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A robust method to determine historical annual cone production among slow-growing conifers

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ABSTRACT

Forest and woodland ecosystems may be strongly affected by climate change influences on tree population processes such as seed production and seedling recruitment. Yet climate effects on seed production are generally poorly understood, particularly for trees that exhibit masting behavior (i.e. high synchronicity and high inter-annual variability in seed production). This is largely due to the limited amount of long-term datasets on seed production, which are necessary to characterize the highly variable reproductive outputs of masting species. The cone abscission scar method provides a promising approach to accurately determine historical (past 10–20 years) annual cone production, but the method has not been rigorously validated. Here we use a long-term dataset of cone abundance on individually monitored pinyon pine (*Pinus edulis*) trees to validate the cone abscission scar methodology. Tree cone production estimated using abscission scars was positively associated with observed mature cone and conelet abundances from 8 to 13 years previously (Spearman's $\rho = 0.52$ and 0.66, respectively), the time period of our observed historical cone production data. Further, we show that between 4–5 branches per tree and 4–6 trees per site need to be sampled to minimize the variance in cone abundance estimates. Thus, only approximately 3–4 h are needed to obtain an estimate of historical annual cone production in a stand. Overall, we show that the cone abscission scar method provides a robust and time efficient approach to accurately determine historical annual cone production for *P. edulis* and likely other slow-growing conifer trees.

1. Introduction

Forest ecosystem response to changing climate and land-use practices will depend upon species-specific effects on fundamental tree population processes, including reproduction, growth, and mortality. Whereas we are able to obtain long-term data on tree mortality and growth through dendrochronology studies, satellite imagery, and long-term monitoring plots, we have limited long-term data on tree reproductive potential due to the difficulty in obtaining historical seed production data (but see Crone et al., 2011; Krebs et al., 2012; Mutke et al., 2005a; Pérez-Ramos et al., 2010; Redmond et al., 2012). Of particular interest are the potential climate change responses of the many tree species that exhibit 'masting' behavior, or high synchronicity and high inter-annual variability in seed production. The necessary long-term data are generally lacking to evaluate the endogenous and exogenous drivers of tree reproduction among masting species.

The historical reproductive output of certain coniferous species can be estimated using the visible abscission scars that remain when female cones are dropped from cone-bearing branches. Cone abscission scars allow temporal variations in seed cone production to be observed by counting scars (as well as any remaining seed cones) at each terminal bud scale scar on a subset (generally 5–10) of cone-bearing branches. Because seed cones of many pine species take multiple years to mature, this methodology estimates potential reproductive output as the total number of conelets (immature cones) that were subsequently aborted, in addition to mature cones. Thus, the cone abscission scar method provides a promising approach to estimate seed cone production over the past 10–20 years among several pine species, including *Pinus albicaulis*, *Pinus edulis*, *Pinus halepensis*, *Pinus pinea*, *Pinus pinaster*, *Pinus pumilo*, and *Pinus silvestris* (Crone et al., 2011; Forcella, 1981a, 1981b; Girard et al., 2011; Kajimoto et al., 1998; Mutke et al., 2005b; Thabeet et al., 2009; Weaver and Forcella, 1985). With

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increased drought and projected impacts of climate change on cone production, the ability to reconstruct past cone production will become increasingly important for both basic and applied research.

Yet despite the breadth of studies using this methodology (Crone et al., 2011; Forcella, 1981b; Girard et al., 2011; Kajimoto et al., 1998; Mutke et al., 2005b; Redmond et al., 2012; Thabeet et al., 2009; Vennetier et al., 2013; Weaver and Forcella, 1985), there has been limited validation, likely due to the necessity of obtaining long-term data on individually monitored trees. Forcella (1981a) found that cone abscission scars of the recent year were strongly correlated with the total number of observed new cones on the tree and ground surface in pinyon pine (*P. edulis*), yet it remains unclear how effective this methodology is at quantifying cone production further back in time. Morgan and Bunting (1992) also conducted a validation study using historical cone production data on whitebark pine (*P. albicaulis*), yet this study did not have individually monitored trees and was thus only able to assess whether the cone abscission scar method could distinguish between qualitatively different levels of cone production (e.g. high vs. low cone production years). Given the considerable effort required to accurately date cone scars on a given branch, it is also important to quantify how many branches are necessary to obtain a robust estimate of cone production in a tree, as well as how many trees need to be sampled to accurately estimate cone production at the stand level.

Here we use a long-term dataset of cone abundance on individually monitored pinyon pine trees to validate the cone abscission scar methodology. Our specific objectives were to: 1. Evaluate whether the cone abscission scar methodology is effective at measuring conelet and/or mature cone abundance 8–13 years previously; 2. Determine the sample size necessary to obtain a robust estimate of cone production within an individual tree and among trees within a stand.

2. Materials and methods

Nineteen individually tagged pinyon pine trees, previously sampled between 2003 and 2008 to determine conelet and cone production, were revisited in 2015 for our validation study. These trees were located near Sunset Crater National Monument (5 trees) and Red Mountain (14 trees) in northern Arizona, USA (see Cobb et al., 2002 for site location and tree selection details). On average, sampled trees were 21.9 cm in basal trunk diameter (range: 15.5–29 cm), 9.8 m^2 in canopy area (range: 4.2–19.6 m^2), and 3.7 m in height (range: 1.9–5.3 m).

2.1. Pinyon pine seed cone production and cone abscission scar methodology

Similar to many pine species, pinyon pine seed cones require multiple growing seasons to mature (Little, 1938; Mirov, 1967). At cone initiation in August or September, microscopic buds develop and not until early that following summer, when pollination occurs, do the microscopic buds develop into visible seed conelets (or 1st year cones), which then overwinter. Mature seed cones form the following fall, 26 months after cone initiation (Little, 1938; Mirov, 1967). Similar to other pine species (Crone et al., 2011; Kajimoto et al., 1998; Thabeet et al., 2009; Weaver and Forcella, 1985), pinyon pine seed cones and conelets leave visible abscission scars on tree branches (Fig. 1). These abscission scars allow temporal variations in seed cone production to be observed by counting cone scars (as well as any remaining cones or conelets) at each terminal bud scale scar on cone-bearing branches (see Fig. 1 for a description; Forcella, 1981b). Cone-bearing branches of pinyon pine are noticeably more erect and sturdy than purely vegetative branches and are generally in the top two thirds to top third of the tree canopy. Following the methodology in Forcella (1981b), for each branch sampled, all cones, conelets, and cone abscission scars were counted on the dominant branch stem as well as all recent (<13 years old) lateral offshoots. To ensure accurate dating of annual growth increments along tree branches, offshoots without any cone scars were also dated to confirm cone abscission dates by cross-dating within each branch system. Finally, the total number of cone-bearing branches on each tree was counted to obtain an estimate of total cone production for each year by multiplying the mean scar number per branch for a given year by the total number of branches.

2.2. Field sampling

Between late July and early September of each year from 2003 to 2008, all individually tagged trees were visited and all conelets (i.e. juvenile 1st year cones) and mature cones (i.e. mature 2nd year cones) were counted by two independent observers, and the observer counts were then averaged. These two observers were present in the field together, but each observer counted the total number of conelets and mature cones on the tree without prior knowledge of the other observer's estimates. In October of 2015, we revisited each tree and used the cone abscission scar method to quantify cone production during that same time period. To do this, we counted the number of conelets, mature seed cones, and seed cone abscission scars at each annual node from 2003 to 2008 on 6–10 cone-bearing branches on each tree following the methodology outlined above (see Fig. 1 for details). We had difficulty determining cone scars past 2004 (year of maturity, i.e. conelets of 2003), likely due to a drought event that occurred in 2002 and resulted in extensive pinyon pine mortality in the area (Clifford et al., 2011; Floyd et al., 2009; Mueller et al., 2005). We were thus able to compare the cone abscission scar abundance to mature seed cone abundance from 2004 to 2008, whereas we were able to compare the cone abscission scar abundance to seed conelet abundance from 2003 to 2008 (years of maturity: 2004–2009).

2.3. Statistical analyses

To determine whether the cone abscission scar method accurately measures conelet and/or mature cone abundance, we performed Spearman's rank correlation analyses to evaluate the relationship between estimated cone abundance (calculated for each tree and each year) and observed conelet abundance (analysis 1) and mature cone abundance (analysis 2). We performed these two separate analyses to assess whether our estimated cone abundance is a better estimate of conelet abundance, which includes conelets that were subsequently aborted in addition to conelets that developed into mature cones, or a better estimate of mature cone abundance. We also assessed the accuracy of the cone abscission scar method at distinguishing between years of high and low cone production across our study area. To do this, we calculated the mean estimated cone abundance and mean observed cone and conelet abundance for each year (averaged across all trees in our study area) and then performed Pearson's correlation analyses. We similarly assessed whether the cone abscission scar method accurately detects high and low cone-producing trees by calculating the mean estimated cone abundance and mean observed cone and conelet abundance for each tree (averaged across all years) and then performing Pearson's correlation analyses.

To evaluate the appropriate branch sample size needed to determine cone production for each tree, we assessed how the variance and mean of estimated cone abundance changed with an increasing sample size (from 1 branch to 8 branches). For this