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Landscape-scale variation in canopy water content of giant sequoias during drought☆

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ABSTRACT

Recent drought (2012–2016) caused unprecedented foliage dieback in giant sequoias (*Sequoiadendron giganteum*), a species endemic to the western slope of the southern Sierra Nevada in central California. As part of an effort to understand and map sequoia response to droughts, we studied the patterns of remotely sensed canopy water content (CWC), both within and among sequoia groves in two successive years during the drought period (2015 and 2016). Our aims were: (1) to quantify giant sequoia responses to severe drought stress at a landscape scale using CWC as an indicator of crown foliage status, and (2) to estimate the effect of environmental correlates that mediate CWC change within and among giant sequoia groves. We utilized airborne high fidelity imaging spectroscopy (HiFIS) and light detection and ranging (LiDAR) data from the Carnegie Airborne Observatory to assess giant sequoia foliage status during 2015 and 2016 of the 2012–2016 droughts. A series of statistical models were generated to classify giant sequoias and to map their location in Sequoia and Kings Canyon National Parks (SEKI) and vicinity. We explored the environmental correlates and the spatial patterns of CWC change at the landscape scale. The mapped CWC was highly variable throughout the landscape during the two observation years, and proved to be most closely related to geological substrates, topography, and site-specific water balance. While there was an overall net gain in sequoia CWC between 2015 and 2016, certain locations (lower elevations, steeper slopes, areas more distant from surface water sources, and areas with greater climate water deficit) showed CWC losses. In addition, we found greater CWC loss in shorter sequoias and those growing in areas with lower sequoia stem densities. Our results suggest that CWC change indicates sequoia response to droughts across landscapes. Long-term monitoring of giant sequoia CWC will likely be useful for modeling and predicting their population-level response to future climate change.

1. Introduction

California experienced its most severe drought in more than a century between the years 2012 and 2016, characterized by historically low precipitation combined with particularly warm temperatures and forest insect outbreaks (Diffenbaugh et al., 2015; Swain et al., 2016). These factors generated a large pulse of canopy water loss and tree mortality throughout the state (Asner et al., 2016a; Young et al., 2017). In addition, the ongoing drought generated a severe reduction in soil moisture, groundwater levels, and reservoir stocks (Diffenbaugh et al., 2015). One area that experienced extensive drought stress was the Sierra Nevada region, which had undergone a dramatic decline in winter snowpack and an increase in the length of the summer drought period (Griffin and Anchukaitis, 2014). Large-scale tree mortality was observed throughout the Sierra Nevada, with observations of millions of dead trees (Asner et al., 2016a; Young et al., 2017). During the third year of the drought (2014), giant sequoias (*Sequoiadendron giganteum*) exhibited foliage dieback (Stephenson et al., this issue). As a result, there has been a growing concern regarding giant sequoia responses to drought stress.

Giant sequoias are endemic to the western Sierra Nevada, are generally confined to a narrow mid-elevation range (1400–2150 m), and are restricted to roughly 70 groves that occupy about 14,600 ha (Stephenson, 1999). Giant sequoias are the most massive tree species on

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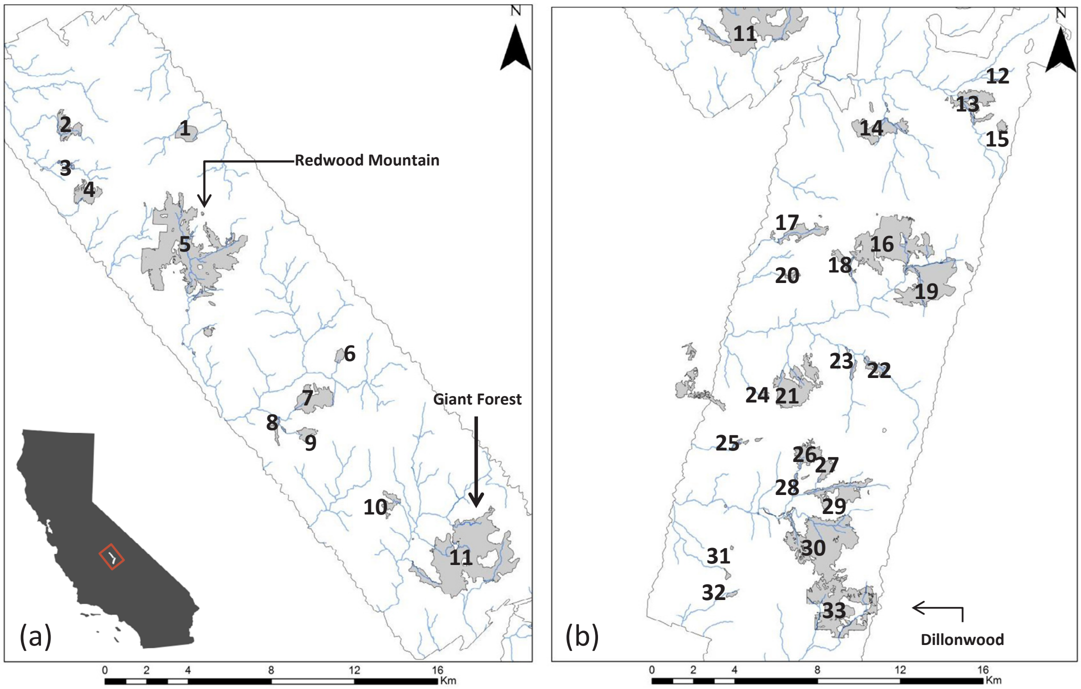

Fig. 1. (a) Carnegie Airborne Observatory (CAO) flight coverage throughout 33 giant sequoia groves and aggregated groves (small groves adjacent to each other) in the northern (a) and the southern areas (b) on the western slope of the southern Sierra Nevada in central California, together with the grove map and rivers and streams. Grove numbers correspond to those in Table 4.

earth, among the tallest, reaching heights of up to 95 m, and among the oldest, sometimes having a life span of 3200 years or longer (Stephenson, 1996; York et al., 2011). Giant sequoias are known for their remarkable pest, pathogen, and fire resistance (Hartesveldt et al., 1975), and their present species range appears to be based on abundant soil moisture (Rundel, 1972).

Giant sequoias deploy multiple adaptation strategies to cope with water stress, including shoot and leaf succulence, leaf toughness, and optimization for heat accumulation in the transpiration tissues (Ambrose et al., 2016). The ability of giant sequoias to tolerate water stress is possible, in part, because its leaves are responsive to environmental change. Chin and Sillett (2016) have shown that phenotypic plasticity allows giant sequoias to adapt their foliage to within-crown environments, maximizing limited windows of stomatal openness through rapid hydraulic throughput and resistance to water stress-induced damage. Additional adaptations to cope with water stress in giant sequoias have been found, including tight stomatal control of water loss and increasing xylem cavitation resistance with height (Ambrose et al., 2015; Ambrose et al., this issue). These findings provide insight into the isohydric approach through which giant sequoias regulate their stomatal conductance, transpiration, and resultant water loss rates (Tardieu and Simonneau, 1998). Isohydric trees regulate stomatal conditions to maintain minimum water potential within a relatively narrow range, thereby reducing the risk of damaging xylem cavitation (Roman et al., 2015). However, this strategy causes them to close their stomata in response to even mild water stress, which reduces carbon uptake.

While our knowledge about physiological responses to drought at the leaf and whole tree level is growing, the understanding of crown-level responses in giant sequoias at local (grove) to a regional scale still remains a challenge. Ground-based measurements provide insight into the mechanisms of drought responses in trees, but are often limited to relatively few individuals, especially in trees of tall stature such as giant sequoias. These measurements are expensive and time-consuming, and thus cannot meet the requirements of landscape-scale assessment and management. Remote sensing offers a means to measure the canopy condition of a large number of trees, which may provide insight into whether giant sequoias are responding at the canopy and/or landscape level. Remote sensing technologies, such as high fidelity imaging spectroscopy (HiFIS) and light detection and ranging (LiDAR) measurements, may improve our understanding of giant sequoia responses to drought stressors at landscape scales. The combination of high spatial and spectral resolutions provided by HiFIS is particularly suitable for this task, providing a powerful technique for mapping specific species at the crown level, based on the reflectance properties of tree canopies (Asner and Martin, 2015; Asner et al., 2015; Baldeck et al., 2015). HiFIS can also be used to study foliage status as part of the trees' physiological and biophysical status (Asner et al., 2014; Asner et al., 2015). The LiDAR data can be used to study the giant sequoia's responses to environmental control via both topographic characteristics and canopy characteristics such as top-of-canopy height above ground (Omasa et al., 2007).

One of the most applied HiFIS measurements of foliage status is canopy water content (CWC), which is defined as the total amount of liquid water in the foliage of a canopy expressed in L m^{-2} (Asner et al., 2004; Farooq et al., 2009). CWC is broadly correlated with the combination of leaf water content and leaf area index, thus serving as an indicator of progressive drought-related stress (Ustin et al., 1998; Cheng et al., 2006; Asner et al., 2016a). Martin et al. (this issue) combined the airborne HiFIS remote sensing measurements taken in 2015 and 2016 to assess the biophysical responses of giant sequoias to drought. In 49 studied trees, CWC was related to leaf water potential in both years and non-structural carbohydrates (NSC, %) in one year, but not to other foliar traits including leaf water content, leaf mass per area (g m^{-2}), foliar δ13C, and total nitrogen (%) suggesting that changes in CWC were made at the whole-canopy rather than the leaf scale. Martin et al. (this issue) detected a clear relationship between CWC and foliage dieback, even without taking into account new or prior variability in leaf growth. This connection between CWC and foliage dieback suggests that CWC of giant sequoias might serve as an indicator of water stress in giant sequoia canopies using HiFIS. In particular, foliage dieback was most likely a controlled process of drought-induced senescence and not