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LIMITING FACTORS ON THE SEED PRODUCTION OF *LINDERA ERYTHROCARPA* IN THE KASUGAYAMA FOREST RESERVE, NARA, JAPAN

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The limiting factors in seed production of *Lindera erythrocarpa* (Lauraceae) trees were examined using the key factor analysis. We compared three submortality factors, which were represented by *k*-values of reproductive organs in the seed production process. The first factor is the abortion of female flowers in flowering stage ($k(1)$). The second is the death of immature fruits by abortion in fruiting stage ($k(2)$). The third is the seed abortion in seed maturation stage ($k(3)$). The key factors staggered with respect to tree size through the development of reproductive organs. In smaller trees, the major submortality factor of reproductive organs was $k(3)$ or seed abortion possibly caused by the resource limitation. In larger trees, the submortality factor $k(1)$ was distinguished from the other two submortality factors, suggesting the prominent rate of flower abortion possibly caused by the pollination limitation and selective abortion. Thus the switching of the submortality factors with respect to tree size was clear in *L. erythrocarpa*, although the mechanism was still unknown. In general, forest trees represent broad differences in size and fecundity among individuals. Therefore, our results are considered to offer a new aspect in the forest management plan, since the relationship between limiting factors in seed production and tree size has seldom been the subject of research. The size dependency of limiting factors in seed production should be tested by more detailed analyses in the future studies.

Key Words: abortion, Kasugayama forest, key factor analysis, *Lindera erythrocarpa*, seed production

Introduction

Evaluating limiting factors of seed production of forest tree species is essential for understanding the forest dynamics and offers the effective conservation scheme of the forest. The period of seed development on a mother tree is considered to be one of the most hazardous phases in a plant's life cycle (Fenner & Thompson, 2005). Many plants produce mature fruits from only a small portion of their female flowers (Stephenson, 1981; Bawa & Webb, 1984). Many female flowers and immature fruits fail in developing mature fruits with viable seeds. The lack of resources for seed development has been indicated as a proximate factor of fruit abortion in the later period of seed maturation

(e.g., Lee & Bazzaz, 1986). On the other hand, the pollination limitation (e.g., Bierzychudek, 1981; Owens et al., 1991) and selective abortion (e.g., Stephenson, 1981) have been considered as the causes of flower abortion in earlier phase of reproduction. To examine the relative contribution of these factors to the seed production, quantification of the reproductive organs at all stages from flowering to fruiting is necessary.

In our previous study, the reproductive variables, such as the amount of female flowers, fertilized flowers, mature sized fruits, and seeds, in *Lindera erythrocarpa* (Lauraceae) trees were clarified at individual basis at the Kasugayama forest reserve, Nara, Japan (Hirayama et al., 2004). Based on the data of the former study, we examine the limiting factors in seed production of *L. erythrocarpa* trees, using the key factor analysis (Varley & Gradwell, 1960; Podoler & Rogers, 1975) in this study. The key factor analysis has been adopted widely in the studies of insect population dynamics as a standard procedure to discover main factors responsible for the variations in abundance (Kuno, 1971; Yamada, 1995).

The objectives of this study are as follows: (1) to assess the relative influence of the abortion of female flowers, fruits, and seeds on the total mortality of reproductive organs, (2) to clarify the relationship between the major lethal factors of seed production and tree size.

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Materials and methods

Study species

Lindera erythrocarpa Makino (Lauraceae) is a deciduous tall tree species and usually begins to bloom in April and fruit in September and October. Since it is dioecious and animal pollinated, a pollinator's visit is necessary for reproduction (Dupont & Kato, 1999a). According to Dupont and Kato (1999b), the *Lindera* species have a wide spectrum of the pollinators which consist of dipteran and coleopteran. The ovary of the female flower contains a single ovule. The fruit is a drupe and dispersed by birds, such as brown-eared bulbuls (*Hypsipetes amaurotis*) and dusky thrushes (*Turdus naumanni*).

Key factor analysis in female reproduction

Figure 1 shows the flowchart of the seed production process of female trees in *L. erythrocarpa*. All of the components in the flowchart, i.e., the number of female flowers ($N(1)$), fertilized flowers ($N(2)$), mature-sized fruits ($N(3)$), and seeds ($N(4)$), which were produced by an individual, were estimated for 5 trees at the 5.06 ha research plot in the Kasugayama forest reserve by using the seed-trap method and a numerical

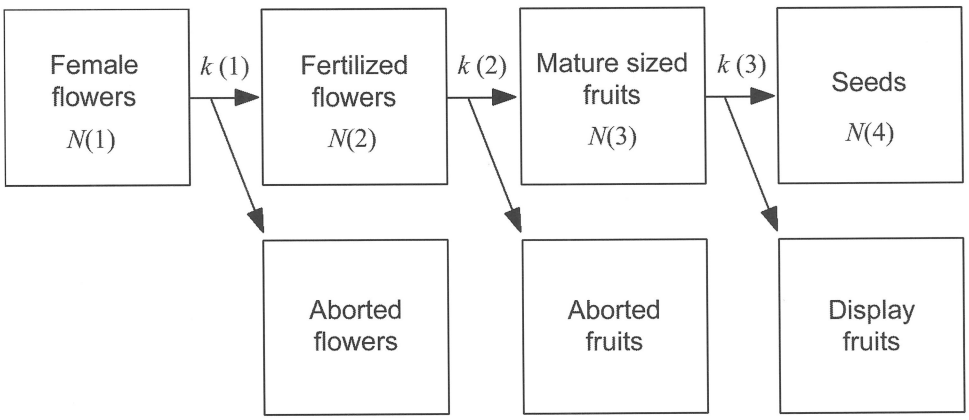


Fig. 1. A flowchart of the seed production process of female trees in *L. erythrocarpa*. The three submortality factors, $k(1)$, $k(2)$ and $k(3)$ were compared in the key factor analysis to determine major factors of the seed set determination.

analysis of seed dispersal (Hirayama et al., 2004) (Table 1). In the study, the spatial distribution pattern of dispersed reproductive organs was expressed using a mathematical model with a probability density function. This new approach is effective for investigating the reproductive investment of individual trees wherein a direct count of all reproductive organs is not actually possible. The Kasugayama forest has been protected for 1100 years as the sacred forest of the Kasuga Shinto shrine, and densely covered by the original vegetation with oak-laurel dominants. Details of the method and the research plot are described in Hirayama et al. (2004). Based on the data, the key factor analysis (Varley & Gradwell, 1960; Podoler & Rogers, 1975) was performed to determine the major lethal factors of the seed production in *L. erythrocarpa*.

Table 1. Numbers of reproductive organs produced per tree. The number of reproductive organs was estimated using the seed trap method and a numerical analysis of seed dispersal in our previous study (Hirayama et al., 2004).

Tree No.	DBH (cm)	Female flowers $N(1)$	Fertilized flowers $N(2)$	Mature sized fruits $N(3)$	Seeds $N(4)$
1	13.4	6590	1690	1580	0
2	16.7	1.06×10^5	2.06×10^4	1.40×10^4	106
3	22.4	2.29×10^5	6.20×10^4	4.45×10^4	2083
4	28.6	6.20×10^5	1.39×10^5	1.08×10^5	3.64×10^4
5	44.4	3.16×10^6	1.60×10^5	1.23×10^5	4.67×10^4

We compared three submortality factors, which were calculated by k-values (Varley & Gradwell, 1960) of reproductive organs, in the entire reproductive process from flowering to fruiting (Fig. 1). The first factor is the abortion of female flowers in flowering stage ($k(1)$). The second is the death of immature fruits by abortion in fruiting stage ($k(2)$). The third is the seed abortion in seed maturation stage ($k(3)$). The k-value of each stage is calculated as follows,

$$k(1)=\ln(N(1))-\ln(N(2))$$

$$k(2)=\ln(N(2))-\ln(N(3))$$

$$k(3)=\ln(N(3))-\ln(N(4)).$$

The total mortality (K) of reproductive organs is given by the sum of three k-values,

$$K=k(1)+k(2)+k(3)$$

The connection between the total mortality K and submortality k is diagrammatically given in Fig. 1. The major submortality of k, which contributes much to the total mortality K of reproductive organs, can be discernible by a visual comparison between different submortalities (Varley & Gradwell, 1960). The data of 4 sample trees (tree number 2, 3, 4, and 5) with different DBHs in Table 1 were used for the key factor analysis because the tree number 1 produced no seeds and was not available in the analysis.

Results

The results are graphically represented in Fig. 2. The total mortality (K) was the lowest in the second largest sample tree. However, the K of each sample tree was not determined by a single submortality factor which was common for all the sample trees (Fig. 2).

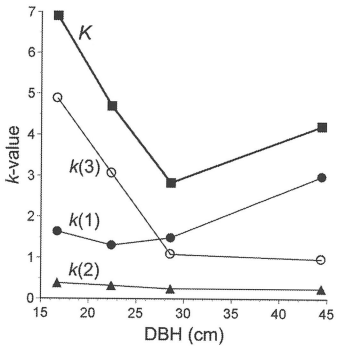


Fig. 2. The result of the key factor analysis in *L. erythrocarpa* trees. The switching of key factors with respect to tree size is clear.

The key factor $k(1)$ in a flowering stage was not parallel to the total mortality K of small sized trees but resembles the pattern of larger trees in DBH vs. k diagram (Fig. 2). The $k(2)$ working at the earlier stage of fruit maturation represents a modest and uniform effect on the total mortality K for all the sample trees. The last key factor $k(3)$ has conspicuous contributions to K in smaller trees but minor contributions to that of larger trees.

Discussion

The key factors staggered with respect to tree size through the development of reproductive organs (Fig. 2). A major submortality factor of reproductive organs in smaller trees was $k(3)$ or seed abortion occurring inside the mature sized fruits. The fruit and seed

abortion at seed maturation stage has been considered to result from a resource limitation in reproduction (Stephenson, 1981; Sutherland & Delph, 1984). Therefore, the smaller trees in our study appear to abort their seeds due to the shortage of their resources such as dry matter.

The key factor $k(1)$ was distinguished from the other two submortality factors in larger trees, suggesting the prominent rate of flower abortion. Since the flowers should be cheaper than fruits in dry matter allocation, the observed behavior of large trees is less extravagant than that of smaller trees in investing the resources in reproduction. The abortion of female reproductive organs in flowering stage has been discussed in conjunction with the pollination limitation and the selective abortion (Stephenson, 1981). The pollination limitation of seed production is a common phenomenon in plants (Bierzychudek, 1981). Many animal-pollinated species have been found to have quite low rates of pollination under natural conditions (Fenner & Thompson, 2005). On the other hand, the hypothesis of selective abortion states that the abortion represents an adaptive mechanism for imposing quality control on the progeny (Stephenson, 1981; Fenner & Thompson, 2005). The pollinated flowers and juvenile fruits may selectively mature on the basis of the order of pollination, number of developing seeds, pollen source, or some combination of these (Stephenson, 1981). The evidence to support this hypothesis is the inferior quality of the aborted fruits, and has been reported in some plant species (Lee & Bazzaz, 1982; Bookman, 1983; Stephenson & Winsor, 1986). In the present study, we have no data for testing whether the study species fit the predictions of the hypotheses about pollination limitation versus selective abortion. The hand pollination test is necessary to confirm the possibility of these hypotheses.

In this study, switching of the submortality factors with respect to tree size in *L. erythrocarpa* became clear using the key factor analysis but the mechanism was still unknown. In general, forest trees have broad differences in size and fecundity among individuals. Therefore, our results are considered to offer a new aspect in the forest management plan, since the relationship between limiting factors in seed production and tree size has seldom been the subject of research. The size dependency of limiting factors in seed production is of interest and should be tested by more detailed analyses in the future studies.

Seed production has a great influence on the demography of the plant populations. Therefore, the further accumulation of knowledge of reproductive processes of forest tree species is necessary for understanding a forest dynamics and suggesting effective conservation schemes of a forest.

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要　約

奈良県春日山のカナクギノキの種子生産を制限する要因．平山大輔・山倉拓夫（大阪市立大学大学院理学研究科）

奈良県春日山保護林に生育するクスノキ科カナクギノキの種子生産を制限する要因を明らかにするため，変動主要因解析（Key factor analysis）の手法を用いて，繁殖器官の３つの死亡要因

（k 値）を比較した。一つ目の要因は，開花期の雌花の中絶（$k(1)$），二つ目は，未成熟果実の中絶（$k(2)$），そして三つ目は，結実期の種子の中絶（$k(3)$）である。胸高直径の異なる雌 4 個体の繁殖器官生産数のデータをもとに解析を行った結果，以下の事項が明らかとなった。開花結実過程全体の繁殖器官の死亡率は，単一の死亡要因では決まっていなかった。小個体の繁殖器官の死亡率には，結実期の種子の中絶（$k(3)$）が大きく寄与していたが，大個体のそれにはほとんど影響を与えていなかった。一方，大個体の繁殖器官の死亡率には，開花期の雌花の中絶（$k(1)$）が大きく寄与していた。また，どのサイズの個体においても，未成熟果実の中絶（$k(2)$）は繁殖器官の死亡率にほとんど寄与していなかった。以上のように，カナクギノキの種子生産を制限する要因が個体サイズとともに変化することが明らかとなった。小個体で種子の中絶の寄与が大きい理由には，種子成熟に必要な資源の不足（resource limitation）が考えられた。また，大個体で顕著な雌花の中絶には，受粉制約（pollination limitation）と繁殖器官の選択的中絶（selective abortion）が考えられたが，これらの仮説の検証には強制受粉実験など今後のさらなる調査が必要である。樹木の種子生産の制限要因が個体サイズにより変化することはこれまであまり明らかにされていない。本研究の結果は，様々なサイズの個体からなる森林の効果的な保全を考える上で有用である。