant communities and ecosystem processes

Wrapping up this focus issue are several papers that addressed the dynamics of landscape type, the non-woody component of the vegetation, and ecosystem processes. Including the Villarreal et al (2012) paper mentioned above, three of the articles focused on different aspects of ecosystem change at Barrow, Alaska. In addition to contributing to the shrub change discussion, Villarreal et al (2012) found that plant communities in general had changed between 1972 and 2010. Plant diversity, in terms of both species richness and Shannon’s index, had increased over that time period. A slight drying of the tundra over this 38 year period (also shown by Lin et al 2012, for Barrow) could be the explanation for greater changes in the wetter plant communities relative to dry and moist communities. Lichen cover increased consistently over the sampling period, whereas other vegetation types varied substantially among sampling times (1972, 1999, 2008, 2010). Periodic lemming outbreaks and the resulting herbivory could however be masking long-term changes. Johnson et al (2011) looked specifically at the effects of brown lemming herbivory on coastal tundra vegetation at Barrow, using 50+ year-old lemming exclosures. Whereas lemming exclosures did not influence species richness, the Shannon index was greater in lemming exclosures for the dry and moist sites, but greater in the control plots for the wet sites. The exclusion of lemmings yielded increases in the abundance of lichens and bryophytes and decreases in graminoids, although the magnitudes of these responses varied across landscape moisture regimes. An interesting conclusion here is that lemming herbivory actually promoted higher biomass of vascular plants (graminoids in this case). In the Yu et al (2011) grazing simulation study, as mentioned above, they found that grazing might benefit evergreen shrubs due to reduced competition with the more palatable deciduous shrubs. However, when evergreen shrubs were constrained in the model (through nitrogen limitation), heavy grazing by reindeer led to the conversion of shrub tundra to a moss, graminoid-dominated tundra.

With regard to ecosystem function, Gamon et al (2012) examined the surface energy balance components across features of a peat plateau with degraded high-centered polygons (baydjarakh) near Churchill, Manitoba; these polygonal peat plateaus had been observed in aerial photographs as being relatively stable for >80 years. This study analyzes field measurements of albedo, thaw depth, snow depth, snow heat transfer, surface temperature, and surface reflectance (visible and near-infrared wavelengths) over varying periods between 2002 and 2011, for both troughs between the polygons and the centers of the baydjarakh. They found that the troughs, dominated by graminoids and standing water, had lower albedo, with particularly lower reflectance in the near-infrared, relative to the shrub and lichen covered baydjarakh. The troughs also had substantially greater snow
depth, surface temperatures, and therefore much greater thaw than the baydjarakh, leading to differential thermal feedbacks that could promote the stability of these features over time. Lara et al. (2012) examined changes in ecosystem function at Barrow, Alaska between 1972 and 2010. They measured numerous variables, including land–atmosphere exchange of CO\(_2\) and CH\(_4\), albedo, water table, soil moisture, NDVI, and plant species cover and abundance at 14 new sites in proximity to 43 historic sites from the International Biological Programme (established in 1972). They found that moist and dry sites were generally stable with regard to ecosystem functioning over time, although there was a decrease in soil moisture at these sites. Aquatic and wet sites, on the other hand, showed increased soil moisture, greater CH\(_4\) efflux, and variable productivity over time.

6. Summary/synthesis

This collection of 22 research articles, in addition to effectively clarifying much of what we have been observing with regard to vegetation changes in the Arctic and sub-Arctic, has advanced our understanding of the spatial patterns of vegetation changes, the mechanisms for change, and the implications of dynamic vegetation for northern ecosystems and climate. For the boreal forest, remote sensing studies continue to support the ‘browning’ of forest vegetation; however, this reduction in photosynthesizing vegetation (NDVI) appears to be related to the fractions of evergreen trees and deciduous trees on the landscape—with greater declines in evergreen-dominated areas (Beck and Goetz 2011). Field observations, in these cases tree-ring studies, also suggest that boreal vegetation responses to temperature (the studies here focused on white spruce) can be highly variable in both space and time (Andreu-Hayles et al. 2011, Ohse et al. 2012). With regard to arctic tundra, remote sensing, field observations, and simulation modeling all continue to concur that there is a generally widespread ‘greening’ of tundra vegetation (Beck and Goetz 2011, Fraser et al. 2011, Buizer et al. 2012, Epstein et al. 2012, Lin et al. 2012, Villarreal et al. 2012, Yu et al. 2011, Zeng et al. 2011). A major component of this increase in photosynthetic vegetation is the proliferation of shrubs, largely in the more southern subzones of arctic tundra (Beck and Goetz 2011, Fraser et al. 2011, Myers-Smith et al. 2011, Naito and Cairns 2011, Ropers and Boudreau 2012, Epstein et al. 2012, Lin et al. 2012, Tremblay et al. 2012). However, these studies additionally reveal that while shrub expansion is occurring, there is also a more general background increase in tundra vegetation; in other words, shrubs are not the only plant life form that is responding positively to warming Arctic (Beck and Goetz 2011, Fraser et al. 2011, Johnson et al. 2011, Epstein et al. 2012, Lin et al. 2012, Villarreal et al. 2012). The studies here also indicate that shrub expansion and other tundra vegetation changes are highly spatially variable, and that certain species and landscape types are likely more conducive for change than others (Johnson et al. 2011, Naito and Cairns 2011, Lin et al. 2012, Ropers and Boudreau 2012, Tremblay et al. 2012). With regard to implications of shrub expansion, the modeling studies concurred that the effect of shrubs on reducing albedo, and therefore increasing regional heating, will outweigh the local effects of shrubs on summer soil cooling (Lawrence and Swenson 2011, Bonfils et al. 2012). A field study however suggested a contrasting outcome—that increasing shrubs on the landscape will not always decrease albedo (particularly in the summer), depending on the landscape type that is being replaced by the shrubs (Blok et al. 2011). Collectively these studies increase our knowledge of the spatial and temporal variability of recent vegetation changes at northern high latitudes and their effects on ecosystems and climate. Furthermore, they provide a basis for the development of new research questions on dynamic vegetation influences on land–atmosphere exchange of carbon (CO\(_2\) and CH\(_4\)), landscape hydrology, permafrost, plant–herbivore interactions, and other relevant high-latitude system properties and processes.

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