

Nobuhiko Suzuki · Shin Teranishi

Phenology and life cycle of the annual, *Chamaesyce maculata* (L.) Small (Euphorbiaceae), with multiple overlapping generations in Japan

Received: 15 October 2004 / Accepted: 5 January 2005 / Published online: 9 March 2005
© The Ecological Society of Japan 2005

Abstract The phenology of germination, vegetative growth and sexual reproduction in the annual *Chamaesyce maculata* (L.) Small (Euphorbiaceae) were investigated in a natural population in western Japan. Seedlings emerged from mid-June to early October, with three peaks: mid-June, late July and late August. Plants that emerged in June commenced sexual reproduction from late July, and thereafter both vegetative growth and sexual reproduction occurred together until early November, the plants showing no switching from vegetative growth to sexual reproduction. Seedlings that emerged in June and July suffered high mortality, but most seedlings that emerged from August onward survived until the reproductive stage. The minimum size for reproduction was largest for plants that emerged early in the season, and it decreased with a delay in seedling emergence. The late emergence of seedlings that resulted in low reproductive output may be to some extent compensated for by the increased probability of survival in the seedling stage. A transplant experiment clarified that *C. maculata* can repeat a maximum of three overlapping generations within a year. Multiple generations per year were attained by non-dormant seeds produced in the first and second generations and clearly resulted in an increased reproductive output per year. The life cycle with multiple overlapping generations may have been acquired in habitats where unpredictable disturbance results in temporally unsuitable conditions for germination, vegetative growth and sexual reproduction of annual plants, but where suitable conditions frequently

continue over a period longer than the single generation time of annual plants.

Keywords Annual plants · Seedling emergence · Vegetative growth · Sexual reproduction · Life history strategy

Introduction

Organisms such as fishes, reptiles, woody plants and polycarpic perennial herbs, whose growth (body size) and longevity are not limited, survive over long periods and reproduce many times (iteroparity) (Cole 1954) over many years under suitable conditions. In contrast, many species of invertebrates such as insects, with a short adult life span and limited body size, undergo multiple generations within a year (multivoltine), resulting in high yearly reproductive potentials. Diverse patterns in semelparous and iteroparous reproduction in animals and plants have been discussed in relation to their life spans (e.g. Stearns 1977; Kirkendall and Stenseth 1985).

The survival probability of plants is susceptible to the influences of changing environments, because plants are generally sedentary. Therefore, many plants have evolved high plasticity in their growth and reproduction to fit to the changing environments (Lloyd 1984). In many plants, a trade-off between their growth and reproduction is likely to occur because of high costs of reproduction. Then, the plasticity against changing environments and the trade-off between growth and reproduction have generated diverse life histories of plants such as monocarpic and polycarpic perennials, biennial and annual herbs (Silvertown 1987).

Annual plants may have evolved from perennial plants by rapid vegetative growth and early sexual reproduction as adaptations to temporally and/or spatially disturbed environments (Watkinson 1990). Most annual plants predominate in environments in which disturbance prevents a full cover of vegetation by

N. Suzuki (✉)
Department of Applied Biological Sciences,
Faculty of Agriculture,
Saga University, 1 Honjo,
Saga 840-8502, Japan
E-mail: suzuki@cc.saga-u.ac.jp

S. Teranishi
Centre for Ecological Research,
Kyoto University, Otsu,
Shiga 520-2113, Japan

perennials (Watkinson 1990); i.e. annual plants acquired a new niche in those environments. Timing of the disturbance has a major impact on the phenology of these annuals. In many of them, germination, vegetative growth and sexual reproduction are each limited to a particular season within a year. In temperate regions, seedlings of many annual plants emerge in either the spring (summer annuals) or the autumn (winter annuals), by predictable disturbance in either the winter or summer, respectively (Grime et al. 1981; Baskin and Baskin 1988; Watkinson 1990; Masuda and Washitani 1990).

Seeds of most annuals have high dormancy in seasons other than their active life seasons (Baskin and Baskin 2001). Accordingly, the life cycle of annual plants in temperate regions generally comprises a long seed dormancy period and a short active period. Therefore, the body size (vegetative growth) and longevity (sexual reproductive period) of annuals are limited, as seen in insects. There are a few species of annual plants, however, that produce multiple generations within a year, in temperate regions.

In unpredictable environments, timing of disturbance in relation to timing of vegetative growth and sexual reproduction has a major impact on the phenology of annuals. Unpredictable disturbance may be expected to have been a selective force in determining the germination and dormancy strategies of annuals (Watkinson 1990). Cohen (1966, 1968) demonstrated theoretically that how fractions of seeds are expected to germinate is determined by environmental predictability. The bet-hedging strategy of germination and dormancy of seeds has been theoretically examined by many authors (e.g. Templeton and Levin 1979; Ellner 1985a, 1985b; Brown and Venable 1986; Venable and Brown 1988).

In addition, although most annual species have a definite germination period, mainly spring or autumn, there are some annuals that are known to have two or more periods, depending on the difference in timing of disturbance in their habitats (e.g. Roberts and Lockett 1978; Roberts and Boddrell 1983; Baskin and Baskin 1983, 1988; Ankei 1989; Hurka 1990; Masuda and Washitani 1990, 1992; Ishikawa and Abe 1995). Such a polymorphism in germination time is generated by a seed dimorphism, spring and autumn emerging ecotypes and continuous germinations in habitats in which suitable conditions for germination fluctuate within a year and among years. The evolution of polymorphism in germination time has been theoretically considered (e.g. Westoby 1981; Venable 1985). Although these plants produce a portion of seeds which germinate in a particular season or seedlings that emerge successively over a long period, it has not been confirmed whether these annual species undergo multiple generations within a year.

We have found that *Chamaesyce maculata* (L.) Small (Euphorbiaceae) has a unique phenology, in which there are multiple overlapping generations per year. A schedule of vegetative growth and sexual reproduction of *C. maculata* is conspicuously different from typical patterns

of growth and reproduction in annual plants. Thus, we expect that such a phenology has evolved in a habitat in which unpredictable disturbance results in temporally unsuitable conditions for germination, vegetative growth and sexual reproduction of annual plants, but in which suitable conditions frequently continue over a longer period than the generation time of these plants.

To confirm these expectation, we examined the schedules of germination, vegetative growth and sexual reproduction in the annual *C. maculata* and discuss its life history strategy with reference to such events as the timing of germination and reproduction, seedling survival rate and the critical size for reproduction.

Materials and methods

Study species

C. maculata is an annual weed of the Euphorbiaceae tribe Euphorbieae. It was introduced from North America to Japan about 100 years ago and has become naturalized (Kurosawa 2001). The species is distributed throughout Japan (Kurosawa 2001), where it grows in open land such as waste ground, footpaths and crevices in rock. In western Japan, seedlings emerge from June, develop several primary shoots spreading over the ground, and produce many lateral (secondary, tertiary, etc.) shoots by repeated branching. Vegetatively growing plants begin sexual reproduction from early summer, and seed production continues to late autumn, when plants wither.

C. maculata is a self-compatible plant, and most of its flowers are likely to be fertilized by selfing in a natural population because of conspicuously high fruit and seed sets in such a population and under a flower-visitor-free condition (Suzuki and Ohnishi, unpublished data).

The seed size is very small (about 0.15 mg fresh weight) and its variation is also small throughout the reproductive periods (Ohnishi and Suzuki, unpublished data). Seeds produced in summer are automatically dispersed by the dehiscence of capsules (autochory). In contrast, seeds that are produced in autumn are dispersed by ants (myrmecochory) (Suzuki et al., unpublished data).

Census of a natural population

The phenology and life history characteristics of a natural population of *C. maculata* on wasteland on the campus of Kobe University, Kobe City, western Japan (34°41'N, 135°11'E) were investigated. A rectangular area of 1×7 m was selected in a 2×11-m study area; 28 quadrats of 50×50 cm were placed within the rectangular area. The rectangular area was divided into a 1×5-m census area (20 quadrats) and a 1×2-m sampling area (eight quadrats).

The census for seasonal emergence and distribution of seedlings of *C. maculata* was carried out principally at 10-day intervals from June to early November 1999. Newly emerged seedlings were individually marked using a small tag, and their location was noted. Thereafter, we investigated survival and phenology (vegetative growth, flowering, fruiting and withering stages) of these individually marked plants in the census area and in the sampling area.

Vegetative growth and reproduction

Seasonal changes in vegetative growth and reproductive allocation of plants that emerged in different seasons (June–October) were examined by sampling plants in the sampling area in which the emergence time of all seedlings was examined by the census at 10-day intervals as described above. Ten plants were sampled monthly from June to October. Sampled plants were oven dried at 60°C for 48 h, and the dry biomass of each organ (roots, leaves, shoots, flower buds and flowers and fruits) was determined. The biomass of reproductive organs could reflect the number of seeds, because the seed size is likely to be less variable throughout the reproductive periods (Ohnishi and Suzuki, unpublished data). The length of all shoots in each plant was also measured.

Transplant experiment

It is impossible to confirm whether seedlings emerging in a natural population originate from buried seeds produced in a previous year or from fresh seeds produced by the plants growing in the current year. Hence, a transplant experiment was carried out at an experimental field at Kobe University where buried seeds were not present in the soil. *C. maculata* plants had not appeared in the experimental field for at least 5 years. Furthermore, there was no possibility of seed migration into the experimental field by wind, because it was surrounded by buildings of ca. 10 m in height. Vegetative cover was removed before and during the experiment.

Twenty-three reproductive plants (first generation) were collected from a natural population in Kobe City in June 2000 and transplanted at 50-cm intervals within a 3×3-m site (first site) that was free of buried seeds. We could not exclude the possibility that the seedlings which emerged at the first site grew from seeds buried in the soil that was carried with parent plants from a natural population. But almost all of the seedlings emerged far from the base of parent plants. Therefore, the seedlings emerging at the first site could be regarded as offspring (second generation) derived from seeds that the transplants produced. When these seedlings reached the reproductive stage (flowering), they were removed from the first site, and some of them were transplanted into a new 1×2-m site (second site). Seedlings emerging at the second site could be regarded as offspring (third gener-

ation) which grew from seeds produced by plants of the second generation. When these seedlings reached the reproductive stage, they were removed from the second site, and some of them were transplanted into another 1×2-m site (third site). These procedures were repeated until October, when plants withered. Survival of transplanted plants and the phenology of their offspring plants at each site were examined at 10-day intervals.

Results

Seedling emergence and survival in a natural population

The seasonal change in the number of plants that appeared in the 5-m² census area is shown in Fig. 1. Seedlings emerged from mid-June to early October, with three peaks (mid-June, late July and late August) (Fig. 1a). The total number of plants attained a peak in mid-September, thereafter abruptly declining and disappearing in November due to withering (Fig. 1b). Reproductive plants with flower buds, flowers or fruits appeared from late July, and their number increased until early October (Fig. 1b).

Survivorship curves for each cohort of plants, i.e. those emerging during each 10-day interval from mid-June to early October, are shown in Fig. 2. Initial mortality rate of seedlings that emerged in June and July was high, whereas it was low for many cohorts that emerged from August onward, except for the cohort that emerged in mid-August. The high mortality rate of plants in almost all cohorts after late September was caused by the withering which terminated seed production.

Vegetative growth and reproduction

Seasonal changes in biomass of vegetative and reproductive (flower buds, flowers and fruits including seeds) organs of plants that emerged in June are shown in Fig. 3. The vegetative organs grew from July, and their biomass attained a peak in September. Similarly, the biomass of reproductive organs increased from July to October, and was positively correlated to the total length of shoots in each plant from July to October ($n=23$, $r=0.96$, $P<0.0001$).

The average minimum size for reproduction among plants differed significantly depending on the time of seedling emergence [early season (June and July) $n=12$, (mean \pm SE) 273.96 ± 91.18 ; middle season (August) $n=12$, 33.72 ± 10.43 ; late season (September and October) $n=4$, 2.11 ± 0.40 ; ANOVA, $P=0.0174$]. The minimum size for reproduction in plants that emerged early in the season (June and July) was largest and decreased with a delay in seedling emergence (Fisher's PLSD; early season vs. middle season, $P=0.0099$; early season vs. late season, $P=0.0348$). Plants that emerged late in the

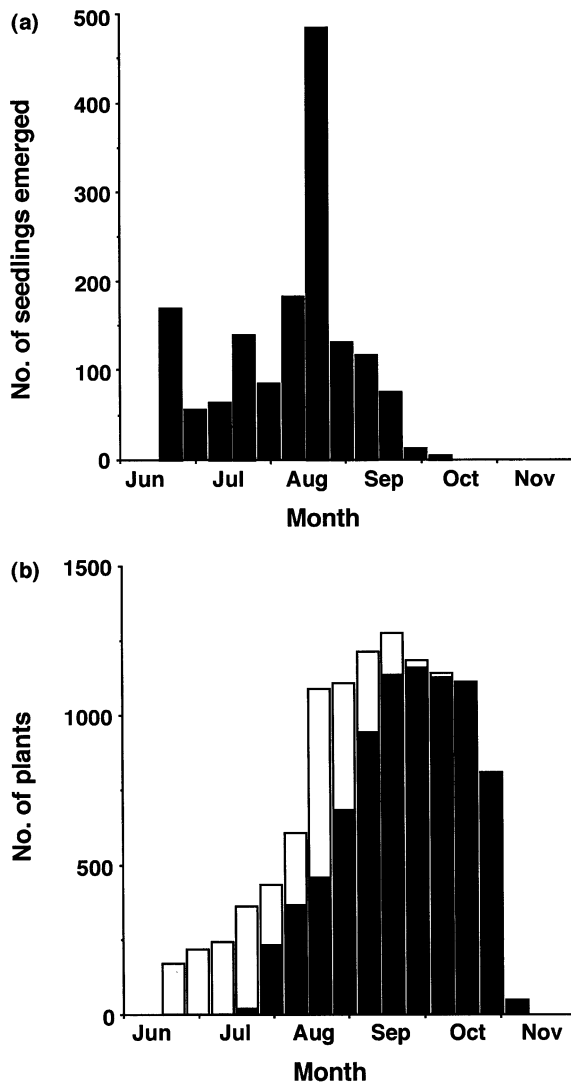


Fig. 1a, b Seasonal change in the number of plants that appeared in the 5-m² census area at the study site. **a** Number of seedlings which emerged. **b** Total number of plants (open bars) and the number of reproductive plants (filled bars). *Jun* June, *Jul* July, *Aug* August, *Sep* September, *Oct* October, *Nov* November

season (September and October) began to produce their fruits when they had developed only a few leaves, and their average minimum size for reproduction was about 1% of that of plants that emerged early in the season.

Reproductive output of plants that emerged in early, middle and late seasons

Almost all plants that survived until October, even those that emerged in October, produced fruits before withering. The biomass of fruits in October, when most plants had completed reproduction, differed significantly depending on the time of seedling emergence (early season $n=9$, 479.61 ± 85.63 mg; middle season $n=17$, 99.86 ± 44.24 ; late season $n=4$, 0.42 ± 0.12 ; ANOVA, $P=0.0001$). Biomass of fruits was largest in plants that

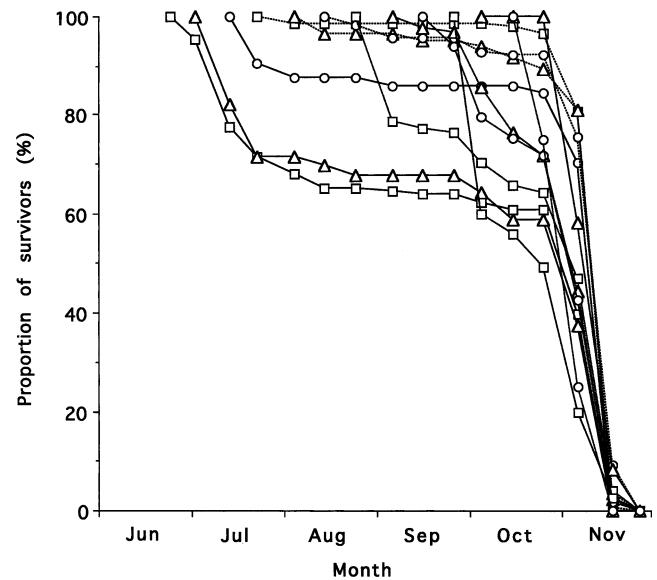


Fig. 2 Survivorship curves for each cohort of plants that emerged during each 10-day interval from mid-June to early October. For abbreviations, see Fig. 1

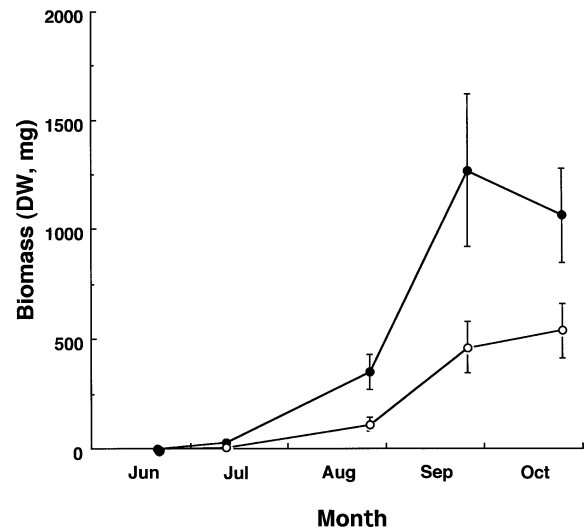


Fig. 3 Seasonal changes in the biomass [dry weight (DW), mg] of vegetative organs (filled circles) and of reproductive organs (flower buds, flowers and fruits including seeds) (open circles) of plants that emerged in June. For other abbreviations, see Fig. 1

emerged early in the season (June and July) and decreased with a delay in seedling emergence (Fisher's PLSD; early season vs. middle season, $P < 0.0001$; early season vs. late season, $P = 0.0004$). The biomass of fruits of plants that emerged late in the season (September and October) was about 0.1% of that of early-emerging plants.

Multiple overlapping generations

Results of the transplant experiment are shown in Fig. 4. Offspring (second generation) derived from plants of the

first generation germinated from late July. They began to reproduce from August and their number abruptly increased from September to early October (Fig. 4a). Further, transplanted second-generation plants produced a third generation. Reproductive plants of the third generation appeared from September, and their number increased from September to October (Fig. 4b). Transplanted third-generation plants produced seeds, but these seeds did not germinate (Fig. 4c). Most parent plants of the first to third generations survived through late October and withered in November (Fig. 4).

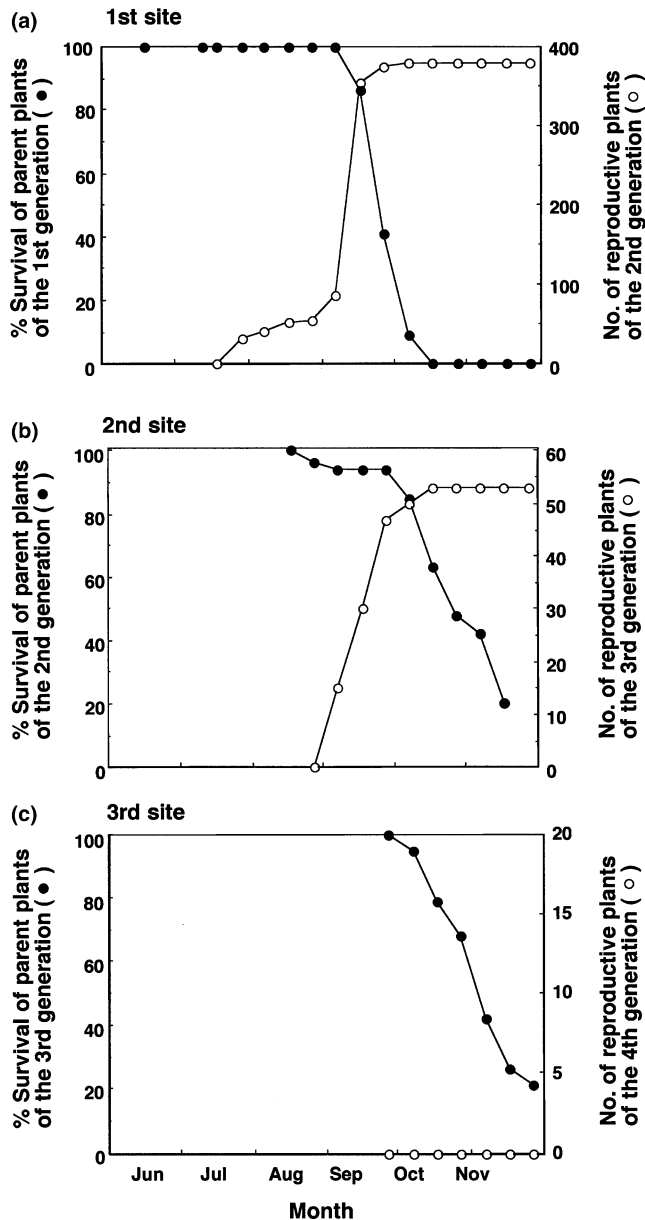


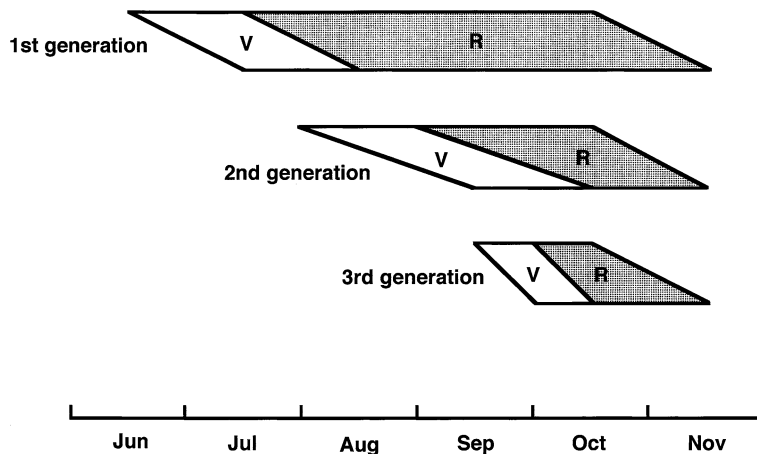
Fig. 4 Results of transplant experiment. Survivorship curves for parent plants of the first, second and third generations (filled circles) and numbers of reproductive plants of the second, third and fourth generations (open circles) that appeared at three sites. Seedlings of the fourth generation did not emerge at the third site. For abbreviations, see Fig. 1

Discussion

We showed that plants of *C. maculata* emerging in June commenced sexual reproduction in late July and that both vegetative growth and sexual reproduction occurred together until early November (Fig. 3). This shows that plants did not switch from vegetative growth to reproductive growth. This phenological pattern appears to be unique. It does not correspond with the theoretical expectation that annual plants switch instantaneously from vegetative growth to reproduction, resulting in the maximum reproductive output (e.g. Cohen 1971, 1976; Vincent and Pulliam 1980; King and Roughgarden 1982a; Kozłowski and Wiegert 1986). In unpredictable environments in which suitable conditions fluctuate within a year and among years, it is likely that the instantaneous switching from vegetative growth to reproduction is not adaptive, because both vegetative growth and reproduction should occur together to avoid the risk of death due to the unpredictable disturbance of habitats (King and Roughgarden 1982b; Amir and Cohen 1990). In addition, it may be considered that if the maintenance cost of vegetative organs increases with aging, switching from vegetative growth to reproduction would not be advantageous, regardless of the unpredictability of an environment. Switching from vegetative growth to reproduction also may not occur in plants with indefinite inflorescences (Masuda and Yahara 1994) and in plants in which branching during vegetative growth generates new meristems that can differentiate into reproductive organs in the future (Geber 1990; Bonser and Aarssen 2001). The switch from growth to reproduction of *C. maculata* could not be explained by an analysis of the pattern of growth and reproduction with respect to meristem allocation (Suzuki and Ohnishi, unpublished data).

Seedlings emerged over a long period, and three peaks in seedling emergence were found (Fig. 1a). In the field experiment for germination of buried seeds, seedlings emerged from June to August in Saga, western Japan (33°14'N, 130°18'E) (Suzuki, unpublished data). Baskin and Baskin (1979) reported that seedlings of *C. maculata* emerged throughout the summer in Kentucky, because the seeds require a high temperature (about 30–35°C) for germination. Although the second and third peaks in seedling emergence may be caused primarily by germination of the second and third generations, as mentioned below, germination of buried seeds occurs over a prolonged period (June–August) in this population. Although there are some annual species known to have two or more periods of germination depending on the timing of disturbance in their habitats (e.g. Roberts and Lockett 1978; Roberts and Boddrell 1983; Baskin and Baskin 1983, 1988; Ankei 1989; Hurka 1990; Masuda and Washitani 1990, 1992; Ishikawa and Abe 1995), continuous germination occurring over a long period as seen in this study has rarely been seen before (Marks and Prince 1981).

Fig. 5 Schematic illustration of the life cycle of *Chamaesyce maculata* with multiple overlapping generations. *V* Vegetative growth stage, *R* sexual reproductive stage with a vegetative growth; for other abbreviations, see Fig. 1



In many plant species, the seedling stage is usually vulnerable to environmental risks, accompanied by high mortality (Harper 1977). In our study, seedlings that emerged in June and July had high mortality, but many seedlings that emerged from August onward survived until the reproductive stage (Fig. 2). The exceptionally high mortality rate in the initial stage of seedlings that emerged in mid-August may have been caused by a crowding effect, because the number of seedlings emerged in mid-August was extremely high (Fig. 1). Gross (1980) and Stanton (1985) reported that seedling mortality is affected by the timing of seedling emergence.

A positive correlation between plant size and reproductive output has been found in many plant species (Samson and Werk 1986; Klinkharmer et al. 1992; Shitaka and Hirose 1993; Clauss and Aarssen 1994; Stöcklin and Favre 1994), and a delay in seedling emergence generally causes a low reproductive output (Shitaka and Hirose 1993, 1998). In the present study, such a tendency was found: the later seedlings emerged, the lower the biomass of fruits. Therefore, the late emergence of seedlings that resulted in low reproductive output may be to some extent compensated for by an increased probability of survival in the seedling stage. Similar results were reported for the wild lettuce, *Lactuca serriola*, which has two distinct germination periods (Marks and Prince 1981).

The minimum size for reproduction in plants was largest for plants that emerged in the early season (June and July) and decreased with a delay in seedling emergence. The critical size for reproduction is known for many perennial plants and facultative biennial plants (Kelly 1985), in which the timing of reproduction is determined primarily by size rather than age (Meijden and Waals-Kooi 1979; Gross 1981; Kachi and Hirose 1985; Kachi 1990). In annual plants, however, seasonal environments strictly constrain reproductive growth by determining a time limit for reproduction (Shitaka and Hirose 1998). Therefore, variations in timing of seedling emergence and in vegetative productivity may strongly affect the minimum size for reproduction, in turn causing variation and plasticity in the timing of reproductive growth (Clauss and Aarssen 1994).

The transplant experiment proved that *C. maculata* can have a maximum of three overlapping generations within a year (Fig. 4, schematically shown in Fig. 5). Multiple generations per year clearly result in an increase in annual reproductive output, meaning the increase in fitness of individual plants. This phenological pattern was attained by non-dormant seeds produced in the first and second generations under continuously suitable conditions for germination, vegetative growth and reproduction (Fig. 4). Baskin and Baskin (1979) reported that the seeds of *C. maculata* require a high temperature for germination and that buried seeds do not remain viable in soil for long periods of time. Therefore, we would expect that annual plants with multiple overlapping generations have evolved in habitats in which unpredictable disturbance within a year and among years results in temporally unsuitable conditions for germination, vegetative growth and sexual reproduction of annual plants, but in which suitable conditions frequently continue over a period longer than the generation time of annual plants.

However, multiple overlapping generations of annual plants are hardly known in temperate regions. A somewhat similar life cycle has been found in a population of *Poa annua* (Law 1981). Since parent plants in an initial colonizing population of *P. annua* have a 2-year maximum lifespan (non-annual plants), the recruitment of seedlings occurs when parent plants are still living. However, when the population density has increased to a ceiling, the longevity of *P. annua* shortens to < 1 year (likely annual plants). Therefore, the life cycle of *P. annua* is conspicuously facultative, depending on population densities, and the overlapping of generations occasionally occurs for biennial plants.

In Japan, there is a possibility that *Galinsoga parviflora* Cav., *G. quadriradiata* Ruiz et Pav. (Compositae), and *Amaranthus retroflexus* L. (Amaranthaceae) are annual plants with multiple generations per year (Shimizu et al. 2001), but their life cycles and phenologies have been hardly investigated. In future work, we shall elucidate the evolutionary and ecological significance of the life cycle of annual plants with multiple generations per year. Then, we plan to investigate the timing and phenology of germination, vegetative growth and sexual

reproduction in these plant species and other species of annual plants in relation to unpredictability and seasonal suitability of habitats.

Acknowledgements We thank the members of the Laboratory of Ecology, Kobe University for valuable advice and support during this study. This study was partly supported by Grants-in-Aid from the Ministry of Education, Science, Sports and Culture of Japan (no. 14540582).

References

- Amir S, Cohen D (1990) Optimal reproductive efforts and the timing of reproduction of annual plants in randomly varying environments. *J Theor Biol* 147:17–42
- Ankei T (1989) Phenology and life cycles of *Stellaria* (Caryophyllaceae) with special reference to the evolution of their life forms. *J Phytogeogr Taxonomy* 37:43–52
- Baskin JM, Baskin CC (1979) Timing of seed germination in the weedy summer annual *Euphorbia supina*. *Bartonia* 46:63–68
- Baskin JM, Baskin CC (1983) Germination ecology of *Veronica arvensis*. *J Ecol* 71:57–68
- Baskin CC, Baskin JM (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *Am J Bot* 75:286–305
- Baskin CC, Baskin JM (2001) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, Calif.
- Bonsler SP, Aarssen LW (2001) Allometry and plasticity of meristem allocation throughout development in *Arabidopsis thaliana*. *J Ecol* 89:72–79
- Brown JS, Venable DL (1986) Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am Nat* 127:31–47
- Clauss MJ, Aarssen LW (1994) Phenotypic plasticity of size-fecundity relationships in *Arabidopsis thaliana*. *J Ecol* 82:447–455
- Cohen D (1966) Optimizing reproduction in a randomly varying environment. *J Theor Biol* 12:119–129
- Cohen D (1968) A general model of optimal reproduction in a randomly varying environment. *J Ecol* 56:219–228
- Cohen D (1971) Maximizing final yield when growth is limited by time or by limiting resources. *J Theor Biol* 33:299–307
- Cohen D (1976) The optimal timing of reproduction. *Am Nat* 110:801–807
- Cole LC (1954) The population consequences of life-history phenomena. *Q Rev Biol* 29:103–137
- Ellner S (1985a) ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theor Popul Biol* 28:50–79
- Ellner S (1985b) ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. *Theor Popul Biol* 28:80–116
- Geber MA (1990) The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. *Evolution* 44:799–819
- Grime JP, Mason G, Curtis AV, Rodman J, Band SR, Mowforth M AG, Neal AM, Shaw S (1981) A comparative study of germination characteristics in a local flora. *J Ecol* 69:1017–1059
- Gross KL (1980) Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. *J Ecol* 68:919–927
- Gross KL (1981) Predictions of fate from rosette size in four “biennial” plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia* 48:209–213
- Harper JL (1977) Population biology of plants. Academic Press, New York
- Hurka H (1990) Differentiation and adaptation in the genus *Capsella* (Brassicaceae). In: Kawano S (ed) Biological approaches and evolutionary trends in plants. Academic Press, London, pp 19–32
- Ishikawa S, Abe J (1995) Germination strategies of *Capsella bursa-pastoris* in the orchard (in Japanese with English summary). *Weed Res Jpn* 40:209–214
- Kachi N (1990) Evolution of size-dependent reproduction in biennial plants: a demographic approach. In: Kawano S (ed) Biological approaches and evolutionary trends in plants. Academic Press, London, pp 367–385
- Kachi N, Hirose T (1985) Population dynamics of *Oenothera glazioviana* in a sand-dune system with special reference to the adaptive significance of size-dependent reproduction. *J Ecol* 73:887–901
- Kelly D (1985) On strict and facultative biennials. *Oecologia* 67:292–294
- King D, Roughgarden J (1982a) Multiple switches between vegetative and reproductive growth in annual plants. *Theor Popul Biol* 21:194–204
- King D, Roughgarden J (1982b) Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. *Theor Popul Biol* 22:1–16
- Kirkendall LR, Stenseth NC (1985) On defining “breeding once”. *Am Nat* 125:189–204
- Klinkharmer PGL, Meelis E, Jong TJD, Weiner J (1992) On the analysis of size-dependent reproductive output in plants. *Funct Ecol* 6:308–316
- Kozlowski J, Wiegert RG (1986) Optimal allocation of energy to growth and reproduction. *Theor Popul Biol* 29:16–37
- Kurosawa T (2001) Taxonomy and distribution of weedy taxa of *Chamaesyce* S.F. Gray (Euphorbiaceae) in Japan (in Japanese with English abstract). *Acta Phytotaxonomy Geobot* 51:203–229
- Law R (1981) The dynamics of a colonizing population of *Poa annua*. *Ecology* 62:1267–1277
- Lloyd DG (1984) Variation strategies of plants in heterogeneous environments. *Biol J Linn Soc* 21:357–385
- Marks M, Prince S (1981) Influence of germination date on survival and fecundity in wild lettuce *Lactuca serriola*. *Oikos* 36:326–330
- Masuda M, Washitani I (1990) A comparative ecology of the seasonal schedules for “reproduction by seeds” in a moist tall grassland community. *Funct Ecol* 4:169–182
- Masuda M, Washitani I (1992) Differentiation of spring emerging and autumn emerging ecotypes in *Galium spurium* L. var. *echinospermon*. *Oecologia* 89:42–46
- Masuda M, Yahara T (1994) Reproductive ecology of a cleistogamous annual, *Impatiens noli-tangere* L., occurring under different environmental conditions. *Ecol Res* 9:67–75
- Meijden EVD, Waals-Kooi REVD (1979) The population ecology of *Senecio jacobaea* in a sand dune system. I. Reproductive strategy and the biennial habit. *J Ecol* 67:131–153
- Roberts HA, Boddrell JE (1983) Seed survival and periodicity of seedling emergence in ten species of annual weeds. *Ann Appl Biol* 102:523–532
- Roberts HA, Lockett PM (1978) Seed dormancy and periodicity of seedling emergence in *Veronica hederifolia* L. *Weed Res* 18:41–48
- Samson DA, Werk KS (1986) Size-dependent effects in the analysis of reproductive effort in plants. *Am Nat* 127:667–680
- Shimizu N, Morita H, Hirota S (2001) Plant invaders in Japan (in Japanese). Zen-no-kyo, Tokyo
- Shitaka Y, Hirose T (1993) Timing of seed germination and the reproductive effort in *Xanthium canadense*. *Oecologia* 95:334–339
- Shitaka Y, Hirose T (1998) Effects of shift in flowering time on the reproductive output of *Xanthium canadense* in a seasonal environment. *Oecologia* 114:361–367
- Silvertown JW (1987) Introduction to plant population ecology. Longman, London

- Stanton ML (1985) Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia* 67:524–531
- Stearns SC (1977) The evolution of life history traits. *Annu Rev Ecol Syst* 8:145–171
- Stöcklin J, Favre P (1994) Effects of plant size and morphological constraints on variation in reproductive components in two related species of *Epilobium*. *J Ecol* 82:735–746
- Templeton AR, Levin DA (1979) Evolutionary consequences of seed pools. *Am Nat* 114:232–249
- Venable DL (1985) The evolutionary ecology of seed heteromorphism. *Am Nat* 126:577–595
- Venable DL, Brown JS (1988) The selective interactions of dispersal, dormancy, and seed size as adaptation for reducing risk in variable environments. *Am Nat* 131:360–384
- Vincent TL, Pulliam HR (1980) Evolution of life history strategies for an asexual annual plant model. *Theor Popul Biol* 17:215–231
- Watkinson AR (1990) Annual plants: a life-history and population analysis. In: Kawano S (ed) *Biological approaches and evolutionary trends in plants*. Academic Press, London, pp 351–366
- Westoby M (1981) How diversified seed germination behavior is selected. *Am Nat* 118:882–885