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Reproductive Phenology and Allocation in *Rubus palmatus* var. *coptophyllus* in the Understory of a *Pinus densiflora* Stand

By

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Summary : Flowering and fruiting phenology, and reproductive allocation were investigated in a *Rubus palmatus* var. *coptophyllus* population which developed on the forest floor of an 86-year old *Pinus densiflora* stand. About 70% of the suckers in the population ranged from 6–15 years, and the average sucker age was 10.6 years. Flowers began to open on the floricane in the middle of April, and fruits ripened one month later. There were allometric relationships between the cane size and the number of flowers and fruits per cane. According to these regression lines, as the cane size increased, the fruit/flower ratio increased. The mean value of reproductive allocation (RA) in the fruiting stage was 4.6%, which was three times as much as that of the flowering stage. There were no significant relationships between sucker biomass and RA in both stages. Reproductive outputs increase with increasing sucker size, independent of RA.

1. Introduction

Energy investment for sexual reproduction, as well as the number of offsprings produced, is an important factor for understanding adaptive strategies of plants (HARPER, 1967; PIANKA, 1970). GRE, NRE and CRE as measures of reproductive effort (RE) were proposed by HARPER and OGDEN (1970), and the reproductive effort was measured in many herbaceous plants (KAWANO, 1975; NEWELL and TRAMER, 1978; OGDEN, 1974). These studies showed that RE or reproductive allocation (RA) vary among species, and are greatly affected by the growing conditions, such as population density, soil fertility, light and water conditions (OGDEN, 1974; PITELKA *et al.*, 1980; KAWANO and HAYASHI, 1977; HARA *et al.*, 1988).

RA (sexual reproductive allocation) values in some *Rubus* species belonging to a "nonintegrated clonal" plant (PITELKA and ASHMUN, 1985) were investigated (ABRAHAMSON, 1975a and b; NARUHASHI and KOBAYASHI, 1982). However, RA values of integrated clonal *Rubus* species, the so-called "underground branching" type (SUZUKI, 1987), have not been measured in detail, because of difficulty in investigating the underground parts of a clone individual without destruction (NARUHASHI and SATOMI, 1972; SUZUKI, 1990). In many integrated clonal plants, ramets composing a clone become independent with increasing age (PITELKA and ASHMUN, 1985). Moreover, according to previous studies by this author about integrated clonal *Rubus* species (SUZUKI, 1989 and 1990), the suckers composing a clone individual are independent from each other for reproduction as well as vegetative growth, in spite of be connected with perennial underground runners. These results suggest the possibility of considering reproductive ecology at sucker level for integrated clonal *Rubus* species.

In a previous paper (SUZUKI, 1987), the structure and seed production of *R. palmatus* var. *coptophyllus* populations under different light conditions were critically described.

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In this study, flowering and fruiting phenologies of *Rubus palmatus* var. *coptophyllus*, one of the *Rubus* types mentioned above, the sucker size structure of a well-developed population and RA values of this species at the sucker level were investigated. RA variation among some *Rubus* species in relation to growth habitats was then discussed from the aspect of reproductive ecology.

2. Materials and Methods

The field for this study is in a plantation of *Pinus densiflora* approximately 86 years old located in the Takizawa-mura (Lat.39° 45′, Long.141° 15′), Iwate Prefecture. The *R. palmatus* var. *coptophyllus* population had developed well on the forest floor of this stand, and other main dominant species composing undergrowing vegetation were *Sasa nipponica* and *Lonicera gracilipes*. The light conditions just above the undergrowth were relatively good, in spite of crown closure, about 6% in relative illuminance.

A study quadrat (2m×2m) was established in the population of this *Rubus* species, and five suckers were chosen in order to investigate the reproductive phenology. On each sucker chosen, the number of leaves, flowers and fruits on the floricane (second-year-cane) were counted. The length of the primocane newly sprouting from the stool was measured and the number of leaves on the primocane was counted every week from April to December, 1989.

In both the flowering and fruiting stages, 20 suckers of various sizes, including underground organs within 15cm around the center of the stool, were harvested to estimate RA around the study quadrat. The diameter at the cane base (D_0) and cane height (H) were measured, and the number of flowers and fruits were counted in order to establish the relationships between cane size and flower and fruit production. Each sucker was divided into sexual reproductive organs (flowers or fruits), above -ground parts without flowers or fruits, and underground organs. These were dried in a ventilated oven for 72 hours at 80℃ and weighed.

One of the life history characteristics of *R. palmatus* var. *coptophyllus* is the short life span of above-ground-canes, for one and a half years, and the alternating of above-ground parts every year (SUZUKI, 1987). A new above-ground cane (primocane, A in Photo.1) sprouts from the stool every year. In the next year, the primocane becomes floricane (B in Photo.1), and produces flowers and fruits. After fruiting, it dies in the same year (withered cane, C in Photo.1). However, a new primocane sprouts from the stool at the same time, replacing the floricane. Thus, the number of traces of above-ground canes having sprouted on the stool was counted to estimate sucker age.

Another study quadrat (2m × 4m) was established in the same population in 1990, and all suckers appearing in the quadrat were harvested, including the underground organs. The D_0 and H of all canes, both living and withered were measured, and the number of cane traces on the stool were counted in order to determine the population structure and its dynamics.

3. Results

3.1 Population structure

The *R. palmatus* var. *coptophyllus* population in this study was mostly composed of old suckers of more than 6 years. About 70% of the suckers in the population were aged between 6–15 years on the sucker age-class (Table 1). The oldest sucker in this population was more than 20 years old, and the youngest ones were those formed in the investigated year by underground branching (SUZUKI, 1987). The average sucker age was 10.6 years. The number of canes appearing in the population and their size-class distribution did not change much during the past three years (Fig.1). There were no significant relationships between sucker age and sucker biomass ($r=0.4$: n.s. at 5%).

3.2 Vegetative and reproductive phenology

The leaves of the floricane of *R. palmatus* var. *coptophyllus* sprouted rapidly in April, increasing by about 80% in the number, and reached the maximum number in the middle of May. Following this, the amount of leaves remained at the 90% level of the maximum until with all the leaves being shed gradually from September to November as the cane withered (Fig.2). On the other hand, a new above-ground cane (primocane) began to sprout in the middle of May, and continued to grow until September. As the primocane grew, the number of leaves on it increased rapidly, and reached its maximum in the middle of September, when the primocane stopped growing. The primocane began to shed its leaves, from the middle of October until all leaves shed in November (Fig.2). The floricane as an above-ground part was alternated with the primocane, on account of withering. Alternation required about six months.

Flowers began to open on the floricane in the middle of April. About one month after flowering, this *Rubus* species fruits. However, about 45% of the flowers failed to fruit (Fig.2). This failure was largely due to the predators, mainly insects, while other reasons are unknown. Both flowering and fruiting seasons were short, less than two weeks. However, some fruits did not drop to the ground until they had completely dried on the cane.

3.3 Flower and fruit production

There were allometric relationships between the cane size and the number of flowers and fruits produced per cane (Fig.3). The regression line at the fruiting stage significantly differed from that at the flowering stage (at the 5% level, *t*-test). The number of fruits per cane was lesser than that of the flowers in the same size. According to these regression lines, the number of fruits was about 50% of flowers for canes of 50 cm^3 in D_0^2H of canes, and about 80% for those of 200 cm^3. That is, as the cane size increased, the fruit/flower ratio increased.

3.4 RA in the flowering and fruiting stage

In this study, RA was estimated as the ratio of reproductive organs (flowers or fruits) to the sucker

Table 1. Age-class distribution of suckers (per $8m^2$)

Age-class(year)									
1	2	3	4	5	6-10	11-15	16-20	20-25	Total
3	1	1	1	1	15	19	6	1	48

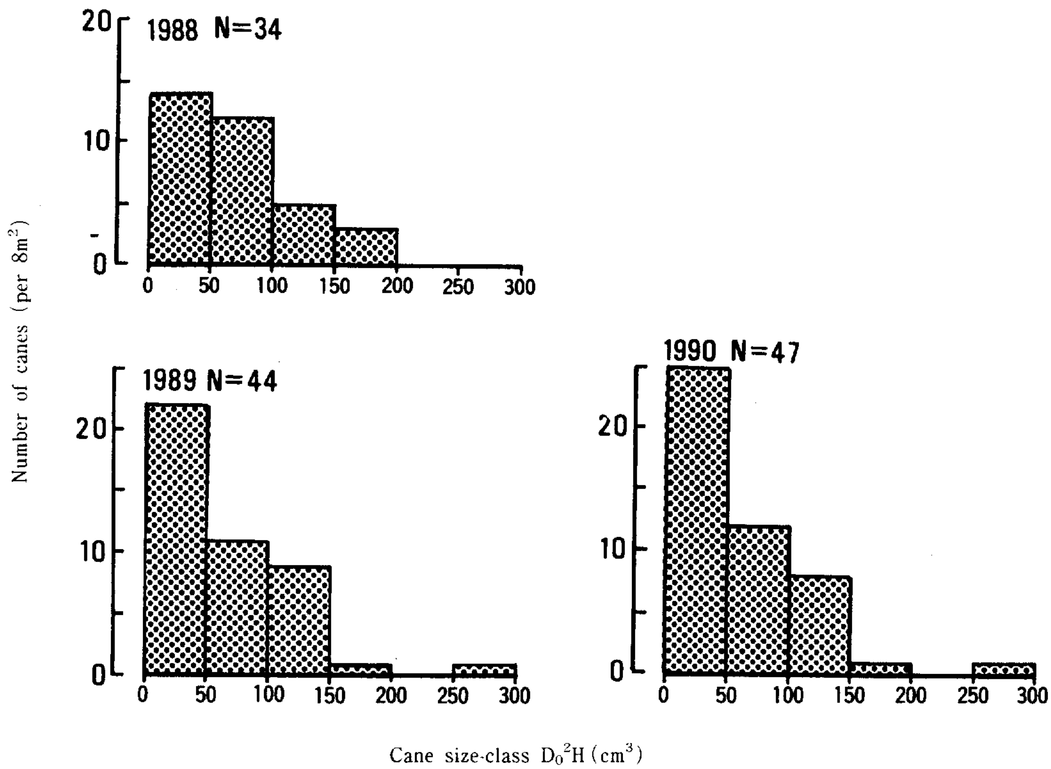

Fig. 1. Cane size-class distribution of the population of *R. palmatus* var. *coptophyllus*

biomass, including subterranean parts. RA varied from 0.5 to 3.5% in the flowering stage, and from 1.0 to 8.5% in the fruiting stage. The mean value of RA in fruiting stage was about 4.6%, which was three times as much as that of the flowering stage (Fig.4). There was no significant relationship between the total dry weight of suckers and RA (n.s. at 5%).

4. Discussion

The population of *R. palmatus* var. *coptophyllus*, here under consideration, developed well on the forest floor of crown closed *P. densiflora*, and was mainly composed of old suckers, with an average sucker age of 10.6 years. Stool longevity was negatively correlated with shoot height and sucker density, indicating sucker vigor in *R. fruticosus* and *R. idaeus* (PELOUZAT and LEVACHER, 1981; WHITNEY, 1978). NYBOM (1987) reports a similar relationship between shoot height and short depletion time, turnover being quicker in vigorously growing stands of *R. nessensis*. According to these reports, sucker age structure in this population may be caused by low vegetative sucker production under unfavorable growing conditions caused by the crown closure of the canopy trees. On the other hand, size-class structure of above-ground canes in the population had not changed in the past three years (Fig.1). These results suggest that this population was very stable in sucker number and size structure, in spite of increasing sucker age.

Flowering of this *Rubus* species occurs simultaneously in late April, before all the floricane leaves have been expanded (Fig.2). Flowering with these phenological characteristics may attract many insects

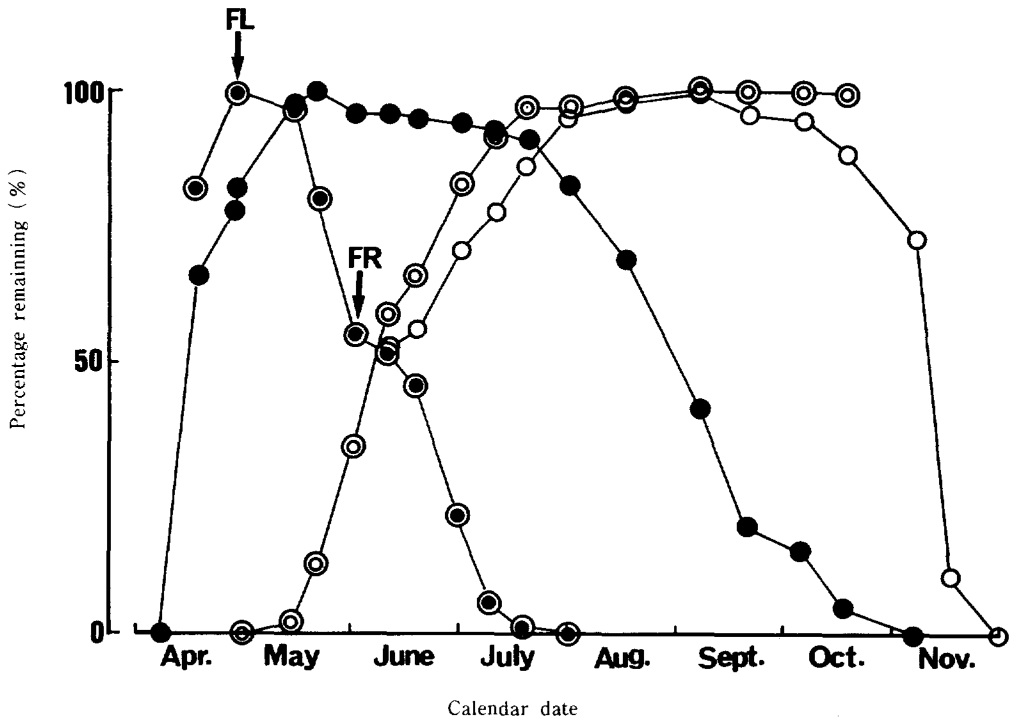

Fig. 2. Seasonal changes in number of leaves and fruits, and length of primocane of *R. palmatus* var. coptophyllus

Open circles, leaf of primocane; filled circles, leaf of floricane; open circles with spot, fruits; double circles, growth pattern of primocane; FL, flowering; FR, fruiting. Amounts are expressed as percentages of the maximum quantities.

as pollinators, and make fertilization more efficient (HANDEL, 1983).

After flowering, unripe green fruits grow, with about 55% of ripening. The failure of fruiting can be attributed to predator activity, since some beetles such as *Byturus atricollis*, which prey on the flowers were observed (unpublished data). On the other hand, it was found that there was a difference in the ratio of fruits to flowers produced per cane between the open-site and closed-site population of this species (SUZUKI, 1989). These results suggest that many factors, such as resource and pollinator limitation as well as predator activity, are closely related to fruit production.

The RA value of *R. palmatus* var. *coptophyllus* investigated on Mt. Tsukuba, about 500 km south of Takizawa, was about 5.7 ± 1.2% in the fruiting stage (SUZUKI, 1990), slightly larger than that in the present study. The difference in RA between the two sites may be due to the different developing stage of each population. That is, the population on Mt. Tsukuba had been developed on an open site, while the population in the study was on a closed site. Such trends in the flower and fruit production are noted between open- and closed-site populations of this species (SUZUKI, 1989).

NARUHASHI and TERAO (1978) reported that RA at the clone level of *R. hirsutus*, belonging to the "underground branching" type, was only 1.97% in the fruiting stage. RA at sucker level was 5.1% in *R. idaeus* in the fruiting stage (SUZUKI, unpubl.). On the other hand, some Japanese native *Rubus* species be-

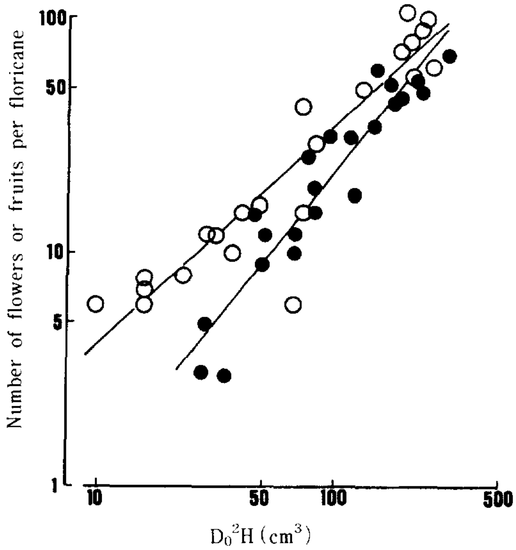

Fig. 3. Allometric relationships between cane size and number of flowers and fruits.

Open circles, flowering stage; filled circles, fruiting stage.
A, log Y = −0.339+0.938 log X (r=0.926)
B, log Y = −1.193+1.270 log X (r=0.936)

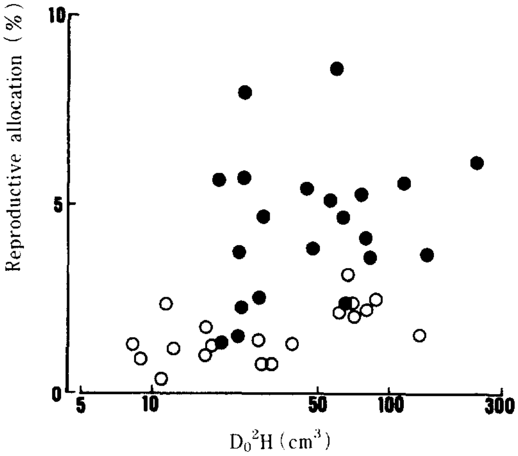

Fig. 4. Relationships between sucker biomass and RA (Reproductive allocation)

Open circles, at flowering stage; filled circles, at fruiting stage.

longing to the "stepping stone" type showed RA values ranging from 0.5−1.6% in the flowering stage and 0.8−2.9% in the fruiting stage (NARUHASHI and KOBAYASHI, 1982). However, RA variation among the populations was affected by habitat conditions, such as light conditions and/or population density (ABRAHAMSON, 1975).

Although RA values in the flowering stage in *R. palmatus* var. *coptophyllus* were comparatively constant with increasing sucker biomass, RA values at the fruiting stage varied widely, independent of sucker size (Fig. 4). As there were fundamentally allometric relationships between the dry weight of reproductive organs and total sucker biomass in both flowering and fruiting stages (SUZUKI, 1987; 1990), RA variation in the fruiting stage was caused by the accidental events such as pradation, in the process of fruiting on each sucker. In addition, fruit weight variation ranging from 0.06 to 0.16g (mean dry weight per fruit = 0.09±0.02g) may affect the RA values.

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アカマツ林床におけるモミジイチゴの繁殖季節相と繁殖分配

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摘　要

86年生アカマツ人工林の林床に発達するモミジイチゴ個体群において，開花・結実の繁殖季節相と繁殖への物質分配を調査した。個体群を構成するサッカー（株個体）の約70％は６～15年生であり，サッカーの平均齢は10.6年であった。開花は，２年生地上茎において４月中旬に始まり，果実は１か月後に成熟した。地上茎当りの開花・結実数と茎サイズの間には相対成長関係が認められた。これらの回帰直線から，茎サイズが大きくなるにしたがって，果実数／開花数の値は増加した。結実期におけるRA（繁殖器官への物質分配率）の平均値は4.6％で，この値は開花期の３倍に当たった。また，両時期のRAとサッカーのバイオマス量との間には明らかな関係は認められなかった。繁殖体（種子）数は，RAとは無関係にサッカーサイズが増大するにしたがって増加した。

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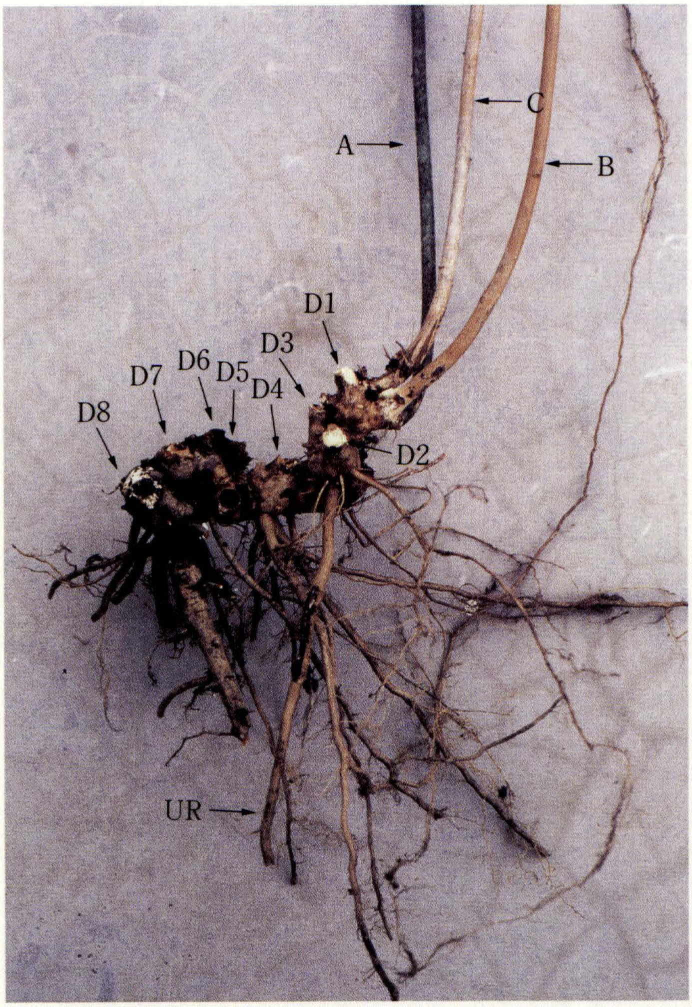

Photo. 1. Stool of *Rubus palmatus* var. *coptophyllus* and above-ground canes sprouting from it.

Sucker age can be estimated from the number of traces of withered above-ground canes.
A, primocane; B, floricane; C, withered cane; D1~8, traces of withered canes, UR; underground runners.