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Methods for measuring arctic and alpine shrub growth: A review

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ABSTRACT

Shrubs have increased in abundance and dominance in arctic and alpine regions in recent decades. This often dramatic change, likely due to climate warming, has the potential to alter both the structure and function of tundra ecosystems. The analysis of shrub growth is improving our understanding of tundra vegetation dynamics and environmental changes. However, dendrochronological methods developed for trees, need to be adapted for the morphology and growth eccentricity of shrubs. Here, we review current and developing methods to measure radial and axial growth, estimate age, and assess growth dynamics in relation to environmental variables. Recent advances in sampling methods, analysis and applications have improved our ability to investigate growth and recruitment dynamics of shrubs. However, to extrapolate findings to the biome scale, future dendroecological work will require improved approaches that better address variation in growth within parts of the plant, among individuals within populations and between species.

Contents

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1. Introduction

The recent observed increases in the growth and abundance of shrubs are one of the most prominent ecological changes currently occurring in many tundra ecosystems (Sturm et al., 2001; Tape et al., 2006; Post et al., 2009; Naito and Cairns, 2011; Myers-Smith et al., 2011a; Elmendorf et al., 2012; Macias-Fauria et al., 2012). Shrubs form canopies that alter litter inputs to the soil, the tundra microclimate and therefore soil and permafrost temperatures (Myers-Smith et al., 2011a); in addition, they provide important habitat and food sources for other organisms (Kitti et al., 2009; Tape et al., 2010; Ehrich et al., 2012; Ims and Henden, 2012; Li et al., 2013). Therefore, increases in shrub cover, abundance and canopy height will alter biodiversity, soil nutrient cycling, carbon storage, water and energy exchange (Eugster et al., 2000; Sturm et al., 2001; Liston et al., 2002; Chapin et al., 2005; Sturm, 2005; Wookey et al., 2009; Blok et al., 2010). Consequently, there is a growing need to better understand the drivers of arctic and alpine shrub growth and population dynamics to improve projections of tundra vegetation change.

Shrubs provide a multi-decadal record of environmental changes in tundra ecosystems. Shrub dendrochronology, the dating of annual growth rings, has been used to reconstruct climate (e.g., Schmidt et al., 2006; Weijers et al., 2010; Rayback et al., 2012a), measure landscape-level responses to climate and disturbance (Forbes et al., 2010; Hallinger et al., 2010; Blok et al., 2011; Macias-Fauria et al., 2012; Tape et al., 2012), date landslides (Gers et al., 2001) and permafrost disturbances (Gärtner-Roer et al., 2013; Leibman et al., 2014), reconstruct glacial history (e.g., Roer et al., 2007; Owczarek, 2010; Buras et al., 2012), describe rates of isostatic rebound of shorelines (von Mörs and Bégin, 1993), assess land-use history and human impacts in tundra ecosystems (Rixen et al., 2004; Speed et al., 2011) and more. By analyzing growth over time, growth–climate relationships, aging individuals, or examining wood anatomy or wood scarring, both the timing and extent of landscape-level vegetation change or geomorphic disturbances can be determined. Much of the current shrub dendroecological literature focuses on vegetation dynamics in relation to climate, but like with treering research, dendroecology extends far beyond dendroclimatology to applications across the Earth Sciences (Stoffel and Bollschweiler, 2008).

The application of dendrochronological methods requires adaptation of the standard techniques developed for tree-ring analyses (Fritts, 1976; Cook and Kairiūkštis, 1990; Schweingruber, 1996) to the specific morphology and ecology of shrubs. Like trees, shrubs typically add a layer of wood each year, which leads to shoot and root elongation and is visible as growth rings in the cross-sections of wood. However, unlike many tree species, tundra shrubs: (1) exhibit prostrate or multi-stemmed growth forms; (2) can reproduce clonally; (3) have below-ground connections among individuals; and (4) can allocate growth to different stems both above and belowground in complex ways (reviewed below). These physiological and ecological characteristics of shrubs often confound age determination and analyses of radial and axial growth. Modified or novel approaches are thus needed for sample collection, processing, analysis, and interpretation of shrub growth from annual rings and stem increments (Fig. 1).

Shrub growth measurements have been used to: (1) quantify climate-sensitivity of growth; (2) reconstruct climate; (3) establish linkages to satellite-derived vegetation greening; (4) document advances of the shrubline ecotone; and (5) investigate landscape-level disturbances (Table 1).

The application of dendroecological analysis to shrub species is a relatively recent advance of the last three decades (Woodcock and Bradley, 1994; Schweingruber and Poschlod, 2005). As the number of studies using shrub growth measurements increases, so too, does the need for better coordination of methods to promote inter-study comparisons and the integration of data among sites and species. In this paper, we review the dendrochronological methods for the measurement and analysis of shrub growth (Fig. 2). We hope that this review can serve as a guide for future dendroecological research on tundra shrub species, stimulating further advances in this field.

2. Important botanical considerations of shrub species

2.1. Growth form

Shrubs exhibit varied growth forms as a result of genetic differences or phenotypic plasticity in response to the growing environment (e.g., extreme cold, shade; snow cover, soil accumulation, and soil movement), which influences the interpretation of radial and axial growth measurements. Reduced apical dominance in shrubs may lead to the development of multiple stems and large clonal patches and competition or facilitation among species (interspecific), individuals of the same species (intraspecific), and stems within the same plant (e.g., self-shading; Carlsson and Callaghan, 1991; Pajunen, 2009;