

# Clonal Strategy and Physiological Integration of a Rhizomatous Perennial, *Convallaria keiskei*.

## I. Ramet Growth and Clonal Structure

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# 지하경쟁식물인 은방울꽃의 영양생장전략과 생리적 통합. I. 라메트의 생장과 클론의 구조

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## ABSTRACT

To explain the horizontal expansion of a rhizomatous perennial, *Convallaria keiskei* (lily-of-the-valley), in a study site of Chunchon, Kangwon Province, Korea, ramet growth and clonal structure were studied. Remarkable growth strategies were clarified. First, the timing for the successive phenological events such as sprouting, flowering and rhizome growth for lily-of-the-valley was fitted to exploit early spring when the canopy of overstory was opened. Second, these events were supported by effective matter allocation pattern: for example, two-year investment for new rhizomes enabled the first year ramets to mature in six weeks after sprouting and to grow up to 85% of the leaf area of perennial ramets. Finally, the ramet population was increased by local disturbances such as freezing, herbivory and collection by human. The rule that a clone was supposed to produce one new rhizome per year was broken by occasional disturbances. Then, up to 5 rhizomes from latent bud could be redeveloped. Based on clonal structure, 80% of total clones have from 1 to 4 ramets. This means there have occurred minor disturbances. Therefore, in conclusion, the successful flourishing of lily-of-the-valley came from its effective growth strategy to take advantage of site disturbance.

**Key words:** Clone, *Convallaria keiskei*, Disturbance, Growth strategy, Population, Ramet, Rhizomatous plant

## INTRODUCTION

Dominance of clonal plants has been well known over diverse environments such as for-

est understory in temperate regions, polar regions, alpine areas and water regimes (Abrahamson 1980, Cook 1985). Salisbury (1942) estimated that more than two-thirds of the perennials of the British flora showed clonal growth pattern. Likewise, when Mt. Gumbung, which has a typical vegetation of central region in Korea, was investigated, the number of species with clonal habits were 60, 63 and 53 % of total herbaceous species in *Pinus*-, *Quercus*- and *Larix*-dominated forests, respectively (unpublished). This might be attributable to their growth strategies (Harper 1980). Most of clonal plants, especially for rhizomatous and stoloniferous species, have physical connections among ramets even though its level of persistency is highly variable among species and habitats (Sobey and Barkhouse 1977). The connection makes young ramets not only grow fast through the support from the older, but also increase the probability of survival (Pitelka and Ashmun 1985, Cook 1985). These characteristics have been expressed as 'post-natal care' by Callaghan (1984) as equivalent as that of animals. However, physical connection does not always mean that connected ramets are physiologically integrated. Thus, the degree of physiological integration depends highly on species (Sobey and Barkhouse 1977). *Convallaria keiskei* (lily-of-the-valley) as a typical rhizomatous plant has occupied a large area along the south facing edge of the forest in the study site and they seemed to be expanding. Research was conducted to explain the mechanism of the clonal strategy and the level of physiological integration of lily-of-the-valley. Thus, in this paper, the growth strategies and clonal structure which allowed lily-of-the-valley to expand and be dominant were explained. In the next paper, the physiological integration through <sup>14</sup>C-photoassimilates translocation among ramets will be followed.

## MATERIAL AND METHODS

Research has been conducted in a *Larix* community, which is located in Giam-Ri, Chunchon, Kangwon Province, Korea from spring 1991 to spring 1993. The plantation was estimated to be formed about 30 years ago.

Lily-of-the-valley has long branched slender rhizomes over 10 cm long, with clusters of roots from the node. One to three basal leaves, mainly two, rise from rhizome with 4 leaf-like sheaths attached at each stem node. When leaves and sheaths were disintegrated, approximately 6 scars are left at the point of attachment, giving an appearance like a tree annual ring at the stem node. Thus, age of each ramet could be estimated. Hartmann *et al.* (1990) reported a similar growth pattern in *Convallaria majalis*.

Total 467 clones were excavated from the site to clarify morphological structure of clones. Underground parts such as rhizomes and roots were buried 15~20 cm deep. Extreme care was given not to sever the rhizomes. They were rearranged according to original morphology to draw a structural diagram of each clone in the laboratory. Several generations within a clone were identified by the rhizome morphology, mainly rhizome angle attached at parent. Then, the number of ramets was counted, each ramet age

was estimated, and new rhizome length was measured.

To explain seasonal growth pattern, shoot heights were measured every week until shoots stopped to grow. Height was measured from shoot base to apex of leaf blade and it was expressed as the relative growth rate (RGR), the specific increase rate in height per unit time.

For the annual change of ramet size, leaf area was measured instead of height. Height measurement is relatively easy and simple, but it is highly variable depending on the buried depth. Thus, ten  $1 \times 1 \text{ m}^2$  permanent quadrats were established early in spring of 1991 and total 657 ramets were labeled with numbered tags. Then the length and the width of the longest leaf among them were measured and the number of leaves per ramet was counted in mid-May when they were fully matured, and this was repeated for the next year. In order to build a regression equation between the squared area (length  $\times$  width) and the actual leaf area of the longest leaf, the actual leaf area was measured by leaf area meter (LI-3100, LiCor) using the same population of the ramets collected out of the permanent plots. Consequently, three different linear equations were adopted:  $Y = 0.648X$  ( $n=39$ ,  $R^2=0.992$ ) for one-leaf ramet,  $Y = 1.211X$  ( $n=37$ ,  $R^2=0.991$ ) for two-leaves ramet,  $Y = 1.890X$  ( $n=20$ ,  $R^2=0.974$ ) for three-leaves ramet. Here,  $Y$  value is the actual leaf area and  $X$  is the product of length and width.

According to the result of the research for two subsequent years, average growth rate was 1.2. Based on this rate, ramet size by leaf area ( $\text{cm}^2$ ) was classified into 11 classes: class 1, under 50; class 2, 50.1~60.0; class 3, 60.1~72.0; class 4, 72.1~86.4; class 5, 86.5~103.7; class 6, 103.8~124.4; class 7, 124.5~149.3; class 8, 149.4~179.2; class 9, 179.3~215.0; class 10, 215.1~258.0; class 11, 258.1~309.6.

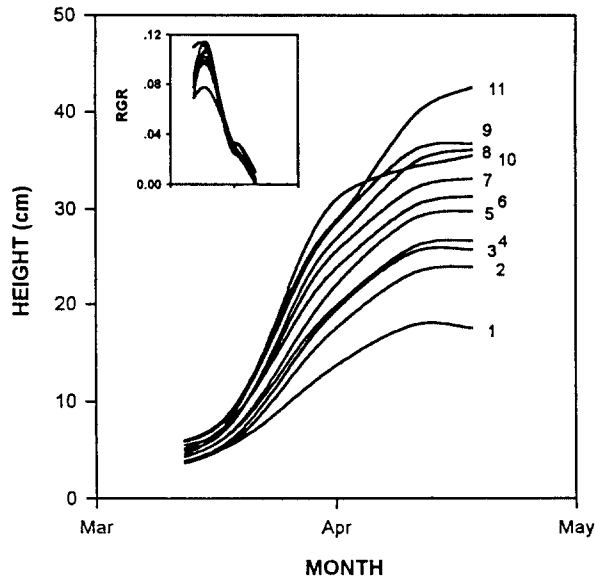
Statistical analyses for linear regression and ANOVA were performed with Excel (ver. 5.0, Microsoft Co.). For nonlinear regression, SYSTAT (ver. 5.03, SYSTAT Co.) was used.

## RESULTS

### Phenology and seasonal growth of ramets

In early April, lily-of-the-valley sprouted when the canopy of overstory was completely opened (Fig. 1). Then its shoot growth speeded up and showed the highest RGR in mid-April. After then, RGR decreased with time and shoot height approached to asymptote in mid-May, about one month after sprouting. Therefore, shoot growth ended before the canopy of the tree layer was closed. Although the final shoot heights among ramets were different, they showed the same trend in growth pattern. When RGR approached nearly zero in mid-May, a flowering stalk came out from the base of a shoot. Soon, it had several bell-like white flowers.

In early June after the cessation of shoot growth, new rhizomes which have been produced during the previous year were about to differentiate. The new roots were deve-



**Fig. 1.** Seasonal growth curve of ramet height. A graph inside is a relative growth rate (RGR,  $\text{cm} \cdot \text{cm}^{-1} \cdot \text{day}^{-1}$ ) curve and the same X-axis label is applied with that of the main graph. Each line represents size class.

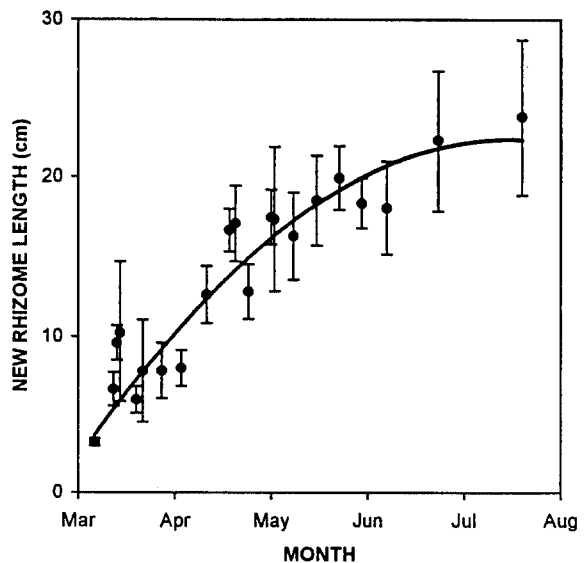
year growth, new rhizome length in average was 4 cm long in early April and increased up to about 18 cm long in June. After then, rhizome apex was differentiated into shoot and root, as mentioned above.

#### Annual growth in ramet size

A ramet is a perennial as well as a clone itself. In fall, shoots died back but resprouted from the base of the shoot in the following spring. From the tagged shoots, the annual change of leaf area was traced (Table 1). The smaller the leaf area was, the higher the increase rate was. The transition of size class was

developed from the first node under the rhizome apex, and then rhizome apex turned upward. Later, new rhizomes were produced from either the first node which developed roots or the second node below the first node. Therefore, there coexisted two different rhizome cohorts: one is the first year rhizome group and the other is the second year group.

The first year rhizome group grew the rest of the year and then regrew the next spring. Thus the growth of the second year rhizome was traced from early April (Fig. 2). The rhizome growth pattern was fitted significantly to the second order non-linear equation ( $F=359.84$ ,  $P=0.000$ ,  $n=247$ ). Due to the first



**Fig. 2.** Seasonal growth in length for the second-year-new rhizome. Data are expressed as mean  $\pm$  s.e. The second order regression line analyzed by nonlinear ANOVA was highly significant ( $N=247$ ,  $F=359.84$ ,  $p=0.000$ ), based on raw data.

**Table 1.** Transition matrix of size class. The figures in the table specify the percentage of the total samples. The cells with the same size between year 1 and 2 were written in bold letter. Total 548 ramets were traced

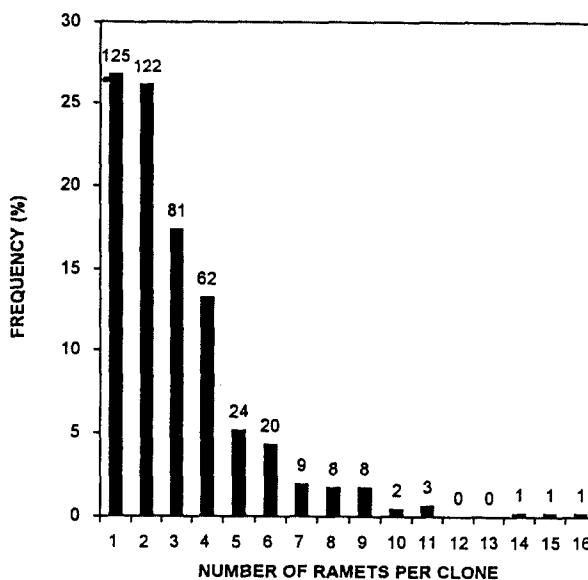
Size class	Year 1									
	1	2	3	4	5	6	7	8	9	
Year 2	1	<b>43.12</b>	35.18	22.68	10.00	9.80	7.27	2.96		
	2	14.22	<b>7.41</b>	4.84	11.67	1.96	1.82			
	3	14.68	12.96	<b>14.52</b>	8.33	9.80	1.82	5.88		
	4	8.71	14.81	17.74	<b>13.33</b>	19.61	9.09	5.88		
	5	9.26	20.38	17.74	11.67	<b>13.73</b>	10.91	11.76		
	6	4.13	5.57	11.29	13.33	7.84	<b>12.73</b>	5.88	9.10	
	7	3.67	3.7	8.06	21.67	21.57	25.45	<b>23.53</b>	9.10	
	8	1.83		3.23	6.67	9.81	18.18	14.71	<b>9.10</b>	33.34
	9	1.38			3.33	3.92	10.91	11.76	27.26	
	10					1.96	1.82	11.76	18.18	66.66
	11							5.88	27.26	

highly variable after one year. Some ramets of the same class got smaller, some stayed and the other got larger. For example, ramets of size class 1 in the first year moved to even size class 9 in the second year. Ramet size seemed to be under the influence of complicated factors such as climate and stored materials rather than that of age.

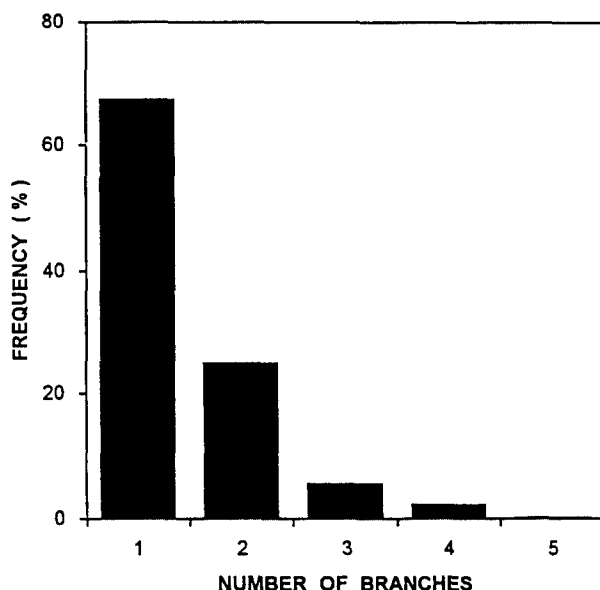
**Morphological structure of a clone**

Number of ramets per clone of lily-of-the-valley showed wide variation from 1 up to 16 (Fig. 3). However, more than 80 % of 467 clones had 1~4 ramets and 27% had only one ramet. High proportion of one-ramet clone indicates the frequency of disturbances. The existence of 16 ramet clone, however, meant that rhizome connections persisted relatively long.

The examination of branching behavior under field condition expressed the extent of severance of rhizomes (Fig. 4). Resulting from the close examination of clonal morphology of lily-of-the-valley, each clone was



**Fig. 3.** Frequencies of clones according to the number of ramets. The figures on each bar indicate the number of clones collected.



**Fig. 4.** Frequency of the number of branches within a clone.

connected shoots, only 25% of all cases showed one year difference while 75% showed more than two year even up to twenty years (data not shown). This means a latent bud can be viable more than twenty years. Disintegration of a clone by disturbances and long lasting viability of latent buds might play a great role for lily-of-the-valley to expand its area successfully where the small scale disturbances continue.

#### **Age structure of a ramet population**

There was no significant size difference with age among over two-year old ramets ( $F=1.030$ ,  $P=0.311$ , Table 2). Only one-year old ramets had smaller leaf area compared to two-year old ones. It suggested that a ramet could be fully grown in terms of size after only one year. Considering that they invested carbohydrates for about six weeks during a growing season (refer Fig. 1), the rapid growth of small size ramets might be resulted from the support by connected ramets.

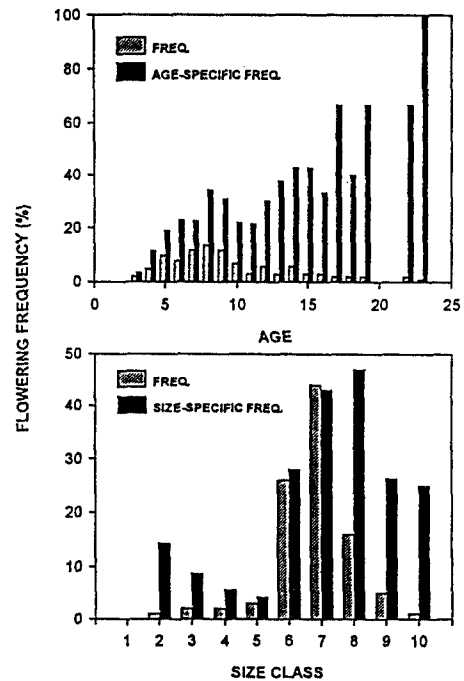
Ramet size did not mean the developmental status of a ramet because size-specific flowering frequencies did not show linear relationship with size class clearly (Fig. 5). On the other hand, age-specific frequencies was increased with age, representing that developmental status in lily-of-the-valley was related to ramet age.

The age structure was formed from the age data of 1,006 ramets collected (Fig. 6). Overall, it showed a reverse J-type curve, which is a characteristic of the stable plant population. The first bar indicating the second year rhizome was the highest. It plays as a source for the next year shoots. Lower frequencies of the young ramet groups, compared with that of a rhizome population, suggested that mortality rate is high either during in

supposed to produce one new ramet per year from the youngest one, meaning the existence of apical dominance over a clone. However, 33% of all rhizome nodes produced branched rhizomes. This suggested that in case the dominance be broken by either biological factors or physical and chemical factors, lateral buds on rhizome node were developed and enabled clones to form large, moderately branched system. Once apical dominance was broken, more than two branches were produced although the frequency was relatively low. In the age difference of two connected

**Table 2.** Leaf area of ramets according to their age

Ramet age	Leaf area (cm <sup>2</sup> )		Numbers
	Mean $\pm$ s.e.		
1	100.2	$\pm$ 8.10	32
2	118.1	$\pm$ 5.67	45
3	117.7	$\pm$ 8.12	33
4	120.0	$\pm$ 5.17	35
5	118.5	$\pm$ 6.71	25
6	125.3	$\pm$ 6.58	38
7	113.1	$\pm$ 5.13	32
8	120.2	$\pm$ 4.83	33
9	121.8	$\pm$ 6.43	26
10	112.7	$\pm$ 9.56	8
11	116.2	$\pm$ 7.80	18
12	120.4	$\pm$ 13.22	6
13	121.8	$\pm$ 5.88	11
14	134.9	$\pm$ 10.77	6
15	113.2	$\pm$ 7.57	8
16	135.1	$\pm$ 2.41	3
17	121.4	$\pm$ 11.30	5
18	118.1	$\pm$ 20.01	3
19	112.2		1
20	110.0		1
21	121.7	$\pm$ 14.54	3
22	124.6		1
23	112.4	$\pm$ 0.11	2
25	113.5	$\pm$ 7.19	2

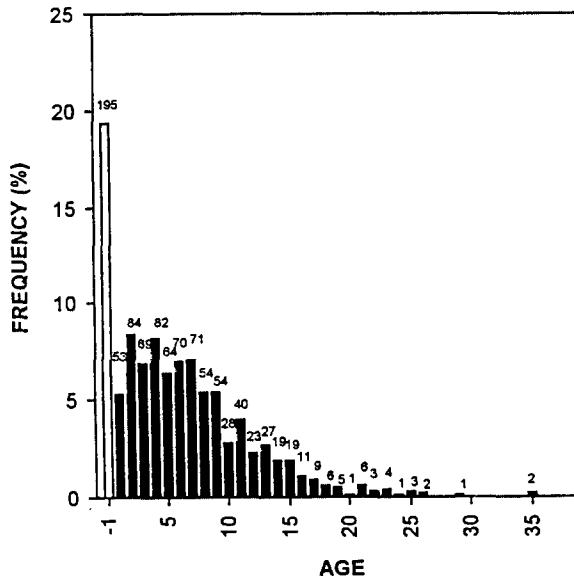
**Fig. 5.** Flowering frequency in relation to age (upper) and size (lower). Hatched bar represents the proportion of flower numbers of a certain age or size class group against total flower numbers while solid bar indicates age-specific or size-specific frequency.

soil or while sprouting in the first year. However, since then there was a trend to be stabilized. Among all the ramets investigated, the age of the oldest one was 35 years old, enabling us to assume the site history.

## DISCUSSION

Why natural selection has favored *Convallaria keiskei* (lily-of-the-valley) as a rhizomatous species? How the species has occupied considerable area and still its population is expanding? One of the answers could be its growth strategy for the timing of phenological events and effective matter allocation pattern during a growing season.

In general, many early spring species sprout early, grow fast and flower before overstory was closed (Harper 1977). These are common among insect-pollinated species. However, it is not well known how shoot growth and underground growth throughout all phenological events are matched in terms of timing and matter allocation. Therefore, it is



**Fig. 6.** Age distribution of ramet population in the study site. Open bar represents the second year rhizome population. The figures on each bar are the number of collected samples.

underlying rhizome apex is thought to be one example of good strategies lowering mortality rate and increasing survival rate of young shoots. After a shoot is emerged from rhizome apex, it is likely to die unless it has enough materials and keeps to be supported by the connected rhizomes. Any dead young plant, however, was not observed during the growing season. Two-year rhizome growth contributes to not only lowering mortality rate of ramets, but also speeding up the growth of the first year shoots. After about 6 weeks from sprouting, the leaf area of the first year ramet was 85% of that of the other older shoots (Table 2). Articles with other species (Harper 1977, Werner and Caswell 1977, Cook and Lyons 1983, Weiner and Schmid 1995) reported that both the probability of death and fecundity was closely related to the size. Therefore, the remarkable size of the first year shoots might be a great benefit for the species (Pitelka *et al.* 1985, Carlson and Callaghan 1991).

No significant difference in leaf area with age supported that vertical growth of shoot is limited by programmed morphological constraint (Watson and Casper 1984, Watson 1984). Instead, a clone size could be expanded through the addition of new modules over large area horizontally.

There was a wide variation among ramets of the same age. Since the population studied seemed to be consisted of a few genets, it is hard to presume that the variation was from a genetic reason.

meaningful to pursue it.

After shoot growth and flowering completion in May, underlying rhizome apices are differentiated into roots and future shoots. Then, from the base node of rhizome apex, another new rhizome is produced subsequently. The rhizome apex from which a new rhizome is produced does not have any photosynthetic organ to support new rhizome production. Thus, the new rhizome production is completely supported by the older connected ramets via the second year rhizomes. New rhizomes, the first year rhizomes, stop growing in August and then regrow in the next spring as the second year rhizomes. Two-year growth of



Considering shoot growth of lily-of-the-valley is accomplished in a short time, the annual size variation results from the reserves of the previous year as well as climatic conditions of the current year (Silvertown 1993). In other words, matter investment on shoot base and rhizome apex of the current year play a great role to the ramet size of the next year.

How long the persistence of the rhizome connection can be lasted? It seems to be at least over 30 years because the oldest ramet found was 35 years old and it was connected by a rhizome to other ramets. This is similar to that of *Carex bigelowii*, a rhizomatous sedge (Carlson and Callaghan, 1991). Even though rhizome connection could be maintained long potentially, occasional disturbances make a clone disintegrate into several clones. Over 80% of 467 clones were consisted of 1~4 ramets (refer Fig. 3). This indicates the magnitude of disturbance. Underlying rhizomes are distributed more or less 15 cm deep in soil, so some rhizomes were exposed around the litter layer. Thus, they were susceptible to be disturbed by animals, insects or men, or freezing during the winter (Choung 1991).

Disturbances seem to be important for lily-of-the-valley to expand. Once the apical dominance is broken by disturbances, up to 5 latent rhizome buds could be elongated from the old dormant buds (refer Fig. 4). This mechanism, then, can be very effective because it may increase population size compared to the situation not disturbed. *Polygonatum humile* and *P. involucreatum* which were found at habitats with similar environmental conditions, showed the same strategy (Choung 1991). Also, the mechanism seems to be still working in reverse J-type age distribution showing high frequency of young age group.

Based on the age of the oldest ramet and the age of *Larix* of overstory vegetation, lily-of-the-valley seemed to expand fast at the study site since *Larix* trees had been planted. It might have existed with low density before the *Larix* plantation. The successful flourishing of lily-of-the-valley came from its effective growth strategy to take advantage of site disturbances by the plantation process.

## 적 요

지하경생장식물인 은방울꽃의 수평성장전략을 설명하기 위하여 강원도 춘천의 조사지역에서 라메트의 성장과 클론의 구조를 연구한 결과, 몇 가지 특이할만한 성장전략이 밝혀졌다. 첫째, 은방울꽃은 개엽, 개화, 지하경생장과 같은 계절현상의 발현시 상층부 낙엽송의 수관이 개방된 이른 봄의 짧은 시기를 집중적으로 이용하였다. 둘째, 이른 봄의 이른 개엽과 빠른 성장 및 개화는 은방울꽃의 물질분배의 기작이 효율적이었기 때문에 가능하였다. 예를 들면, 은방울꽃은 지하경에 2년동안 물질투자를 한 후, 새 라메트로 발달시켰다. 그 결과 1년생의 새 라메트는 개엽 후 6주만에 다년생 라메트 엽면적의 85%에 달하는 크기를 가질 수 있었다. 셋째, 은방울꽃의 라메트 개체군은 교란에 의하여 그 크기가 증가하는 특징을 가졌다. 즉 교란이 없을 때 클론당 매년 1개씩의 지하경을 생산하던 규칙을 깨고, 겨울동안의 동결이나 곤충 또는 사람에 의하여 지하경이 끊어지면 잠재분열조직이 발달하여 5개까지의 지하경을 새로 생산함으로써 라메트의 수를 증가시키는 것으로 밝혀졌다. 은방울꽃의 클론구조를 살펴 본 결과, 라메트 수가 4개 이하인 클

론의 비율이 80%나 된다는 사실은 강도는 낮지만 생육지에 교란이 빈번히 발생하고 있다는 사실을 의미한다. 은방울꽃은 이와 같이 탁월한 성장전략과 교란에 적합한 클론의 구조적 특성을 가짐으로써 조사지에서 넓은 면적의 순군락을 유지 및 확장하고 있는 것으로 판단되었다.

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