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Population Differentiation and Germination Ecology in *Stellaria media* (L.) Vill.

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Summary. Population differentiation in *Stellaria media* was studied with regard to life-cycle strategy and germination ecology. Two populations were identified in the study area, growing side by side, W1 and W2. The life-span of population W1 is much shorter than that of population W2, especially under summer conditions: 1–2 months versus 4–6 months; the time to flowering differs accordingly. Germination properties of seed produced under summer, winter, and field conditions were studied. Fresh seeds produced at 20° C showed good germination (ca. 75%) over a broad range of temperatures in the case of population W1, but seeds of population W2 showed appreciable germination only at high temperatures (ca. 30%). Seeds produced at 7° C showed very little (population W2) or no germination at all (population W1). To simulate seasonal changes in temperature, a "comprehensive" germination scheme was developed which enabled the response of hydrated seeds to two temperature cycles (cold-warm-cold and warm-cold-warm) to be tested. The two populations reacted differently. At the end of the cycles, only a few seeds of population W1, but about half of the seeds of population W2, remained dormant. The data obtained were used to study the effects of differential germination ecology on the dynamics of the two populations. In a reconstruction of the courses of development, the populations were shown to possess different strategies. Population W1 builds up a uniform seed stock, and population W2 a phenotypically diverse seed reserve. The implications for population dynamics are discussed.

1. Introduction

Stellaria media (L.) Vill.—common chickweed—is usually one of the first colonizing species of abandoned, sandy arable fields in dune areas. *S. media* is known as both a winter and summer annual species (Hitzer, 1934–1935; Peter-

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son, 1936; Reinöhl, 1903). In summer more than one generation may occur (Lyre, 1957; Reinöhl, 1903). Baskin and Baskin (1976), however, regard *S. media* as strictly a winter annual.

In the study area, *S. media* may grow all the year through. However, in summer, when the sandy soil dries up this species usually wilts and dies off. Two fluxes of germination can be observed, the main one in September and a minor one at the beginning of June.

A thorough knowledge of germination ecology is indispensable to the study of population dynamics of annual species (Hayashi and Numata, 1967; Harper, 1977). The evaluation of published data on the germination behaviour of *S. media* seeds is difficult because of the differences in material and methods used. The results are not always in accordance with each other. In most studies poor germination and high dormancy of freshly harvested seeds were observed (Baskin and Baskin, 1976; Lyre, 1957; Kolk, 1947, 1962; Krug, 1929; Reinöhl, 1903; Roberts and Lockett, 1975). High percentages of germination of fresh seeds have been mentioned by Evans et al (1974), Salisbury (1974) and Steinbauer et al (1955). Lyre (1957), Peterson (1936) and Salisbury (1974) point to the possible existence of races or ecotypes of *S. media*, each with different germination properties.

The aim of the present investigation was to study the germination properties of *S. media*, notably in view of population differentiation and seasonal seed production, and to analyze the results with respect to population dynamics.

2. Materials and Methods

2.1. Study Area

This consists of two abandoned arable fields lying fallow and situated in the coastal dunes of the western part of the Netherlands. The soil is fine dune sand and poor in nutrients. During the first two years of abandonment the vegetation of the fields was characterized by *Stellaria media* (L.) Vill. and *S. pallida* (Dum.) Piré as the most common species, and by *Cerastium semidecandrum* L., *C. holosteoides* Fr., and a few other species. Briefly, the phenology of *S. media* in the study area is as follows. The great flux of germination is in September, the cover reaches its maximum soon after and is sustained until spring. In March and April most plants die off, but the remaining plants grow for another month or two, or sometimes even longer. Usually, by the end of May or the beginning of June, there is a second, minor flux of germination. These plants die off after about one month during the dry summer period when the groundwater table falls to several meters below the surface of the soil. Only in September do *S. media* plants appear again.

2.2. Seed Harvest and Experimental Growing Conditions

When seeds were harvested special attention was paid to collecting fresh seeds. Seeds were only taken from their capsules when these had opened up less than 1 day before. As an alternative, seed capsules which were almost dehiscent were used. This can be ascertained by the formation of a brownish ring in the stem directly beneath the capsule. This method of collecting seeds is very time consuming, especially in the field, but is to be preferred to the less accurate dating involved in other methods referred to in the literature. Dry storage of seeds took place in paper envelopes at room temperature (20–22° C).

Plants were grown outside under natural conditions, as well as in a greenhouse (20° C; 70% r.h.; 12 h light period by means of mercury-vapor bulbs; dark period dependent on natural light conditions) and in a climate room (7° C; 60% r.h.; 12 h light period by means of Phillips fluorescent lamps, color 33; dark period also 12 h). Light intensity of both artificial regimes was 6000–7000 lux at plant level. The cultures were renewed regularly by growing from seed.

2.3. Germination Experiments

Fresh seeds—used on the day of collection—and dry-stored seeds were laid to germinate in closed trays made of transparent plastic and measuring 10 × 10 × 10 cm. One hundred seeds per tray were put on filter paper on a plastic mat in demineralized water in such a way that the seeds were in contact with the water only via the paper. When necessary the trays were replenished with water of the same temperature to prevent undesirable temperature shocks.

The emergence of the radicle through the testa was used as the criterion for germination. Germinated seeds were removed from the trays. Each treatment lasted for six weeks. During the first 3 weeks the trays were inspected daily for germination, after that twice weekly. If germination took place, this usually happened between the 3rd and 8th day. The variation in germination results between replications was only small. The standard deviation rarely exceeded 10%; therefore, statistical treatment of the data was deemed unnecessary.

At the end of each test, ungerminated seeds were dried and tested for viability by lightly scarifying with sandpaper and laying for germination at room temperature. The percentage of total germination thus found was never below 97%, and percentages of germination and dormancy have been calculated on this basis.

Two schemes were developed for germination tests. In the first, more conventional one, seeds were laid to germinate at the following temperature and light regimes: 4, 8, 12 and 16° C S.D. (Short Day: 8 h light and 16 h dark period) and 20, 24 and 28° C L.D. (Long Day: 16 h light and 8 h dark period); all are at constant temperatures. In addition, two alternating temperature regimes were used: 2–12° C S.D. and 15–25° C L.D. (dark period coincided with the low temperature period). The alternating regimes were chosen to reflect to some extent the natural diurnal fluctuations in temperature during mid-autumn/spring and summer, respectively. Germination experiments were carried out four to nine times (400–900 seeds) per treatment, depending upon the number of seeds available. The second scheme was specially developed for the present investigation. This "comprehensive" germination scheme aims at simulating the effects on germination behavior of seasonal changes in temperature prevailing in the study area. In this paper the results presented are derived from a shortened version of this scheme.

Seeds were laid to germinate at 8, 12 and 2–12° C S.D. and 20, 24 and 15–25° C L.D. regimes. For clarity, germination data are averaged in tables under the heading "cold" (pertaining to the low temperature treatments) and "warm" (pertaining to the high temperature treatments). After 6 weeks one tray from each treatment was brought to each of the other temperatures and one tray remained at its original temperature. After this second period of 6 weeks, the trays changed treatments once more. The ones at 8 and 12° C were brought to 24° C and the ones at 20 and 24° C to 12° C. The trays at the alternating temperatures changed places. After another 6 weeks the experiment was brought to an end. Two important temperature cycles can be studied this way: The cold-warm-cold cycle (winter-summer-winter) and the warm-cold-warm cycle (summer-winter-summer). Apart from the first phase of these cycles, the properties of hydrated seeds were studied this way. Two other cycles, cold-cold-warm and warm-warm-cold, were also included in the experiment, to study the effect of ageing at certain temperatures in hydrated condition. Almost no after-germination took place after the first flux of germination, however long the seeds stayed at that particular regime. For this reason, corrections for after-germination were found to be unnecessary.

The experiments were carried out two or three times, thus involving 7,200–10,800 seeds per experiment.

3. Results

3.1. Population Differentiation

Two growth-forms of *Stellaria media* appeared to exist in the study area. Their properties did not change during cultivation over a number of generations and hence are regarded as genetically fixed. The two forms, called population W1 and population W2, were isolated from seeds collected in spring 1973 and subsequent years, on the strength of differences in life cycle. The data

Table 1. Phenological characteristics of *Stellaria media* populations WI and W2, grown under different conditions

Growing conditions	Life-span of populations (months)		Time to seed setting of populations (months)	
	W1	W2	W1	W2
Greenhouse, 20° C	2–3	4–7	$^{1}/_{2}$–1	3–4 (–6)
Climate room, 7° C	7–12	7–12	2–3	3–4 (–6)
In the field, sown in May	1–2	4–6	$^{1}/_{2}$–1	2–4
In the field, sown in September	7–8	9–10 (–18)	1–2	4–6

in Table 1 are rough averages of a number of cultivations. Lifespan and seed-setting are also dependent on nutrition. High nutrition will prolong the lifespan, in the case of population W1 mainly through the formation of new shoots at the base of the plant while the older parts die off.

3.2. Germination of Fresh and Dry-Stored Seeds

Genotypical Differentiation. The results of germination experiments are summarized in Fig. 1 for seeds produced at 20° C and in Table 2 for seeds produced at 7° C. Data from alternating temperature regimes have been omitted because these scarcely differed from the data obtained at the relevant constant temperatures. However, fresh, half a month old, and one month old seeds of population W2, grown at 20° C, showed 10–20% more germination at an alternating 15–25° C compared with the constant 24° C temperature regime.

Fresh seeds of *S. media*—population W1, grown at 20° C, are characterized by a broad range of optimal temperatures for germination: 8–24° C with 70–80% germination. Dry, 14 day old seed shows even higher germination, notably at the higher temperatures. With the ageing of seeds, germination decreases, not so much at the higher temperatures as at the lower ones. Five month old seed again shows a broad optimum. Seeds more than one year old will germinate fully at all temperatures tested. At first the dormancy of the seeds increases with age, especially when tested at low temperatures. Seeds show decreasing dormancy when older than two months.

The germination behavior of seeds of population W2 grown at 20° C differs considerably from population W1. Optimal temperatures for fresh seeds lie at 20–24° C. The percentage of germination, however, is only about 25%; and at the lower temperatures even less germination occurs. With the ageing of seeds, the range of optimal temperatures becomes broader and germination increases, especially at the higher temperatures. Four month old seeds show the highest percentages of germination: dormancy gradually decreases up to this age. After 5 months, germination is down again and dormancy at low temperatures is considerably increased.

Although there are less data available on the germination behavior of seeds produced at low temperatures, it is clear from Table 2 that the two populations

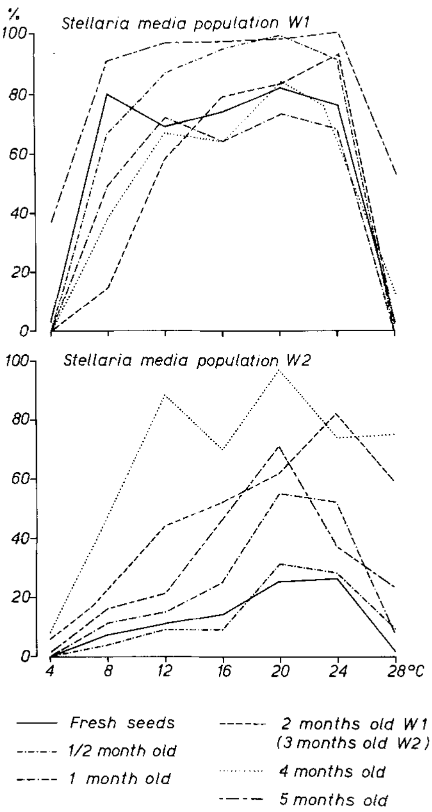

Fig. 1. Germination of fresh and dry stored seeds of two populations of *Stellaria media*, grown at 20° C

Table 2. Germination of fresh and dry-stored seeds of two populations of *Stellaria media*, grown at 7° C

Population	Age of seeds	Percentage of germination at (° C):						
		4	8	12	16	20	24	28
W1	fresh	0	0	0	0	0	0	0
	1 month	0	0	0	0	0	0	0
	2 months	0	0	0	0	0	1	0
	3 months	—	—	2	—	—	6	—
W2	fresh	0	2	1	2	2	1	0
	1 month	0	7	2	3	0	1	0
	2 months	0	4	23	10	4	8	0
	3 months	0	11	58	76	20	25	16

— = data not available

differ significantly in this respect. Seeds of population W1 show virtually no germination. Fresh seeds of population W2 germinate over a broad range of temperatures, though to a maximum of only 2%. With ageing, the germination percentages of population W2 increase gradually to relatively high levels. Optimum temperatures lie between 12 and 16° C, but there is also considerable germination at higher temperatures.

Phenotypically Determined Germination Behavior. When one compares the germination properties with the temperature at which the seed was set (Fig. 1, Table 2), the influence of the environment of the mother plant is striking. Fresh seeds of population W1 show the greatest differentiation: about 75% germination when produced under warm conditions versus no germination when produced at low temperatures. Fresh seeds of population W2 also show a considerable difference: 26% vs 2% respectively. With the ageing of seeds, the discrepancy in population W1 is maintained, whereas in seeds of population W2 the differences gradually decrease.

Germination of Seeds Collected in the Field. On various dates over a couple of years, random samples of fresh seeds were collected from natural stands of *S. media* in the study area. Because of the tangle of plants, no attempt was made to identify specific populations. The results of germination experiments are presented in Table 3. The seeds collected in autumn, winter, and spring show a similar pattern of germination to the seeds of the two populations grown at low temperatures (Table 2). The data on seeds collected in summer are limited to one collection in June 1975. The results from this experiment are in reasonable accordance with those of population W1, but not with population W2 (Fig. 1). A number of seed capsules was marked, left attached to the plants and harvested after 2 weeks. During this interval of time the capsules were subjected to extreme desiccation due to the dry weather. When tested subsequently, all seeds appeared to be dormant (Table 3).

3.3. Germination Behavior with Respect to Temperature Cycles

Genotypical Differentiation. Cold and warm pre-treatments have different effects on the germination of the two populations of *S. media* grown at 20° C (Table 4). The first phase of the cycle cold-warm-cold, the cold pre-treatment, increases the germination percentage of population W1 by less than 10%, except for the seeds originally one month old which germinate fully, an increase of 39%. Population W2 shows a greater increase: about 40–60%.

Virtually all seeds of population W1 germinate after the warm pre-treatment in the second part of the cycle, which represents an increase of 10–70%. Germination of population W2 increases likewise, but less dramatically. At the end of the cycle, virtually no dormant seeds of population W1 are left, in contrast to population W2, of which some 20% of the seeds stay dormant, with the exception of the seeds originally 2 months old.

Table 3. Germination of seeds of natural stands of *Stellaria media* collected at various times of the year

Date of collection	Age of seeds	Percentage of germination at (° C):						
		4	8	12	16	20	24	28
27. 10. 1975	fresh	1	1	0	1	1	1	0
	1 month	0	2	1	1	1	1	0
	2 months	0	10	24	10	4	5	1
17. 11. 1975	fresh	0	0	0	0	0	0	0
	1 month	0	2	1	0	0	0	0
15. 12. 1975	fresh	0	3	4	4	0	0	0
15. 4. 1974	fresh	0	4	4	1	2	2	0
	9 months	26	33	71	55	69	84	19
5. 5. 1977	fresh	0	4	4	1	1	1	0
15. 6. 1975	fresh	–	–	50	–	–	68	–
	$^1/_2$ month	–	–	0	–	–	0	–

– = data not available

Table 4. Results of the comprehensive germination scheme for seeds of two populations of *Stellaria media* grown at 20° C (– = data not available; * = no further test carried out)

Population	Age of seeds	Cumulative germination %			% dormant after cycle	Cumulative germination %			% dormant after cycle
		temperature cycle				temperature cycle			
		cold	warm	cold		warm	cold	warm	
W1	fresh	75	86	98	2	79	100	*	0
	1 month	61	100	*	0	71	100	*	0
	2 months	37	41	100	0	88	100	*	0
	3 months	24	26	100	0	86	100	*	0
	4 months	53	60	100	0	83	92	*	–
	5 months	70	76	98	2	90	100	*	0
W2	fresh	9	70	80	20	31	55	57	43
	$^1/_2$ month	7	44	81	19	37	71	75	25
	1 month	13	–	–	–	62	85	91	9
	2 months	56	92	97	3	48	81	85	15
	5 months	19	67	74	26	54	64	69	31

The second cycle (warm-cold-warm) shows an even greater difference in germination behavior between the two populations. After the first phase, warm pre-treatment, almost all seeds of population W1 germinate. There is also a considerable increase in the germination of seeds of population W2 (10–40%), but after the next phase of the cycle only a minor increase is noticed. The net result, after completing the cycle, is that no seeds of population W1, but a considerable number (up to 43%) of population W2, stay dormant. When viewed as a whole, Table 4 suggests that the germination of population W1

Table 5. Results of the comprehensive germination scheme for seeds of two populations of *Stellaria media* grown at 7° C

Population	Age of seeds	Cumulative germination %			% dormant after cycle	Cumulative germination %			% dormant after cycle
		Temperature cycle				Temperature cycle			
		cold	warm	cold		warm	cold	warm	
W1	fresh	0	6	49	51	0	2	80	20
	$^1/_2$ month	0	0	–	–	0	38	–	–
	1 month	0	0	57	43	0	51	–	–
	2 months	0	0	93	7	0	61	–	–
	3 months	2	21	100	0	6	85	–	–
W2	fresh	2	3	50	50	1	36	43	57
	1 month	4	5	26	74	1	34	35	65
	2 months	14	17	32	68	6	39	–	–

– = data not available

depends largely on the kind of pre-treatment. For population W2, the ageing of the seeds in the course of the cycles in combination with changes in temperature seems to be most relevant. For population W2 the first phase of both cycles is most important, for population W1 it is the change from warm to cold conditions – the warm pre-treatment.

Similar conclusions may be drawn for seeds produced at low temperatures (Table 5). Up to two months old, seeds of both populations show little or no reaction to cold pre-treatment. The germination of three month old seeds of population W1 does increase to some extent. Fresh seeds of population W1 show a great increase in germination after the second phase of the warm-cold-warm cycle. However, more data of a similar kind are not available and no definitive conclusion can be drawn.

Warm pre-treatment clearly increases germination: 40–90% in the case of population W1 and 15–50% in the case of population W2. In contrast to seeds formed at high temperatures, the germination behavior of population W2 exhibits a distinct dependency on warm pre-treatment. Although the data are not complete, the trend seems to be that relatively few seeds of population W1 stay dormant after completing the temperature cycles, whereas in population W2 at least 50% of the seeds stay dormant.

Phenotypically Determined Germination Behavior. When the germination behavior of population W1 is compared with the temperature at which the seeds were formed (Tables 4 and 5), it may be concluded tentatively that the great differences which exist between young seeds decrease a little with ageing. This is especially true for the fraction which stays dormant. Seeds of population W2 produced at low temperatures show on average twice to three times as much dormancy as seeds produced at 20° C. In both cycles, there is no clear tendency of decreasing dormancy with age.

Table 6. Results of the comprehensive germination scheme for seeds of natural stands of *Stellaria media* collected at various times of the year

Date of collection	Age of seeds	Cumulative germination % Temperature cycle			% dormant after cycle	Cumulative germination % Temperature cycle			% dormant after cycle
		cold	warm	cold		warm	cold	warm	
27.10.1975	fresh	1	5	48	52	2	58	64	36
	1 month	2	3	54	46	1	29	51	49
	3 months	17	24	–	–	5	37	–	–
17.11.1975	1 month	2	3	22	78	0	23	27	73
15.12.1975	fresh	4	5	25	75	0	12	14	86
15. 4.1974	fresh	0	0	–	–	2	3	–	–
	9 months	52	88	–	–	65	70	–	–
5. 5.1977	fresh	4	7	14	86	1	21	27	73

– = data not available

Germination of Seeds Collected in the Field. In Table 6, data for seeds collected in autumn, winter, and spring have been summarized. No data are available on seeds collected in summer. The high percentage of dormant seeds at the end of the tests is in general accordance with the findings of Table 5. The October and April data show a reasonable resemblance to the data from population W1. The other data generally show a greater likeness to those from population W2.

4. Discussion and Conclusions

4.1. On the Procedure for Germination Experiments

The two methods used in this investigation yield different information. The first, more conventional, method may be used to study changes in germination properties during ageing when seeds are stored dry. This method has already proved sufficient to show the remarkable population differentiation, with regard to germination in *S. media* present in the study area. By using the "comprehensive" germination scheme, which forms a novel approach, new information is obtained, viz. the properties of fully hydrated seeds, in relation to seasonal changes in temperature. In the field, seeds will be in hydrated condition for most of the time, even in summer, thanks to the almost daily falling of dew. The data thus obtained lend themselves well to the interpretation of the life cycle of the populations and deepen the insight into population dynamics. Also, such data are of high predictive value and are to be preferred to the more conventionally gathered data for use in simulation and modelling studies (e.g. Janssen, 1974).

4.2. On the Germination of *Stellaria media* Seeds

As stated in our introduction, there is no common opinion to be found in the literature with regard to the germination ecology of *S. media*. Kolk (1962) and others have reviewed most of the available data.

The reason for the differences in opinion may arise from differences in experimental methods, such as the range of temperatures used, and from the diversity of seed material used (age, place of origin). The most striking illustration of this is provided by Peterson (1936) who cultivated *S. media* plants from different geographical regions of Europe and North Africa. Although grown under the same conditions, percentages of germination varied between 0% and 96%, and Peterson related these results to the macroclimatic conditions of the original localities of the plants. However, almost the same variation was found between strains originating from four sites within one Swedish province. Peterson does not comment upon this, but it certainly strengthens the argument of Salisbury (1974) that genetically distinct populations of *S. media* may exist locally due to the high intrinsic variability of this species. The findings presented in this paper offer further support for this view.

In most of the investigations cited, seeds harvested in late spring showed low germination. This is in accordance with the data in this paper. The summer generation seems to have been little investigated. Lyre (1957) and Roberts and Lockett (1975) found only small differences between summer and autumn seeds. Salisbury (1974), however, mentions high germination percentages in summer (80%) and low ones in winter (25%).

The positive correlation between the duration of dry storage and the decrease in dormancy of seeds is generally accepted and is confirmed by most of the data from Fig. 1 and Table 2. According to Lang (1965), dormancy can only be measured over a broad range of temperatures and not at one so-called optimum temperature (Lyre, 1957). The evidence of Fig. 1 and Table 2 essentially confirms this view. Both populations possess a broad optimum range only if the seeds are old enough. This range may well differ according to the age of the seeds (see also Fig. 1). In cases where dormancy may be broken by scarifying the testa, this may form the best method to determine the optimum temperature range for germination.

There have been only a few systematically planned investigations into the germination properties of hydrated seeds. Wareing et al (1973) and Roberts (1973) acknowledge the importance of chilling to the subsequent process of germination. The usual effect is a big increase in germination, in the case of *S. media* observed inter alia by Kanipe (1939), Kolk (1947) and Lyre (1957). In the present investigation, the effect of cold pre-treatment was only substantial in the case of seeds produced under warm conditions (Tables 4, 5 and 6). Warm pre-treatment increased germination considerably in all cases, and most dramatically for seeds produced in the cold. Kanipe (1939) and Baskin and Baskin (1976), also found that germination was stimulated by warm pre-treatment.

The dormancy figures resulting from the comprehensive germination scheme (Tables 4 and 5) are quite different from those of dry-stored seeds (Fig. 1

and Table 2). In the latter case, dormancy gradually decreases, while in the former, differentiation between the two populations seems to occur. Population W1 shows very little dormancy, generally speaking, whereas in population W2 there is considerable dormancy in all cases. Possibly, this difference may be explained by differences in physiological dormancy mechanisms between the two populations.

4.3. On the Environmental Conditions at the Time of Seed Production

Plants were grown under conditions of neutral daylength and equal light intensities, in order to avoid any influence of the light regime of the mother plant on the seeds produced (see review by Gutterman, 1973). However, the data from naturally grown plants show a close resemblance to those obtained from plants grown under experimental conditions. It may be concluded that the differential response is attributable to differences in temperature during cultivation (Fig. 1, Tables 2 and 3).

Harrington and Thompson (1952) and Von Abrams and Hand (1956), respectively with *Lactuca sativa* and *Rosa* hybrids, point to the apparent correlation between the percentage of germination and the ambient temperature 10–30 days before seed harvest. Experimental research by Koller (1962) on *Lactuca* and by Grant Lipp and Ballard (1963) on *Anagallis arvensis* subsp. *foemina* proved that high temperatures during seed formation stimulated the germination of these seeds. Datta et al. (1972) showed that in *Aegilops ovata* not only the parental environment played a role in the germination of seeds, but also the grand-parental environment. The results of the present investigation are in general agreement with the conclusions mentioned above, although each of the two population is influenced to a different extent.

Only few data have been reported on this phenomenon with respect to *S. media*. Apart from the single observation by Salisbury (1974), only the investigations by Duer and Watanabe and Hirokawa (l.c. Roberts and Lockett, 1975) are known. Yet, *S. media* is generally regarded as a species which may grow in all seasons (e.g. as an agricultural weed), at least in moderate climates. Thus *S. media* seems ideally suited for fundamental research into the relationship between the environment of the mother plant and the subsequent germination of seeds.

4.4. On Population Differentiation

Intraspecific differentiation forms a well documented phenomenon and has been related to natural selection. This is well known of apomictic species (e.g. Taraxacum) and plants with autogamous reproduction, including many annual species, such as *S. media* (see also Harper, 1977).

In the case of *S. media*, geographical and edaphic ecotypes have been shown to exist with regard to germination and other properties (Salisbury, 1974; Peterson, 1936). The population differentiation as substantiated in this paper (see Table 1) is all the more striking because the plants grow side by side and are literally tangling. By growing rather large numbers of plants individually from seed, these populations could easily be distinguished. It seems a reasonable assumption that further such cases will be detected if more attention is paid to individual plants.

4.5. On Population Dynamics

Germination properties have been used by various authors to explain the occurrence of annual species in certain habitats (Hâjkovâ and Krekule, 1972; Lauer, 1953; Baskin and Baskin, 1971, 1976, 1977; Ratcliffe, 1961). To what extent population differentiation plays a role in determining the occurrence of *S. media* in the study area will be discussed in detail below.

The outcome is presented diagrammatically in Fig. 2, and is based primarily on data from the Tables 1, 4, 5, and 6, together with phenological observations in the field. The diagram forms a qualitative approach to the elucidation of possible population dynamic processes, rather than a numerical elaboration. Therefore, percentages of germination and dormancy have been used throughout, and the scheme refers to one year only.

The course of development of population W1 is represented in the upper part of Fig. 2. Throughout the first winter – the starting point of the scheme – and early spring, only dormant seeds are produced (Tables 5 and 6). With the increase of temperature in spring the life-cycle is completed rather quickly (Table 1). Winter seeds stay dormant for some time. Only when the temperature rises considerably in the beginning of the summer do seeds germinate; about 20% (Table 5). Within 2 to 3 weeks the newly grown plants produce seed (summer seeds) of which a large proportion, ca. 80%, may germinate immediately (Table 4). However, dormancy may be induced under dry weather conditions (Table 3). When conditions are favorable, the summer seeds will germinate, but the young plants are bound to wilt and die off because of the usual dry period in June–July. In September, with the onset of colder weather, a germination explosion will take place: almost all of the stock of summer and winter seeds will germinate (Tables 4 and 5). The net result is that hardly any dormant seeds are left in the soil. After four weeks or so the young plants start producing seeds. Thus, the population structure in the second winter seems to be identical to that of the first winter.

The course of development of population W2 is represented in the lower part of Figure 2. Flowering starts at about the turn of the year and only in the second half of the winter are seeds produced (Table 1). However, some 2% of these will germinate directly after being shed (Table 5), and, depending on competitive ability, plants are able to grow. These plants may find room in the open space created by the dying off of population W1. As dormancy decreases, some after-germination will take place in spring: ca. 10% (Table 5). The original winter plants die at the end of spring (Table 1). The newly established plants will produce seeds at the beginning of summer, about 30% of which may germinate immediately after being shed (Table 4). The summer plants will die off, like those of population W1, without being able to produce

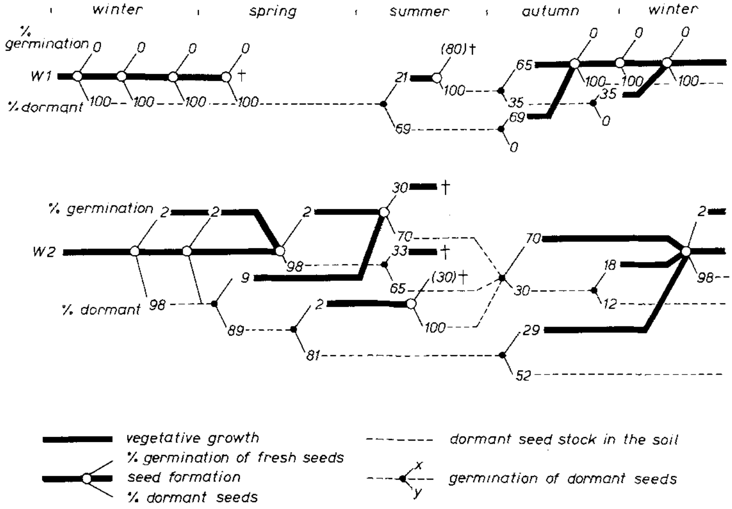

Fig. 2. Theoretical reconstruction of the course of development during one year of two populations of *Stellaria media*, based on field observations and experimental data (for explanation see text)

seeds (Table 1). In September, the majority of seeds (ca. 70%) produced in spring and summer will germinate (Table 4), together with about 30% of the seeds produced in the previous winter (Table 5). In autumn some after-germination of summer seeds will take place. Together these plants will form the new winter germination. However, in contrast to population W1, a considerable seed reserve remains ungerminated.

The population dynamics of the two populations reveal two important aspects (Fig. 2). The two populations differ in life-cycle strategy. Population W1 is able to build up a large, uniform seed reserve, which, under favorable conditions, gives rise to an explosive expansion in autumn: colonizing habit. At the end of the second winter, all seeds of this population once more are of the same phenotype. Population W2, on the other hand, is especially dependent for its expansion on seeds produced in summer. If summer production fails, fewer winter plants will develop. More important, however, is the creation of a diverse seed pool. At the end of the second winter, population W2 has built up three phenotypically different seed reserves. Firstly, there are the fresh, dormant seeds produced in the second winter; secondly, the dormant seeds produced in the previous summer and spring which have been subjected to a kind of chilling treatment in winter; and thirdly, the dormant seeds which have undergone both a warm and a cold treatment, i.e. seeds from the first winter. Extrapolating the evidence contained in this paper, one may assume different germination properties for these different seed reserves.

Thus, population W2 seems to form a more stable part of the vegetation than population W1. Indeed, in the event of unfavorable weather conditions in autumn, a large part of population W1 may be lost. Population W2, by virtue of its diverse seed stock, has a much better chance for re-establishment.

The great uniformity of germination (sensu Heydecker, 1973) adds to the risk for population W1.

The viability of buried seeds forms another important factor of survival for both populations. Data provided by Roberts (1964) and Roberts and Feast (1973) indicate that viability of *S. media* seeds decreases strongly within a couple of years. This lifespan, however, seems to be sufficient to ensure survival of the populations in our case, especially as the soil of the study area is not disturbed artificially.

Weather conditions in summer may also play an important role in the population dynamics of the two populations. Prevailing climatic conditions lead to the scheme elaborated in Fig. 2. A wet first part of the summer will favor seed production by population W1, with its short life-cycle. A longer wet period is of importance for both populations, but will give population W2 a competitive advantage in autumn because of the long lifespan of its plants.

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