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Effects of growth temperature and winter duration on leaf phenology of *Erythronium japonicum*, a forest spring geophyte

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Abstract The effects of growth temperature and winter duration on the leaf phenology of *Erythronium japonicum* were examined in two experiments. Bulbs wintered in the field were cultivated at 10 and 20° C and the bulbs were cultivated at 15° C after chilling treatment at 3° C for 60 and 120 days and without chilling in winter. The plants cultivated at 20° C showed significantly earlier leaf emergence, a more rapid rate of leaf extension and shorter leaf longevity than those cultivated at 10° C. The decrease in the leaf longevity at 20° C resulted from the decreases in the durations of all of the developmental, mature, and senescent phases. The bulbs without chilling treatment did not sprout leaves and those with chilling treatment sprouted leaves. The increase in the length of chilling treatment from 60 to 120 days affected leaf phenology in same manner as the increase in the growth temperature from 10 to 20° C.

Key words Dormant state · Leaf development Leaf emergence · Leaf longevity · Leaf senescence

Introduction

Erythronium japonicum Decne. (Liliaceae) is a spring geophyte distributed mainly in the secondary deciduous broad-leaved forests in the temperate regions of Japan. The growing season of the aerial shoot is limited to the bright light phase before the forest canopy closure in spring (Kawano et al. 1978). Fukuda (1987) reported that emergence, senescence and longevity of the leaf populations of *Erythronium japonicum* varied among years and leaf longevity varied also among the populations emerged at different times in a spring. Change in growth temperature is considered to be one of the factors affecting the variation of these phenological phenomena, as reported for North American *Erythronium* species (Vézina and Grandtner 1965; Caldwell 1969; Muller 1978).

On the other hand, the duration of winter temperatures is also an important factor affecting leaf phenology. Plants which winter in more-or-less dormant states require chilling during winter to break the dormancy and to start growth in spring (e.g. Vegis 1973). In addition, in spring geophytes, the time that the plants remain green decreases with increasing lengths of chilling treatment (Risser and Cottam 1967).

The purpose of this study is to examine how winter duration and growth temperatures affect the leaf phenology of *Erythronium japonicum*.

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Materials and methods

Seeds of *Erythronium japonicum* were collected in 1984 from the populations established in the secondary temperate deciduous broad-leaved forest at Ohizumi, Tokyo, where a previous study (Fukuda 1987) was carried out. They were germinated and the seedlings were cultivated under deciduous trees in the nursery of Tokyo Metropolitan Medicinal Garden, near Ohizumi, until the start of experiments.

Flowering and non-flowering plants were used in the experiments on the effects of growth temperature and winter duration, respectively. The production of flowers depends on the bulb size (Yokoi 1976; Kawano et al. 1982). In natural habitats, emergence and dying of the leaves in non-flowering plants occurs slightly earlier than in flowering plants (Fukuda 1987).

For the experiment on the effect of growth temperature, large bulbs were selected from the nursery in November 1990. They were potted with nursery soils and wintered in the nursery. The potted bulbs were then transferred to the laboratory of Senshu University on 11 March 1991 and were cultivated in the controlled-temperature chamber at $10 \pm 1°$ C and $20 \pm 1°$ C. At the seed-sampling site, leaf emergence of the *Erythronium japonicum* population occurred from late February to late March (Fukuda 1987) and thus the dormancy of the materials was considered to be almost completely broken. Phenology was observed in seven flowering individuals in each treatment. They flowered normally but did not set seeds in the experiment, probably due to the absence of pollinators.

For the experiment on the effect of winter duration, 24 small bulbs were selected from the nursery. They were divided into eight groups based on size, and redivided into three groups so that these had the same size compositions. The bulbs were potted and the pots were transferred to the laboratory on 14 November 1991. The potted bulbs of three groups were cultivated in the chamber at 15±1° C, immediately after transfer and after chilling treatment at 3° C for 60 and 120 days, respectively. The chilling treatment for 120 days was roughly comparable to the winter duration in the natural habitat. The phenology of eight non-flowering individuals in each treatment was observed.

In both experiments, the pots were irradiated with fluorescent light (12 h day length) and the photon flux density (400–700 nm) was 260–290 μmol m^{-2} s^{-1} at the pot surface. The leaves expanded showed normal greeness compared to those in the field. The plants were adequately watered during the experimental period.

Leaf phenological characteristics were observed and expressed in the same manner in both experiments. After the leaves emerged, the length and the rate of dying (10% intervals) were measured at 3-day intervals. Number of days required for 5% and 95% extension of the final leaf length and required for 5% and 95% death of total leaf area were judged from the curves of extension and dying, respectively. The length of the developmental phase was expressed as the period between the time of 5% and 95% extension, length of mature phase was expressed as the period between the time of 95% extension and 5% death, and length of the senescent phase was expressed as the period between the time of 5% and 95% death. Leaf longevity was the sum of the length of these three phases. Mean rate of extension during the developmental phase and mean rate of death during the senescent phase were calculated.

The non-flowering and flowering individuals expanded one and two radical leaves, respectively. Little difference was found in any of the phenological characteristics investigated between the two leaves of each flowering individual and the mean values of two leaves were used for *t*-tests.

Results and discussion

Effect of growth temperature

The leaves of the plants cultivated at 20° C emerged earlier than those cultivated at 10° C (Table 1). The leaves at 20° C showed a higher mean rate of extension and completed extension more rapidly than those at 10° C. The length of the developmental phase at 20° C was about 8 days shorter than at 10° C, but the final leaf length was not significantly different between these two groups. The decrease in time taken for leaf development with increasing temperature has also been reported for other plant species (Dennett and Auld 1980; Rawson and Hindmarsh 1982).

The leaves of the plants at 20° C began to die more rapidly than those at 10° C and the length of mature phase at 20° C was about half of that at 10° C. The leaves at 20° C showed a higher mean rate of death and a shorter senescent phase than those at 10° C. As a result, the leaf longevity at 20° C (34.7 days) was about 1 month shorter than that at 10° C (63.0 days). It is known that adverse temperatures above and below the normal range can accelerate the rate of aging (Thomas and Stoddart 1980). The results of this study indicated that higher growth temperature within the normal range also accelerated the rate of aging of aerial leaves throughout the life span.

Effect of winter duration

The bulbs without chilling treatment did not sprout leaves above the pot soil surface, while the bulbs with chilling treatment sprouted leaves, consistent with the results of previous study (Yoshie and Yoshida 1989). The bulbs that received 120 days (long) of chilling treatment sprouted leaves earlier than those that received 60 days (short) of chilling treatment (Table 2). The results indicated that the dormancy of the leaves was gradually broken by chilling temperatures.

The bulbs that received the long chilling treatment exhibited higher rates of leaf extension and leaf death than those that received the short chilling treatment, but the final leaf length was not significantly different between the two groups. The leaf longevity of the bulbs that received the long chilling treatment was 33.3 days which was roughly comparable to that in the natural habitat (Fukuda 1987). In contrast, the leaf longevity of the bulbs that received the short chilling treatment was 60.5 days.

As to the effects of winter duration on the leaf phenology, other experimental and field studies have mainly investigated the break of dormancy and the time of foliation (see Vegis 1973). However, Risser and Cottam (1967) observed variation in the green-leaf period of

Table 1 Leaf-phenological characteristics of *Erythronium japonicum* flowering individuals grown at 10° C and 20° C

Phenological characteristics	Growth temperature		
	10° C	20° C	*P*
Length required for 5% extension (days)	10.8±5.2	3.5±4.2	<0.05
Length of developmental phase (days)	18.2±4.6	10.5±2.3	<0.01
Length of mature phase (days)	35.5±4.5	18.5±2.8	<0.001
Length of senescent phase (days)	9.3±2.1	5.7±1.7	<0.01
Longevity (days)	63.0±7.9	34.7±3.2	<0.001
Mean rate of extension (mm/day)	4.5±0.9	7.9±1.5	<0.001
Mean rate of dying (% leaf area/day)	10.1±2.4	17.4±5.9	<0.05
Final leaf length (mm)	86.9±11.6	89.2±11.8	ns

Table 2 Leaf-phenological characteristics of *Erythronium japonicum* non-flowering individuals grown at 15° C, after chilling treatment at 3° C for 60 days and 120 days

Phenological characteristics	Length of chilling treatment at 3° C		
	60 days	120 days	*P*
Length required for 5% extension (days)	35.5±12.1	2.1±1.2	<0.001
Length of developmental phase (days)	17.0±3.6	11.1±3.3	<0.01
Length of mature phase (days)	29.1±11.8	14.4±5.0	<0.05
Length of senescent phase (days)	14.4±6.6	7.8±2.0	<0.05
Longevity (days)	60.5±10.6	33.3±3.7	<0.001
Mean rate of extension (mm/day)	3.3±0.7	6.0±1.4	<0.001
Mean rate of dying (% leaf area/day)	7.4±3.3	12.4±3.3	<0.05
Final leaf length (mm)	61.3±10.7	69.5±8.9	ns

spring geophytes in relation to the length of chilling treatment; for example, *Erythronium albidum* bulbs that received 60 days of chilling treatment produced plants which remained green for 85 days, while those receiving 180 days of treatment remained green for only 31 days. The result of this study was consistent with these observations (Risser and Cottam 1967).

The decrease in leaf longevity in the bulbs that received the long chilling treatment resulted from decreases in the durations of all the developmental, mature and senescent phases (Table 2). The results indicated that the long chilling treatment accelerated the rate of aging of leaves throughout the life span.

All of these results indicated that increasing the length of chilling treatment from 60 to 120 days affected the leaf-phenological characteristics in same manner as increasing growth temperature from 10 to 20° C, although the physiological mechanisms are considered to be different between the two.

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