Common noise induced synchrony on coupled and uncoupled oscillators: Case studies for Citrus alternate bearing and Acorns

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Abstract– We investigated common noise-induced synchrony observed in agricultural and ecological systems. Citrus alternate bearing at the national market level is modelled as uncoupled collective dynamics, and acorn masting is modelled as coupled collective dynamics. Isagi's resource budget model (RBM) is employed as a nonlinear oscillator for describing each individual tree. The oscillator is the main element of collective dynamics. Induced common noise can simulate principal features of synchrony observed in citrus alternate bearing and masting.

1. Introduction

Various species of tree crops demonstrate significant fluctuations in annual yield, producing a large amount of flowers and fruits one year (on-year) and significantly smaller amounts in the following years (off-years) until the next on-year. This phenomenon is well known as "alternate bearing" for citrus and "masting" for nuts and acorns (Sakai, 2001).

The term of alternative bearing can be applied not only to an individual citrus tree's production, but also to total production of a population from an orchard or to the national market level. Alternate bearing of *Citrus unshiu* has clearly occurred in at the national market in Japan as shown in Fig. 1.

Masting (mast seeding) is a phenomenon in which acorn production alternates between large and small yields over years (Kelly 1994). Masting is recognized as an important process for both wild-life management and natural regeneration in secondary forests. Large fluctuations in the acorn production of individual trees are due to nonlinear dynamics described as shown in Fig. 2 (Isagi,1996), and collective synchrony can be demonstrated by introducing pollen coupling between trees.
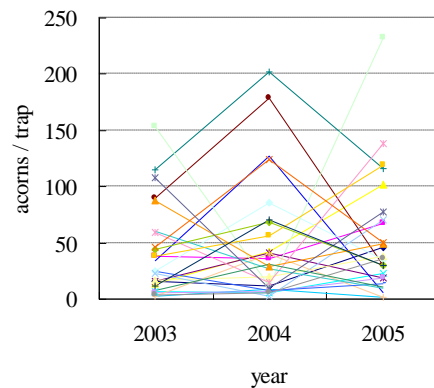
Fig. 2 Time series of 26 individual acorn yields over three years. Global synchrony was not observed. Pearson's correlation coefficient = 0.67 of the yield between 2003 and 2005 (Akita et al., 2008)

2. Mathematical model for resource budget model for *N* trees

2.1 Resource Budget Model

The dynamics of citrus production can be modelled by Isagi's resource budget model (RBM). The photosynthate is used for growth and maintenance of the plant, and any surplus (P_s) accumulates at the plant body's trunk. Let $S(t)$ be the amount of energy reserve at the beginning of year t. If the accumulated photosynthate ($I(t)+P_s$) exceeds the threshold of the pool (L_t), the excess amount ($I(t)+P_s -L_t$) is used for flowering, C_f. The cost of pollinating flowers and bearing fruits is designated as C_a. The ratio C_a/C_f is
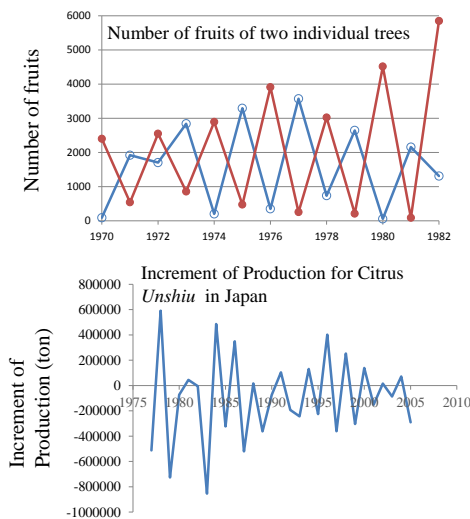
Fig. 1 Citrus alternate bearing data
(a) Number of fruit produced annually from two citrus treesat Nebukawa Experimental Station (b) Increment of total production of *Citrus unshui* in Japan (tons)

assumed to be a constant, R_C. After the reproductive stage, the accumulated photosynthate becomes $L_T - C_a = L_T - R_c C_f$. N denotes the population size of citrus trees. RBM for the tree i can be written as:
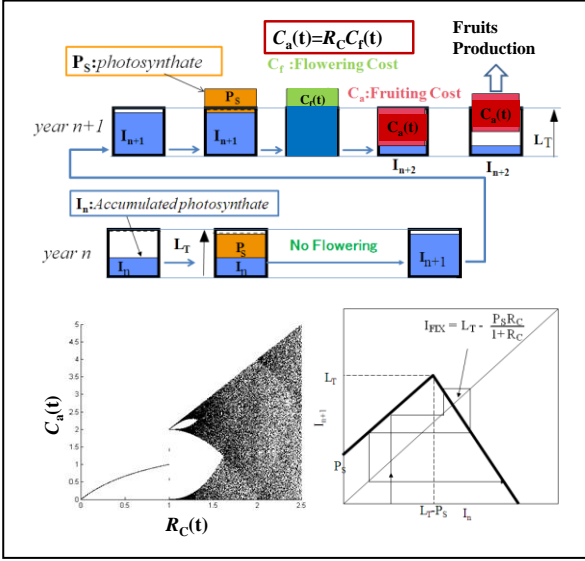

Fig. 3 Resource budget model
(a) Compartment model of RBM (b) Bifurcation diagram of RBM (c) Return map of RBM

$$\begin{cases} I^i(t+1) = I^i(t) + P_s & I^i(t) + P_s \leq L_t \\ I^i(t+1) = I^i(t) + P_s - C_f^i(t) - C_a^i(t) & I^i(t) + P_s > L_t \end{cases} \quad (1)$$

$$C_f^i(t) = I^i(t) + P_s - L_t \quad (2)$$

$$C_a^i(t) = R_c C_f^i(t) \quad (3)$$

where, $I^i(t)$ is the amount of energy reserve at the beginning of year t for tree i; $C_a^i(t)$ is the cost of fruits produced in tree i at the end of year t; $C_f^i(t)$ is the flowering cost for tree i in year t; the system parameters P_s, L_t, and R_c are assumed to be constants over all citrus trees. In this model, the annual production is calculated as the sum of fruits from each single tree, i.e., $C_a^i(t)$ (i=1..N). The annual mean of N trees' production $m(t)$ is defined as:

$$m(t) = \frac{1}{N} \sum_{i=1}^{N} C_a^i(t) \quad (4)$$

Pollen coupling is modelled by replacing Eq. (3) with Eq. (5)

$$C_a^i(t) = R_c C_f^i(t) X(t) \quad (5)$$

where,

$$X(t) = \left[\frac{1}{n P_s} \sum_{i=1}^{n} C_f^i(t) \right]^{\beta} \quad (6)$$

Noise is induced on P_S in the manner of $P_S + \sigma$.
where, σ is a normally distributed random number.
In these numerical experiments, the population size N is set at 10,000. β is set as 0.0 and 0.5 for the uncoupled and the coupled cases, respectively.

2.2 Index for Quantifying Synchrony

Synchrony is quantified with the two indexes. The average correlation coefficient over all possible pairs is defined as:

$$\bar{\rho} = \frac{1}{n(n-1)} \sum_{i=1}^{N} \sum_{j \neq i}^{N} \rho(i,j). \quad (7)$$

where $\rho(i,j)$ is the correlation coefficient between each pair of trees $z^i(t)$ and $z^j(t)$.

$$\rho(i,j) = \frac{\sum_{t=1}^{T} \left(C_a^i(t) - \overline{C_a^i}(t) \right)\left(C_a^j(t) - \overline{C_a^j}(t) \right)}{\sqrt{\sum_{t=1}^{T} \left(C_a^i(t) - \overline{C_a^i}(t) \right)^2 \sum_{t=1}^{T} \left(C_a^j(t) - \overline{C_a^j}(t) \right)^2}} \quad (8).$$

The population coefficient of variance (CV_p) is the coefficient of variance for the annual mean production $m(t)$.

$$CV_P = \frac{\sqrt{\frac{1}{N} \sum_{t=1}^{T} (m(t) - \overline{m}(t))^2}}{\overline{m}(t)}. \quad (9)$$

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3. Numerical Experiments and Discussions
3.1. Uncoupled Dynamics Simulating Alternate Bearing

As *Citrus unshiu* is a self-pollinating tree, it is appropriate to be modelled with uncoupled collective dynamics. In the model described above, β is set to zero in Eq. (6). Fig. 4 demonstrates the behavior of synchrony by changing R_C with (a) the average correlation coefficient $\bar{\rho}$ and (b) the population coefficient of variance CV_P. The noise-free and noise-induced cases are represented by blue and red lines, respectively. In $R_C > 1.5$, There is no significant difference in ρ between the noise-induced case and noise-free case in Fig. 4(a). However, the CV_P in the noise-induced case is apparently larger than that of noise-free case as shown in Fig. 4(b). These results indicate that synchrony did not occurr at the individual level but was clearly observed at the population level. This is the new finding in this experiment and may possibly explain why the national production of citrus shows the oscillating motion annually as demonstrated in Fig. 1. The national production of citrus can be modelled with collective dynamics with common induced noise. In other words, citrus alternate bearing in the national market can be recognized as common noise-induced synchrony. Fig. 4 illustrates the synchrony for two cases in the time domain for R_C=1.5 as a typical case. For the noise-free case, the mean annual production $m(t)$ is almost constant as shown in Fig. 5(a) and (b) with blue lines for $m(t)$ and $\Delta m(t)$. The individual trees behave independently as shown with 20 samples plotted in the green lines of Fig. 5(a). In contrast, for the noise-induced case, significant fluctuation is observed at $m(t)$ and $\Delta m(t)$ in the red lines of Fig. 5(c) and (d). Twenty individual trees (in magenta) look random as well as in the noise-free case, however, as expressed with blue lines of $m(t)$ and $\Delta m(t)$, the common noise induction generates synchrony in the population level. In the collective

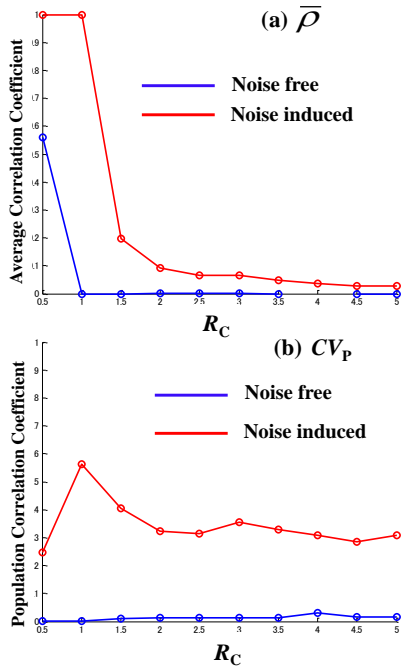dynamics, this mechanism (common induced noise synchrony) can demonstrate Moran's effect.

(a) $\overline{\rho}$

(b) CV_P

Fig.4 Synchrony in the uncoupled dynamics
(a) The average correlation coefficient $\overline{\rho}$
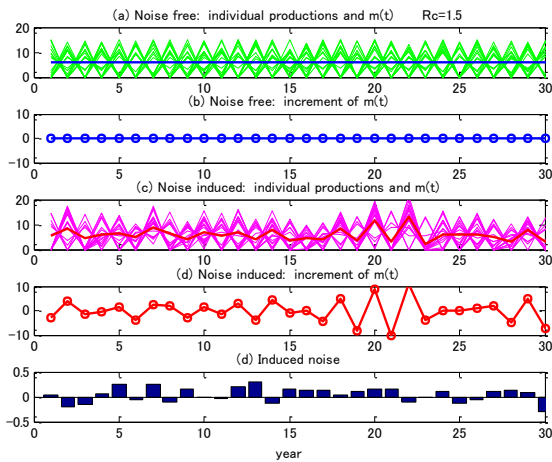(b) The population coefficient of variance CV_P

Fig. 5 Numerical experiment for $R_C=1.5$ on the uncoupled dynamics. (a) Twenty individual productions (in green) and the annual mean $m(t)$ (in blue) (b) annual increment $\Delta m(t)$ for the noise-free case (in blue) (c) Twenty individual productions (in magenta) and the population mean $m(t)$ (in red) (d) annual mean increment $\Delta m(t)$ for the noise-induced case (e) ratio of induced noise to P_S.

3.2. Coupled Dynamics Simulating Acorn Masting
The proximate factor is the dynamics of individual plants and the collective synchrony (dynamics) are due to pollen coupling. The synchrony is modelled as the mean field

collective dynamics in which the coupling term is implemented by pollen coupling due to self-incompatibility (Isagi et al. 1997; Satake and Iwasa 2000). This is so-called Isagi's RBM, and spatial synchrony are demonstrated with coupled map lattice (Satake and Iwasa 2002) and many experimental studies (e.g. Rees et al. 2002; Crone et al. 2005; Akita et al. 2008). Coupling and induced common noise in collective dynamics, which consists of nonlinear oscillators, are the two main causes of acorn masting. The first corresponds to pollen coupling, and the second is due to Moran's effect in the context of ecology. We investigate how the combination of these two factors works on synchrony in the modelled collective dynamics. Fig. 7 demonstrates the behavior of synchrony by changing R_C with (a) the average correlation coefficient $\overline{\rho}$ and (b) the population coefficient of variance CV_P. The noise-free and noise-induced cases are represented by the blue and red lines, respectively. In $R_C<1.5$, individual level synchrony is apparently observed in the both cases as their $\overline{\rho}$ are close to 1. There is significant difference in $\overline{\rho}$ between the two cases when $R_C=1.5$.

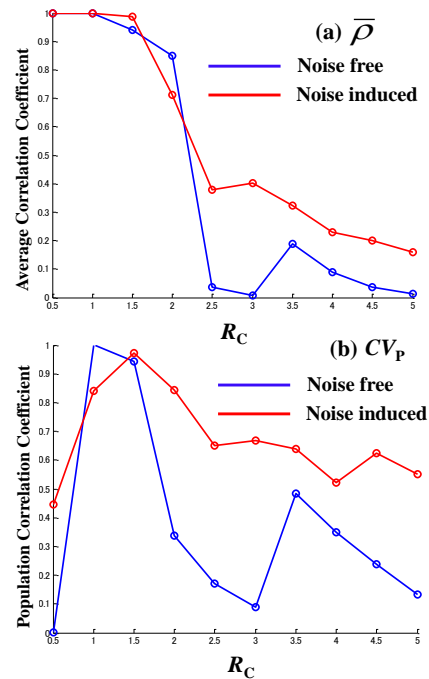**(a)** $\overline{\rho}$

(b) CV_P

Fig.6 Synchrony in the coupled dynamics
(a) The average correlation coefficient $\overline{\rho}$
(b) The population coefficient of variance CV_P

Fig. 7 shows the numerical results for $R_C=2.5$. For the noise-free case, 'out of phase synchrony (period 2)' is very clearly illustrated with 20 samples in the green plots in Fig. 7(a). Because of predominant 'out of phase synchrony', the fluctuation of $m(t)$ is small. In the noise-induced case, 'in-phase synchrony' occurs with 'out of phase synchrony' as shown in Fig. 7(c) with 20 sample productions (in magenta) and leads to large degree of masting.
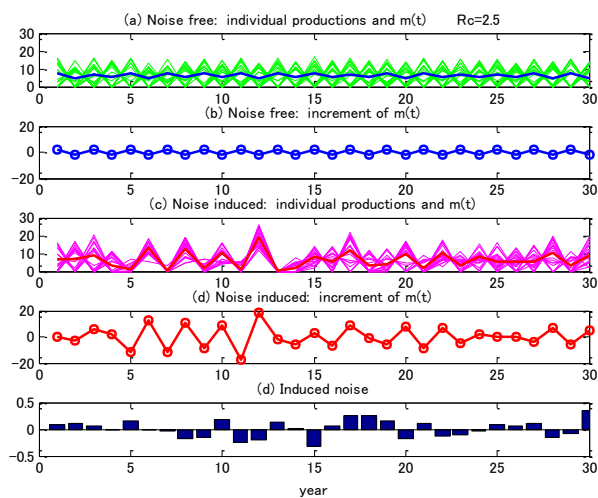
Fig. 7 Numerical experiment for $R_C=2.5$ on the coupled dynamics

(a) Twenty individual productions (in green) and the annual mean $m(t)$ (in blue) (b) annual increment $\Delta m(t)$ for the noise-free case (in blue) (c) twenty individual productions (in magenta) and the population mean $m(t)$ (in red), (d) annual mean increment $\Delta m(t)$ for the noise-induced case (e) ratio of induced noise to P_S.

4. Conclusions

Numerical experiments indicate that national market-level citrus alternate bearing can be modelled as a phenomenon of common noise induced uncoupled collective dynamics. Also, acorn masting can be explained with a combination of pollen coupling and Moran's effect which is modelled with common noise induction. In this modelling, synchrony at the individual level is not observed, however, population level synchrony is clearly observed. This is the most interesting new finding of this paper. The results clearly show that even with independent fruiting (without coupling) of a large enough number of trees, the total production will not be a constant as might be expected statistically, but that alternate bearing appears to be a reason for production fluctuation observed in the national market.

Acknowledgement

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