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ORIGINAL PAPER

Defoliation by gypsy moths negatively affects the production of acorns by two Japanese oak species

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Abstract

Key message **This study showed the negative effects of insect defoliation on the reproduction of canopy trees, where defoliation was not artificially manipulated but rather observed in a natural setting.**

Abstract The gypsy moth (*Lymantria diapar*) is a serious defoliator with the ability to completely defoliate forest canopies. Although the negative effects of defoliation on tree reproduction have been revealed in studies with artificially manipulated defoliation, few studies have examined the effect of insect defoliation on the reproduction of canopy trees under natural condition. In this study, visual surveys were used to clarify the effect of gypsy moth defoliation on the production of acorns by oaks (*Quercus* spp.). Surveys were conducted in an outbreak year at 22 sites in central Japan (13 sites with *Quercus crispula* and nine sites with *Q. serrata*). Five of the *Q. crispula* sites were severely defoliated (mean defoliation ranged from 67 to 88 %), while the remainder of the *Q. crispula* sites and all of the *Q. serrata* sites were lightly defoliated (0–20 %). A negative effect of gypsy moth defoliation on acorn production was detected for *Q. crispula*. However, there was a synchronous decrease in acorn production from the previous year and crop levels were low at all sites regardless of the defoliation severity. The consistent low crop levels were likely the result of weather-related factors. Defoliation also negatively affected the production of acorns for *Q. serrata*; however, severe defoliation was not present at any *Q. serrata* sites. This study suggests that insect defoliation can affect forest ecosystem processes, such as the regeneration of host trees and the behavior of wildlife that depend on seed production, by reducing the reproductive potential of host trees.

Keywords Insect herbivory · Gypsy moth defoliation · Tree reproduction · Mast seeding · *Quercus crispula* · *Quercus serrata*

Introduction

Defoliation has negative effects on tree reproduction and growth (Kulman 1971; Schowalter et al. 1986; Obeso 1993; Morris et al. 2007; Massad 2013). Among the numerous insect defoliators, the gypsy moth (*Lymantria diapar*), which is widely distributed across the northern hemisphere (Alalouni et al. 2013), is well known as a serious defoliator whose larvae can defoliate multiple tree species (Liebhold et al. 1995; Onodera and Hara 2011). Severe outbreaks of gypsy moths can cause complete defoliation of forest canopies (Lovett et al. 2006).

Gypsy moth defoliation induces various responses in trees: refoliation in the same season (Collins 1961; Eschtruth and Battles 2014), reduction of seed production (Gottschalk 1990; Kasbohm 1994), reduction of radial growth (Baker 1941; Muzika and Liebhold 1999; Kosola et al. 2001; Naidoo and Lechowicz 2001; Fajvan et al. 2008), chemical changes in the leaves (Schultz and Baldwin 1982), and even mortality in extreme cases (Campbell

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and Sloan 1977; Gottschalk et al. 1998; Eisenbies et al. 2007). These tree responses affect forest ecosystem processes (Lovett et al. 2006; Gandhi and Herms 2010). For example, ephemeral foliage loss or mortality of canopy trees can facilitate the growth of understory tree species and plant invasions, thus, altering forest species composition (Collins 1961; Fajvan and Wood 1996; Jedlicka et al. 2004; Eschtruth and Battles 2014). Such vegetation changes and diminished seed production caused by defoliation have cascading impacts on wildlife that depend on specific vegetation or seeds (Kasbohm et al. 1995, 1998; Bell and Whitmore 1997). In addition, defoliation can also affect nutrient cycles by altering the nutritional composition and seasonal distribution of litter fall (Grace 1986). Therefore, it is important to monitor the spatial and temporal dynamics of gypsy moth defoliation that occur at a regional scale and to quantify their effect on tree performance to more effectively manage forest ecosystems.

The majority of studies revealing the negative effects of defoliation on tree reproduction to date have involved one of two methods: artificial defoliation, mainly at the branch level and chiefly for small trees or shrubs (Rockwood 1973; Janzen 1976; Stephenson 1980; Marquis 1984; Obeso 1998; Kaitaniemi et al. 1999; Hoch 2005); or the use of insecticide to prevent defoliation in some trees and then compare impacts with naturally defoliated trees (Crawley 1985; May and Killingbeck 1995; Salleo et al. 2003). Consequently, little is known about the effect of insect defoliation on the reproduction of canopy trees under natural condition (Wesołowski et al. 2015), even for the gypsy moth defoliation (Gottschalk 1990; Kasbohm 1994). This is because, first, insect outbreaks that cause severe defoliation are relatively rare events. Second, severe defoliation is short-lived because it is often followed by refoliation (Kulman 1971). Accordingly, surveys of defoliation must be conducted after defoliation reaches a peak but before refoliation progresses: a period of less than 1 month (Collins 1961; de Beurs and Townsend 2008; Eschtruth and Battles 2014). Third, measuring the reproduction of canopy trees is problematic, as the commonly used seed trap method is labor-intensive to place, maintain, and empty. This problem, however, can be overcome by using visual surveys with binoculars (Koenig et al. 1994; Nakajima 2015).

The Asian gypsy moth is widely distributed in Japan (Liebhold et al. 2008; Arimoto and Iwaizumi 2014) with outbreaks recorded intermittently in various regions (Koyama 1954; Akasofu 1973; Higashiura 1987; Liebhold et al. 1998; Kamata 2002; Jikumaru and Sano 2007; Mizutani 2014). Previous studies have quantified defoliation intensity primarily in young coniferous plantation forests (e.g., Ishihama et al. 2011) with few surveys conducted in natural forests (Jikumaru and Sano 2007; Mizutani 2014). Moreover, to date, no study has demonstrated the distribution of defoliation intensity at a regional scale.

The main aim of this study was to evaluate the impact of gypsy moth defoliation on the production of acorns by oaks. The study was conducted in Toyama Prefecture, central Japan, where one of the subspecies of Asian gypsy moth, *Lymantria dispar japonica*, is distributed (Higashiura et al. 2011; Arimoto and Iwaizumi 2014) with outbreaks recorded occasionally (Koyama 1954; Akasofu 1973). The impact of gypsy moth defoliation was quantified in two oak species, *Quercus crispula* and *Q. serrata*, which are temperate deciduous trees requiring about 4–5 months to mature acorns from spring-flowering. These two species were chosen as they are the dominant species in secondary forests in this region (Nakajima and Ishida 2014) and are both susceptible to gypsy moth defoliation (Jikumaru and Sano 2007; Onodera and Hara 2011).

The Toyama Prefectural Government has been monitoring the acorn production of several hundred trees of *Q. crispula* and *Q. serrata* across the prefecture. In this study, visual surveys of defoliation and acorn production of these oak trees were conducted during a gypsy moth outbreak year (2014) at 22 sites (13 sites with *Q. crispula* and nine sites with *Q. serrata*). The aim was to examine the distribution of defoliation intensity throughout the prefecture and evaluate the impact of defoliation on acorn production. As the two oak species exhibit annual fluctuations in acorn production (Imada et al. 1990; Shibata et al. 2002; Maeto and Ozaki 2003; Saitoh et al. 2008; Fukumoto and Kajimura 2011), data on the acorn production in the previous year (2013) were used to compare with the production in 2014.

Materials and methods

Study site

Visual surveys of defoliation and acorn production were conducted in 13 sites for *Q. crispula* (Fig. 1, A–M) and nine sites for *Q. serrata* (Fig. 1, 1–9) in Toyama Prefecture, central Japan. Elevation above sea level ranged from 350 to 1170 m for sites with *Q. crispula* and 90–340 m for sites with *Q. serrata* (Table S1). These sites had been established by the Toyama Prefectural Government to monitor acorn production and predict the mass intrusion of Asiatic black bears (*Ursus thibetanus*) into residential areas in years of poor acorn crops. The government monitoring protocol involves at least 20 trees per site, with the same trees being monitored every year unless the tree declined or died. This study surveyed these same trees (Table S1; $n = 299$ trees for *Q. crispula*; 184 trees for *Q. serrata*).

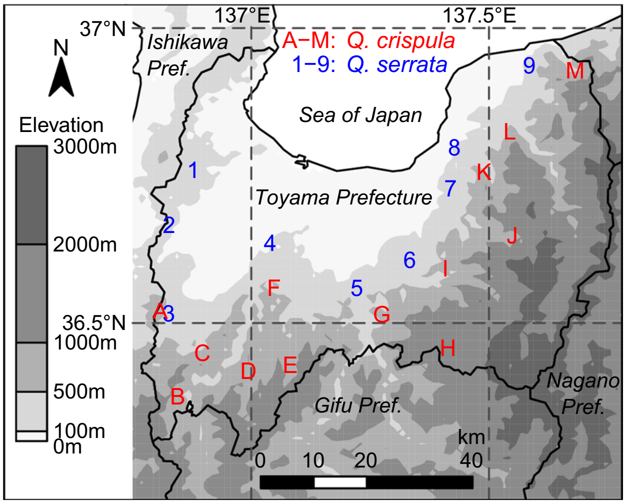

Fig. 1 Map of the study area. *Letters A–M* are the locations of the 13 *Quercus crispula* sites, while numbers *1–9* indicate the nine *Q. serrata* sites

These trees were canopy trees located along the roads and therefore defoliation and acorn-bearing could be visually surveyed easily.

Defoliation

Defoliation was surveyed in 2014 when an outbreak of gypsy moths occurred. In this region, incubation from overwintering egg begins around the middle of April, with pupation starting in late June. Defoliation proceeds rapidly just before pupation because most of the defoliation is caused by the last instar larvae (Furuno 1964). Refoliation induced by severe defoliation is completed within around 1 month of peak defoliation (Collins 1961; Eschtruth and Battles 2014). Therefore, the survey was conducted in July just after peak defoliation.

Using binoculars, tree-level defoliation was visually scored as the percentage loss of crown foliage, in 10 % classes (Williams et al. 1991; Gottschalk et al. 1998; Muzika and Liebhold 1999). Pictures of sample trees in 2012 with little defoliation were used as a reference. Defoliation was rated by the author alone who is skilled in rating crown foliage biomass visually in the forest monitoring program (Nakajima et al. 2011). Site-level defoliation was calculated by the mean of tree-level defoliation. No tree exhibited >20 % defoliation in the previous year, 2013.

Acorn index

In 2013 and 2014, acorn production was visually surveyed in mid- to late-August. The number of acorns was counted with binoculars for 20 branches (50 cm length each) per tree and a tree-level acorn index was calculated from these mean. The observed branches were selected at random from the sun crown in each year. This method was devised by Mizui (1991) and has been used for estimating the seed production of various tree species, including oak (Yasaka et al. 2008; Kozakai et al. 2011; Mizutani et al. 2013). A site-level acorn index was calculated by averaging the tree-level acorn indices, and categorizing this value into four crop levels: few, poor, fair, or good (Mizui 1991). The corresponding boundary values of the crop levels were 0–0.6, 0.6–1.9, 1.9–5.6, and >5.6 for *Q. crispula*, and 0–0.9, 0.9–2.6, 2.6–7.8, and >7.8 for *Q. serrata*. The values of *Q. crispula* were smaller than *Q. serrata* because the boundary values were defined to correlate negatively with the mean acorn weight of the species (Mizui 1991) and *Q. crispula* acorns are heavier. To examine the annual fluctuation in acorn production from 2013 to 2014, the tree-level acorn indices were compared between the 2 years in each site with a Mann–Whitney *U* test.

Relation between defoliation and acorn index

To clarify the effect of defoliation on acorn production, Pearson's correlations between defoliation and acorn indices were calculated at both the site- and tree-level. In the tree-level analysis, pooled data across the sites were used. In addition, to control for variation among sites, a generalized linear mixed model with a negative binomial distribution and a log link function was used. The total acorn count for each tree was used as the dependent variable. Tree-level defoliation was included as a fixed effect, site was included as a random effect, and the log of the number of observed branches per tree (log 20) was included as an offset variable. The model was developed using R 3.1.2 (R Core Team 2014) with the aod package (Lesnoff and Lancelot 2012).

Results

Defoliation

The sites could be divided into two categories according to the intensity of defoliation (Fig. 2; Table S1). Five sites of *Q. crispula* (A–E) were categorized as severely defoliated sites, containing completely defoliated trees and an average (site-level) defoliation of between 67 and 88 %. These sites were located in the south-west of Toyama Prefecture, between 500 and 1000 m elevation (Fig. 1). The remaining eight sites of *Q. crispula* (F–M) and all nine *Q. serrata* sites were categorized as lightly defoliated sites. In these sites, the maximum tree-level defoliation was not greater than 50 % and the site-level defoliation ranged from 0 to 20 %.

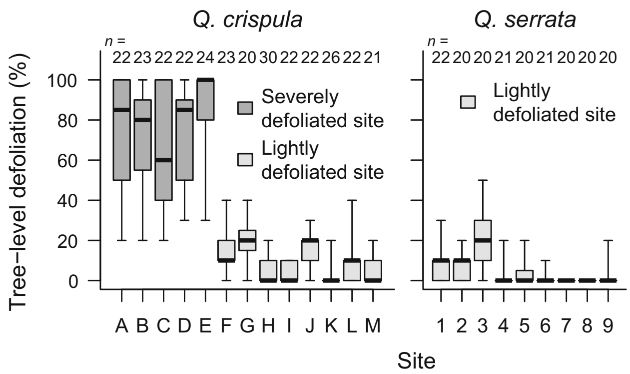

Fig. 2 Distribution of tree-level defoliation throughout the study area in 2014. The box represents the median (*central thick lines*) and quartiles (*box width*). *Letters A–M* and *1–9* correspond to site names listed in Fig. 1. The number of trees in each site is given at the *top*

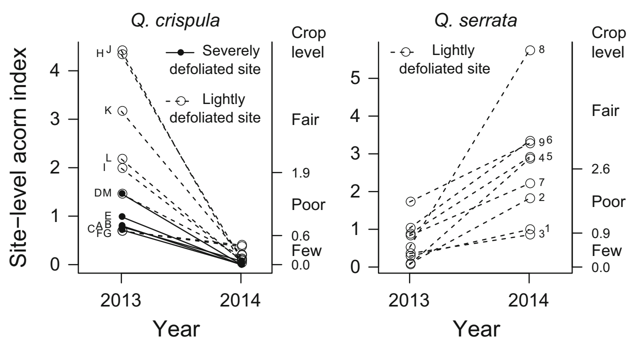

Fig. 3 Fluctuations in site-level acorn index (the mean number of acorns on a 50 cm branch) from 2013 to 2014. *Letters A–M* and *1–9* correspond to site names listed in Fig. 1

In the severely defoliated sites, many cadavers of gypsy moth larvae were observed on the tree trunks, which occur as a result of pathogenic microbes, and characteristic of severe outbreak years (Aoki 1974; Jikumaru and Sano 2007). The larvae, pupae, or imago of gypsy moths were also observed in most of the lightly defoliated sites. Therefore, it was speculated that most of the defoliation was caused by gypsy moth larvae. When acorn production was surveyed in August, about one and a half months after peak defoliation, severely defoliated trees had refoliated and no tree had died.

Acorn production

The site-level acorn indices with *Q. crispula* exhibited a synchronous decrease among sites from 2013 to 2014 (Fig. 3; Table S1). The tree-level acorn index of 2014 was significantly lower than that of 2013 in 12 of the 13 sites ($P < 0.05$). Crop levels in 2013 were classified as 'fair' in five sites and 'poor' in eight sites, while in 2014 crop levels at all sites were classified as 'few', regardless of whether the site was severely or lightly defoliated. In contrast, the acorn indices with *Q. serrata* exhibited a synchronous increase from 2013 to 2014, significantly so in eight of the nine sites ($P < 0.05$). Crop levels in 2013 were mainly classed as 'few' (seven of the nine sites), while in 2014 most sites (five) were classed as 'fair'.

Effect of defoliation on acorn production

There were negative correlations between defoliation and acorn indices at both the site- (Fig. 4) and tree-levels (Fig. 5) for both species. Just 6 % (11/184) of *Q. serrata* trees did not contain any acorns (acorn index equal to zero), whereas 63 % (187/299) of *Q. crispula* trees had no acorns. For *Q. crispula*, 45 % (80/178) of lightly defoliated trees (defoliation ≤20 %) had no acorns, while a notably higher proportion (99 %, 67/68) of severely defoliated trees (defoliation ≥80 %) had no acorns. The results of the generalized linear mixed model revealed the negative effects of defoliation on acorn index at the tree level (for *Q. crispula*, defoliation slope estimate = −0.033, SE = 0.011, $P = 0.0038$; for *Q. serrata*, estimate = −0.029, SE = 0.011, $P = 0.011$).

Discussion

This study has revealed the negative effects of insect defoliation on the reproduction of canopy trees, where defoliation has not been artificially manipulated but rather observed in a natural setting.

Carbohydrate is traditionally considered a limiting resource for seed production in species with mast seeding behavior (intermittent synchronous seed production at regional scale). Meanwhile, recent studies have revealed that temperate deciduous canopy tree species, including oak, primarily use the current year's photosynthate for seed production regardless of their reproductive interval (Ichie

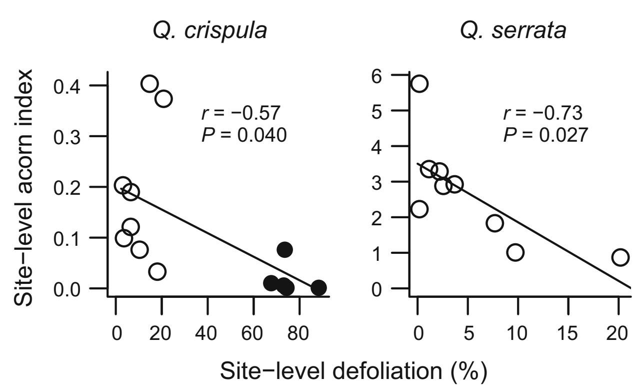

Fig. 4 Relationship between site-level defoliation and acorn indices in 2014. *Closed circles* represent severely defoliated sites, while *open circles* represent lightly defoliated sites

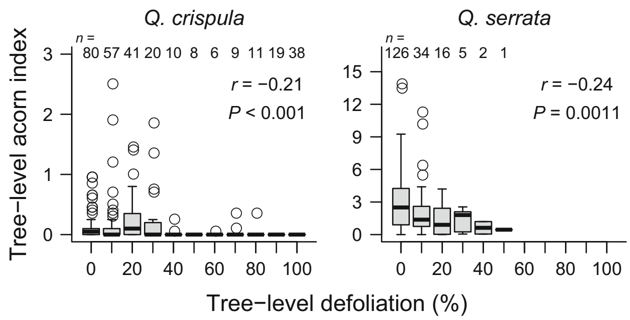

Fig. 5 Relationship between tree-level defoliation and acorn indices in 2014. The box represents the median (*central thick lines*) and quartiles (*box width*). *Open circles* indicate outliers. The number of trees in each defoliation class is given at the *top*

et al. 2013; Hoch et al. 2013). Therefore, seed production of these species is independent from old carbohydrate reserves. Their findings suggest that seed production may be limited by the accumulation of other nutrients, such as nitrogen and phosphorus, rather than carbohydrates (Ichie et al. 2013; Hoch et al. 2013). However, defoliation causes a reduction in the crown leaf area of a tree, decreasing its current year's carbohydrate gain (Palacio et al. 2012). Defoliation also causes a reduction in the stem and root carbohydrate content, especially for severely defoliated trees that subsequently undergo refoliation (Wargo 1972; Wargo et al. 1972; Kosola et al. 2001; Rieske and Dillaway 2008; Palacio et al. 2012; Piper and Fajardo 2014). In addition, defoliation depresses the nitrogen uptake capacity of roots (Kosola et al. 2001). Accordingly, the negative effects of gypsy moth defoliation on the production of acorns by oak revealed in this study (Figs. 4, 5) are likely caused by deficiencies in the availability of carbohydrates or other nutrients that result in the abortion of immature acorns. Another possible explanation for the impact of defoliation on acorn production is that gypsy moth larvae directly consume oak flowers, which bloom just after the leaf flush in spring. However, Gottschalk (1990) suggested that the abortion of immature acorns has more significant effect than the consumption of flowers.

Although a negative effect of defoliation on acorn production was detected for *Q. crispula* (Figs. 4, 5), acorn production decreased from 2013 to 2014 and crop levels were low ('few') in 2014 at both severely and lightly defoliated *Q. crispula* sites (Fig. 3). Synchronous fluctuations in oak acorn production at geographical scales are thought to be driven by weather-related factors (e.g., Koenig and Knops 2013, 2014), and these may also explain the consistent low crop levels recorded for this species in 2014. If a gypsy moth outbreak occurred in a year with high crop potential, driven by weather-related factors, it is possible that only severely defoliated sites exhibit low crop levels (Kasbohm 1994).

For *Q. serrata*, defoliation also negatively impacted acorn production (Figs. 4, 5), even though no site was severely defoliated (Fig. 2). This result suggests that relatively low level defoliation can negatively impact acorn production.

In Japan, there are years when many Asiatic black bears intrude into residential areas in autumn. These are thought to coincide with years of poor acorn crops (Oka et al. 2004; Mizutani et al. 2013; Nakajima 2013) because acorns are a key food for bears during autumn, and because bears will alter their home ranges and foraging behaviors depending on annual fluctuations in acorn production (Kozakai et al. 2011). Therefore, increased human–bear conflicts are predicted to occur as a result of the reduced production of acorns by oaks following gypsy moth defoliation. However, the results of this study suggest that at a regional scale, the impact of gypsy moth defoliation in 2014 on acorn production was not great, because severe defoliation was observed only in *Q. crispula* sites (Fig. 2) where crop levels were low regardless of the defoliation severity (Fig. 3).

In North America, it is common for gypsy moth defoliation to cause tree mortality, with mortality rates higher in less vigorous trees, suppressed trees, and in trees that suffer severe defoliation for two consecutive years (Campbell and Sloan 1977; Gottschalk et al. 1998; Eisenbies et al. 2007). No tree deaths was observed in this study, at least between peak defoliation and the acorn production survey approximately one and a half months later. The resilience of trees in this study to defoliation might be because they were not suppressed, and did not experience consecutive years of severe defoliation, or because Japan's moist climate creates an environment of generally low tree mortality from insect defoliation (Kamata 2002). Nevertheless, studies have shown that severe defoliation does negatively affect tree growth and vigor, with effects persisting for the following years (Campbell and Sloan 1977; Muzika and Liebhold 1999; Fajvan et al. 2008). Hence, the defoliation observed in this study (in 2014) will likely affect acorn production for the coming years.

Interestingly, the gypsy moth infestation did not cause severe defoliation at any *Q. serrata* site (Fig. 2). This is not because *Q. serrata* are less susceptible to gypsy moth defoliation, but rather because the gypsy moth outbreak in 2014 was elevation-dependent. The most severely defoliated area during the outbreak occurred between 500 and 1000 m elevation (A–E in Fig. 1), where *Q. crispula* dominate. *Quercus serrata* oaks occur mainly at lower elevations (Nakajima and Ishida 2014). In support of this theory, there were completely defoliated *Q. serrata* in site A at 570 m a.s.l. (pers. obs.), where *Q. crispula* trees were surveyed and mixed with *Q. serrata* trees. The cause of this elevation-dependent outbreak is likely to be related to factors such as the density of host trees and natural enemies (Kamata 2002; Haynes et al. 2012).

Studies from North America have shown interesting relationships among gypsy moth populations, acorn production, and small mammal populations: failed acorn production lead to reductions in the population sizes of small mammals that depend on the acorns, which subsequently lowers predation rates on gypsy moths leading to outbreaks (Liebhold et al. 2000). If outbreaks diminish acorn production as revealed in this study, positive feedback loops could be present. It is possible that relationships such as those observed in North America also operate in Japan (Liebhold et al. 1998) because acorn masting also affects rodent population dynamics in Japan (Saitoh et al. 2008) and because the predation of gypsy moths by rodent has been observed (Fukuyama et al. 1990; Liebhold et al. 1998). However, the main predators of gypsy moths in Japan are birds (Higashiura 1980; Furuta 1982). Long-term monitoring studies are needed to clarify the existence of such interactions among gypsy moths, small mammal populations, and oak trees.

In conclusion, this study has shown that gypsy moth defoliation reduced the production of acorns by two oak species. This finding lends further support to the suggestion that insect defoliation can dramatically affect forest ecosystem processes, such as the regeneration of host trees and the behavior of wildlife that depend on seed production, by reducing the reproductive potential of host trees.

Author contribution statement HN conceived, designed, and executed this study and wrote the manuscript.

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Conflict of interest The author declares that he have no conflict of interest.

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