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The ground plot counting method: A valid and reliable assessment tool for quantifying seed production in temperate oak forests?

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ABSTRACT

Masting, or mast-seeding, defined as a synchronized and highly variable seed production from year-to-year within a population of plants, is one of the most common example of pulsed resources in terrestrial ecosystems. In oaks, the dramatic fluctuations of acorn production impact its reproductive success and regeneration, the dynamics of a large diversity of seed consumers that rely on it, and, by cascade effects, the dynamics of the entire forest community. However, reproductive effort is difficult to quantify and there is therefore an urgent need of a reliable assessment of the dynamic of acorn production based on a low-cost, unbiased, and robust tool. One of the most commonly used method, the "visual on-tree" method, is very easy and quick to carry out, but is biased under high seed production or when branches are difficult to see. We here assessed the robustness of an alternative method, the "ground plot" (GP), based on a unique annual ground survey after peak of acorn fall, which has not been tested so far. We compared this method at tree and site levels (10 forests throughout France) with the costly and time-consuming trap acorn collection (TNR) method (used here as a reference method). We show that results from the GP method closely matched with those obtained using the TNR method, which demonstrates the efficiency and robustness of the GP method at both tree and forest site levels. Despite some limitations in specific environmental contexts we review, this GP method offers a powerful tool to quantify acorn production and should be deployed to understand mechanisms underlying oak masting and/or to assess its ecological or economic consequences.

1. Introduction

The dynamics of many terrestrial and aquatic ecosystems are characterized by pulsed resources, typically defined as low frequency, large magnitude, and short duration episodes of increased resource availability (Yang et al., 2008, 2010). These events are known to affect a wide range of communities at multiple trophic levels (i.e. individual, population and community) (Ostfeld and Keesing, 2000; Schmidt and Ostfeld, 2008). Masting, or mast-seeding in perennial plants, which involves the synchronous production of large seed crops within a tree population (Silvertown, 1980; Kelly, 1994; Pearse et al., 2016) is one of the most common type of pulsed resources in terrestrial ecosystems (Ostfeld and Keesing, 2000). By affecting the demography of seed consumers, masting not only impacts the reproductive success of plants, but also drives their recruitment and regeneration success, and as a result, forest plant species assembly (Loftis and McGee, 1993; Alejano et al., 2011). One well-supported selective advantage of masting is the predator satiation hypothesis, which states that when seed production is low, seed consumers are maintained at low density. However, when seed production is unpredictably high, seed consumers are satiated and a large proportion of seeds are likely to escape from predation

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(Janzen, 1971; Kelly, 1994; Kelly and Sork, 2002; Bogdziewicz et al., 2018). Oak trees are found in both temperate and Mediterranean regions (McShea, 2000; Gea-Izquierdo et al., 2006) and provide an illustrative case study of the dramatic among-year variation in seed production (Koenig et al., 1994b; Koenig and Knops, 2000; Liebhold et al., 2004a, 2004b). The high fluctuation of oak acorn production shapes the dynamics of acorn consumers such as insects (Venner et al., 2011; Bogdziewicz et al., 2018), birds (Haney, 1999; McShea, 2000), rodents (Wolff, 1996; Stapp and Polis, 2003; Bergeron et al., 2011) and ungulates (Servanty et al., 2009; Gamelon et al., 2017), and impacts by cascade effects the dynamics of the entire community (Ostfeld and Keesing, 2000; Yang et al., 2010; Bogdziewicz et al., 2016). Moreover, by influencing the regeneration of oak forests (Loftis and McGee, 1993; Alejano et al., 2011), masting affects the production of wood of high economic value, and has thereby a strong socio-economic impact (Ostfeld and Keesing, 2000).

Considering the high scientific and societal significance of acorn dynamics, a lot of efforts have been devoted to measure acorn crops (e.g. Graves, 1980; Koenig et al., 1994a; Perry and Thill, 1999). Up to now, two main methods for counting mature acorns have been used. The “trap acorn collection” (named hereafter TNR) corresponds to a method where acorns fall into collectors (e.g. nets, buckets, cans) evenly located beneath the crown (Carevic et al., 2014). This method prevents post-acorn fall seed predation by using protection devices and performing frequent collects during the acorn fall period but does not account for the removal of acorns in the canopy pre-fall. It seems to be the most accurate method to estimate acorn crop (Perry and Thill, 1999; Gea-Izquierdo et al., 2006), but has several drawbacks: the equipment required to collect and protect acorns from consumers may be costly (Perry and Thill, 1999), the conspicuous devices have to be frequently visited to ensure these are not subject to human disturbance, and exhaustive counting of the collected seeds is time consuming (Gea-Izquierdo et al., 2006). The second method, the “visual on-tree” (VOT) method, involves direct counting of mature acorns while still on trees (Koenig et al., 1994a). For this method, observers stand beneath the crown of the focused tree and count as many acorns as possible during a timed period. As used in California oak woodlands, two observers count separate parts of the tree, each for 15 s (Koenig et al., 1994a). This method requires very little equipment (Carevic et al., 2014) and is quick to apply. However, the number of acorns counted in any given period of time is limited by the counting speed of the observer, which may bias the results especially on mast years (Koenig et al., 1994a; Perry and Thill, 1999; see Supplementary Material Appendix 1; Fig. S1; and Table S1). Furthermore, visual access to branches could be compromised either by the location of the acorns inside the tree or by high tree density leading branches from different trees mixing up and canopy closure, which can generate biases when assessing the acorn production in forest landscape (Koenig et al., 1994a; Perry and Thill, 1999; see Supplementary Material Appendix 2; Fig. S2; and Table S2).

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As these limitations are inherent to any TNR or VOT method previously used, we aimed to set up a new low-cost method that would be easily and quickly applicable in any forest landscape to obtain accurate estimates of acorn production at both tree and population scales. To do so, we proposed and tested the efficiency of the “ground plot” counting method (GP). This sampling method is based on counting acorns on the ground under the tree crown, in quadrats of known area, with no protection against seed predators. The survey took place during a single annual visit soon after main acorn fall. We applied this new GP method on one hundred oak trees from 10 forests (i.e. 10 trees per study site) and we compared the estimates of acorn production with the ones obtained with the TNR reference method deployed on the same individual trees. We assessed the robustness of the GP method at both individual tree and site scales.

2. Methods

2.1. Study sites and selection of oak trees

To test the performance of the GP counting method, we selected 10 forest sites widely distributed throughout France (see Supplementary Material Appendix 3; Fig. S3), with the sessile oak tree (*Quercus petraea*) as the dominant species. The distribution of the studied forests allowed encompassing a large range of environmental conditions with contrasting density and diversity of seed predators. At each site, 10 mature and reproductive trees (i.e. at least 45 cm in diameter) were randomly selected. Every year from 2013 to 2016, a single observer surveyed every tree by applying both TNR and GP methods.

2.2. The Trap-Net reference method (TNR)

Seed traps (i.e. nets of 20 m^2 (4 × 5 m)) were laid under the crown of the studied trees to collect mature acorns falling from mid-August to mid-November. Acorns that dropped in the net were forced, once a week, to fall into a collecting device (80 cm in height and diameter) closed with a lid and surrounded by a wooden fence, thus preventing seed consumption by predators (i.e. birds, rodents and ungulates) (see Supplementary Material Appendix 4; Fig. S4). Each year, acorns were collected in December and counted. The annual acorn production of a tree was estimated as the number of acorns collected per square meter.

2.3. The ground plot counting method (GP)

Soon after the main drop of mature acorns (from mid-October to early November), four sampling points were evenly distributed under the half canopy that was free of any seed trap device (used for the TNR method). To do so, the observer placed himself between two and four meters (depending on crown size) away from the tree trunk and defined four evenly spaced counting points following a circular transect fitting the crown shape (see Supplementary Material Appendix 5; Fig. S5). At each counting point, a quadrat of 0.25 m^2 (50 × 50 cm) was settled on the ground and the number of acorns inside was recorded by a single observer, who remained the same throughout the study period. A unique visit made at each tree was required to implement the method. The acorn production was estimated as the number of acorns per square meter.

2.4. Statistical analyses

2.4.1. Assessment of the GP method performance to estimate the number of acorns produced by a tree

We compared the number of acorns produced by individual trees as estimated by the GP and the TNR methods. First, we explored the ability of the GP method to detect very low amounts of acorns produced by trees. To do so, we fitted a logistic regression to estimate the probability for acorns to be detected by the GP method (i.e. presence or absence of acorns in the quadrats) from the number of acorns harvested with the TNR method. Second, we examined the relationship between the number of acorns counted using the GP and the TNR methods for every tree and year. Trees for which no acorn was found in the quadrat a given year were analyzed separately from the other trees having at least one acorn. This allowed us to account for the lack of power of the GP method when very low amounts of acorns are produced. For non-null GP counts, we explored the relationship between the production of the GP method and the one of the TNR method by fitting constant, linear, and quadratic models. To account for repeated measures performed on the same trees over several years and then avoid pseudo-replication issues (sensu Hurlbert, 1984), we included in the model the tree identity as random effect. Year was not included as a random effect because acorn production is synchronized at the population scale and varies among years within a given population (Koenig et al., 1994b).