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A COMPARATIVE STUDY OF THE GERMINATION ECOLOGY OF SOME MICROSPECIES OF TARAXACUM WIGG.

P. J. VAN LOENHOUD and H. DUYTS[1]

Hugo de Vries-Laboratorium, Universiteit van Amsterdam, Plantage Middenlaan 2a, 1018 DD Amsterdam

[1]present address: Milieudienst Provinciale Waterstaat Noord-Holland, Zijlweg 245, 2015 CL Haarlem

SUMMARY

Of the large genus *Taraxacum* Wigg. about 200 agamospermous (micro-)species occur in the Netherlands. The maintenance of this opulence of taxa is presumably attributable to ecological factors. In order to obtain a better insight, experiments were carried out to determine the effect of temperature and light on the germination and the possible changes after a period of storage. Eleven micro-species were comparatively studied.

Appreciable differences between species were recorded: the optimum germination temperature varies from 10°C to 30°C; in some species the germination process is stenothermic and in other ones it is eurythermic. Also the dependance upon light for germination differs. Storage outside of the seed bank did not change the germination pattern of the various species to a great extent, nor did it change the mortality per unit of time appreciably. Within the seed bank the temperature dependence decreases whereas the light dependence increases, and the mortality appears to be related to the time of the year.

The various germination strategies seem to be adaptations to the respective habitats on the one hand (dune dandelions, for instance, only germinate at low soil temperatures), and on the other hand they seem to be correlated with inter-specific niche differentiation (e.g., when of two sympatric species the one has a germination optimum at 10°C, and the other one at 20°C).

The results of the present inquiry strongly suggest that in the Netherlands an ecological differentiation is of common occurrence among microspecies of *Taraxacum*, and apparently plays an important part in the maintenance of the taxonomic diversity within the genus.

1. INTRODUCTION

The genus *Taraxacum* Wigg. is differentiated into a large number of (micro-) species. DOLL (1977) recognised about 2000 taxa which he referred to 23 sections. This diversity is partly attributable to the systems of reproduction found in this genus. A number of species, expecially those belonging to more primitive, Central-Asiatic sections, is diploid, sexual, and self-incompatible. Many other ones, in particular those of younger and more highly evolved sections of Eurasia are polyploid and obligatorily, or sometimes facultatively, agamospermous (DOLL 1977), but they may also contain some sexually reproducing diploids (DOLL 1977, MALEČKA 1973, DEN NIJS & STERK 1980, RICHARDS 1968, 1973). As was shown by FÜRNKRANZ (1961, 1965) and by RICHARDS (1970), new agamospermous clones originate continually as the result of incidental hybridisations between di- and polyploids, both within and between sections. Whether such

hybridisations lead to the advent of novel microspecies is, as argued by KROES (1977), largely dependent on ecological factors.

In the Netherlands *Taraxacum* is represented by 5 sections together comprising 196 described species (HAGENDIJK et al. 1975, and in prep.). The most common dandelions belong to sect. *Vulgaria* (with 153 species). As far as could be ascertained all Dutch forms are polyploids and obligatorily agamospermous (VAN SOEST 1955, STERK & DEN NIJS 1978). Diploid, sexual plants never having been recorded, the formation of new microspecies by hybridisation between the present ones is most improbable, so that the Dutch dandelions must have originated elsewhere, or earlier when other circumstances prevailed. The maintenance of their specific diversity is, therefore, presumably attributable to ecological factors. Two aspects are of importance in this connection, *viz.*,

(1) dandelions belonging to different sections occur, generally speaking, in different habitats: in dunal grasslands mainly species of the sections *Erythrosperma* and *Obliqua* are found, in moist hay-fields species of the sects. *Palustria* and *Spectabilia*, and in more anthropogenously influenced vegetation especially of sect. *Vulgaria* (HAGENDIJK et al. in prep.); also within the sections a habitat differentiation is manifest; even in adjacent fields of pasture one often encounters a different dandelion flora (A. A. Sterk, oral comm.).

(2) It is of significance that at one site usually several microspecies occur sympatrically (VON HOFSTEN 1954, KAPPERT 1954, DEN NIJS & VAN DER HAMMEN 1978).

This last point is contrary to expectation because, as suggested by JANZEN (1977), at a local scale ultimately only a single apomict would survive by ousting all other ones (HARPER 1977: 753), but it is by no means unusual to find up to 20 microspecies of *Taraxacum* in the same piece of meadowland, as reported by NILSSON (1947) in Sweden, and also encountered in the Netherlands (Sterk, oral comm.).

In such a situation two alternative explanations are possible. Conceivably, such sympatrically growing dandelions differ morphologically but do not exhibit any in their common habitat relevant ecological differences, so that they are ecological equivalents and occur in ratios entirely determined by chance. Alternatively, the dandelions do indeed show ecological differences, and in this case one must suppose that these differences largely decide their relative frequencies of occurrence. The second alternative was reported for *Taraxacum* by SOLBRIG & SIMPSON (1974, 1977).

The general problem of co-existence of closely related species in the same habitat has been a moot point since Darwin's time (see *e.g.*, GRANT 1963, GRIME 1979, GRUBB 1977, HARPER et al. 1961). VAN DEN BERGH & BRAAKHEKKE (1978) distinguish spurious co-existance when species occur in a heterogeneous environment in which each of them occupies its own microhabitat and true co-existence when sharing the same homogeneous habitat. GRANT (1963) pointed out the difference between stable co-existence, *i.e.*, a situation in which several species live sympatrically in a homogeneous and permanent habitat *ad infinitum*, and unstable co-existence, i.e., situations in which the co-existence either repre-

sents nothing but a phase in the elimination of less competitive taxa, or is only maintained by immigration, incidental fluctuations in the environmental conditions, etc.

In the case of a stable, veritable co-existence one usually poses that the occurrences of diverse species are limited by different factors, and this is usually connected with the term "niche differentiation" (KROES 1977, GRUBB 1977, VAN DEN BERGH & BRAAKHEKKE 1978).

The present investigation was not aimed at an answer to the question whether co-existence of dandelions is of the spurious, true, stable, or unstable type. This would have required a long lasting, comparative demographic inquiry, which could not be accomplished in the time at disposal. The sole purpose of the study was to establish whether any ecological differentiation between microspecies of *Taraxacum* does exist at all (see ABBOTT 1979), with, on the one hand, the intention to ascertain whether morphologically different dandelions also differ ecologically – which might serve as a confirmation of the taxonomic classification of the micro-species – and, on the other, to find out whether this provides clues regarding the sympatric occurrence of several different microspecies within a single habitat, and, conversely, the differences between the dandelion floras of different habitats.

In a number of experiments a comparative study was made of the ecology of a number of microspecies partly occurring sympatrically and partly occurring allopatrically (and in different habitats). In view of a satisfactory experimental procedure and of the importance of germination in niche differentiation (see GRUBB 1977), the primary choice was a comparison of the respective germination ecologies and the possible changes during storage, the survival of the achenes during storage also being recorded.

2. MATERIALS AND METHODS

2.1. Origin and treatment of the achenes

The microspecies included in the investigation were collected from natural stands and cultivated in the experimental garden of the Hugo de Vries-Laboratorium, Amsterdam. The taxonomic identification was confirmed by the experts on the Dutch dandelion flora A. Hagendijk, Prof. Dr. Ir. J. L. van Soest, and H. Zevenbergen, whose nomenclature is followed here (HAGENDIJK et al. 1975, in prep.). Origin of these taxa and relevant ecological data are shown in *table 1*. Achenes were collected in the experimental garden during the first weeks of June, 1978.

A portion of the freshly gathered achenes was immediately (*i.e.*, on 22 June 1978) used for experiments regarding the influence of the temperature and light (see under 2.2.) on germination. The remainder of each achene gathering was divided into three lots which were stored as from 3 July 1978 in three ways, *viz.*, 1. one lot was kept dry in an exsiccator with silica gel at room temperature and in the dark, 2. a second in thin linnen bags under a shed with a transparent roof (so that they were exposed to varying light, temperature and moisture conditions);

Table 1. Origin and habitat of microspecies studied.

Species	Section	Collecting site	
T. rubicundum	Erythrosperma	Noordhollands Duinreservaat	Dune grassland
T. taeniatum	Erythrosperma	Noordhollands Duinreservaat	Dune grassland
T. obliquum	Obliqua	Noordhollands Duinreservaat	Dune grassland
T. hollandicum	Palustria	Tielerwaard	Mesotrophic hay-field (wet, clay)
T. hygrophilum	Spectabilia	Krimpenerwaard	Mesotrophic hay-field (wet, peat)
T. nordstedtii	Spectabilia	Krimpenerwaard	Mesotrophic hay-field (wet, peat)
T. calochroum	Vulgaria	Tielerwaard	Eutrophic pasture (clay)
T. ekmanii	Vulgaria	Krimpenerwaard	Eutrophic pasture (peat)
T. eudontum	Vulgaria	Krimpenerwaard	Eutrophic pasture (peat)
T. lancidens	Vulgaria	Tielerwaard	Mesotrophic hay-field (wet, clay)
T. sellandii	Vulgaria	Krimpenerwaard	Eutrophic pasture (clay)

this was only done with the species *T. hygrophilum*, *T. nordstedtii*, *T. ekmanii* and *T. eudontum*, as from other species insufficient achenes were available; 3. the third lot was made up into portions of exactly 500 achenes and mixed with c. 1 g of sterilised and sieved humic soil; these portions were subsequently packed into small bags made of nylon gauze with a mesh width of 80 μm and buried at a depth of 2–3 cm in the experimental garden. The intention was to establish whether after fruit shed any mortality and/or change in the germination ecology takes place. To this end a comparison was made between the effects of the unnatural but much practised dry storage (method 1), and the storage under simulated natural conditions either above the soil surface (method 2) or as a part of the seed bank (method 3). After 1, 5 and 8 months, respectively, the stored achenes were used for a number of experiments. Buried achenes were recovered by sieving the contents of the bags. The seemingly intact ones were counted and subsequently used.

2.2. Temperature

All experiments regarding temperature effects were carried out by placing the achenes in petri dishes on two layers of filter paper kept moist with distilled water. Dependant on the available number of achenes lots of 25 to 100 per dish were incubated and each experiment was duplicated. The dishes were kept in climatrons at temperatures of 5, 10, 20 and 30°C (all ± 1°C), respectively and illuminated for 12 hrs per day by three 20W daylight TL tubes. As a criterion for germination "radicle emergence" was chosen. The germinated achenes were counted and removed after 2, 4, 7, 14, 21 and 28 days. The same was done with decomposed ones, which were supposed to have been non-viable or da-

maged before the experiment was started and excluded from the calculations. The percentage of germinated ones at the end of the testing period often proved to be 100%; in those cases in which the germination was not 100% the process of germination was of such a nature that one might anticipate a germination percentage of 100% if the experiment had been prolonged by a few days or weeks. Only in the 30°C series in the case of the dune dandelions, and in the 5°C series in the experiments with the other species, did hardly any germination take place or none at all, so that it did not seem to be very probable that an extended germination time would have altered the results.

For the above mentioned reason a comparison of species and of temperature effects was chosen on the basis of the rapidity of germination and not of germination percentages. An easily computable and useful measure appears to be the median germination time, *i.e.*, the number of days required before 50% of the viable achenes have germinated. When this percentage was not attained within the experimental time-span, the median germination time was assessed by extrapolation from the last two analyses with a maximum estimate of 50 days. A very tardy rate of germination or lack of germination has been registered as "> 50 days". The above mentioned experiments were carried out both with freshly collected achenes and with quantities of achenes stored during 1, 5, and 8 month previously to the testing.

2.3. Light

The effect of illumination was tested by placing achenes in petri dishes on a double layer of filter paper kept moist with distilled water and incubated in a small climatron at 20 ± 1°C with a light regime of 12 hrs illumination provided by three 20W TL tubes/12 hrs darkness. For each experiment, per species two dishes with 100 achenes each were placed in the climatron as such, and two additional ones were sealed in aluminium foil before incubation. After a fortnight the percentage of germinated viable seeds was established. In illuminated dishes this percentage was about 100% in most cases and the percentage of germination in the dark was calculated by dividing the percentage in non-illuminated achenes by the mean percentage of the two illuminated ones.

The recorded differences were tested for significance per species by means of a one-way ANOVA calculated by means of SPSS, version 8.0 (NIE et al. 1975). By dividing the percentages of germination in the dark series by those of the illuminated series, a measure is obtained for the inhibiting effect of darkness in respect of the germinated in light. A percentage below 100% signifies that the achene germination of the species in question is inhibited in the dark, whereas a percentage of 100% indicates that there is no difference in the germination rates in light and in the dark, and a percentage of over 100% a higher rate in the dark. This relative percentage of "darkness germination" was used to test the differences between species for significance by means of a one-way ANOVA.

The experiments were carried out with fresh achenes of all eleven species under investigation and with achenes dry-stored and outside stored for 5 months of the species *T. hygrophilum*, *T. nordstedtii*, *T. ekmanii* and *T. eudontum*; a different

procedure was followed with achenes stored in soil for 5 months: by means of an untransparent cylindrical vessel of each species 4 bags with achenes were dug up and transferred to a dark room, after which the contents of every bag was shaken out in a petri dish and moistened, and two of the dishes were incubated as such and two after sealing in foil as described above. The number of seedlings in each dish was counted after an incubation period of two weeks.

2.4. Survival after storage

In the germination experiments concerning temperature effects also the number of decayed achenes was recorded, so that the percentage of viable seeds could be established. This was done with both fresh and variously aged dry and outside stored lots of achenes (8 petri dishes per species per analysis thus being available); the storage time had been 1, 5 and 8 months per species. Additional analyses with achene samples stored outside for 2 and for 3 months, respectively, were carried out (2 petri dishes per species per analysis at 20°C); of buried bags with achenes per species one was dug up after 1, 2, 3, 4, 5, 8 and 11 months, respectively; in this case the percentage of surviving achenes was calculated by dividing the number of recovered living ones by the original number in the bags (in this case: 500).

3. RESULTS

3.1. Temperature

The effect of the temperature on the germination percentage of fresh achenes is shown in *fig. 1*. The median germination time (MGT) appears to be useful to visualise differences in the rapidity of germination: a low value is indicative of a short germination time, and a high value of a slower rate of germination. There are manifest differences in germination strategy between the species studied: most species germinate fastest at 20°C, but *T. hygrophilum* and *T. calochroum* germinate a somewhat more rapidly at 30°C than they do at 20°C, and *T. rubicundum* does so at 10°C. *T. rubicundum* and *T. obliquum* do not, or hardly, germinate at 30°C, *T. nordstedtii*, *T. calochroum*, *T. eudontum*, *T. lancidens* and *T. sellandii* not, or hardly, at 5°C. *T. ekmanii* does not exhibit an appreciable difference in germination time at its optimum temperature (of 20°C) and the other temperatures tested.

Fig. 2 shows the changes in the MGT at the temperatures tested of the various species after a dry storage of the achenes during certain periods of time. Generally speaking, the germination pattern of all species hardly changes. A number of species, *T. rubicundum*, *T. taeniatum*, *T. obliquum*, *T. hollandicum*, *T. nordstedtii* and *T. calochroum* in particular exhibit a slight acceleration at 10°C after dry storage for some time. The only appreciable changes are found in *T. rubicundum* (at 20°C) and *T. obliquum* (at 30°C): in these species dry-stored achenes germinate at a markedly faster rate than do fresh ones.

Fig. 3 shows changes in MGTs after outside storage. Also in this series of experiments there are no clear indications of changes in the MGTs. Only the

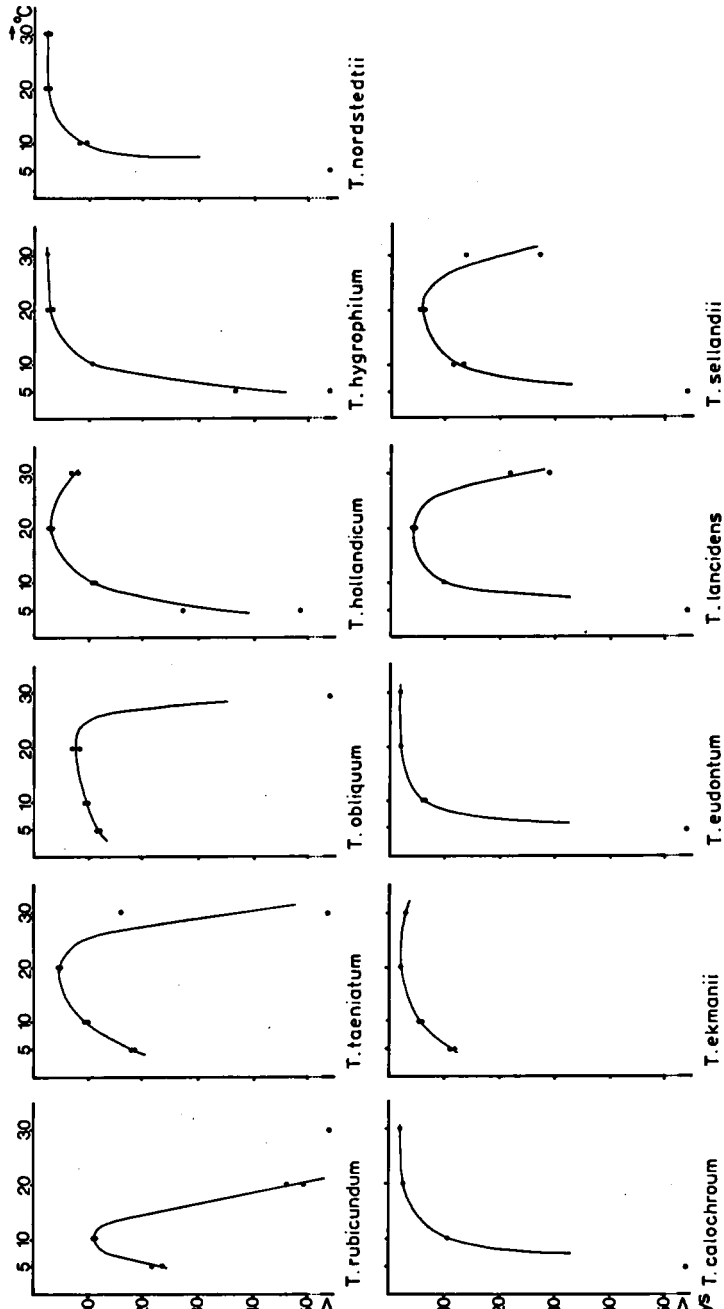

Fig. 1. Relation between temperature in °C and Median Germination Time in days.
N.B. Each symbol in *figs. 1–4* represents the value obtained from a single – or, in the case of coinciding duplicates, two – petri dish(es) with 25–100 achenes each. The curves drawn through the points are personal interpretations not based on calculation.

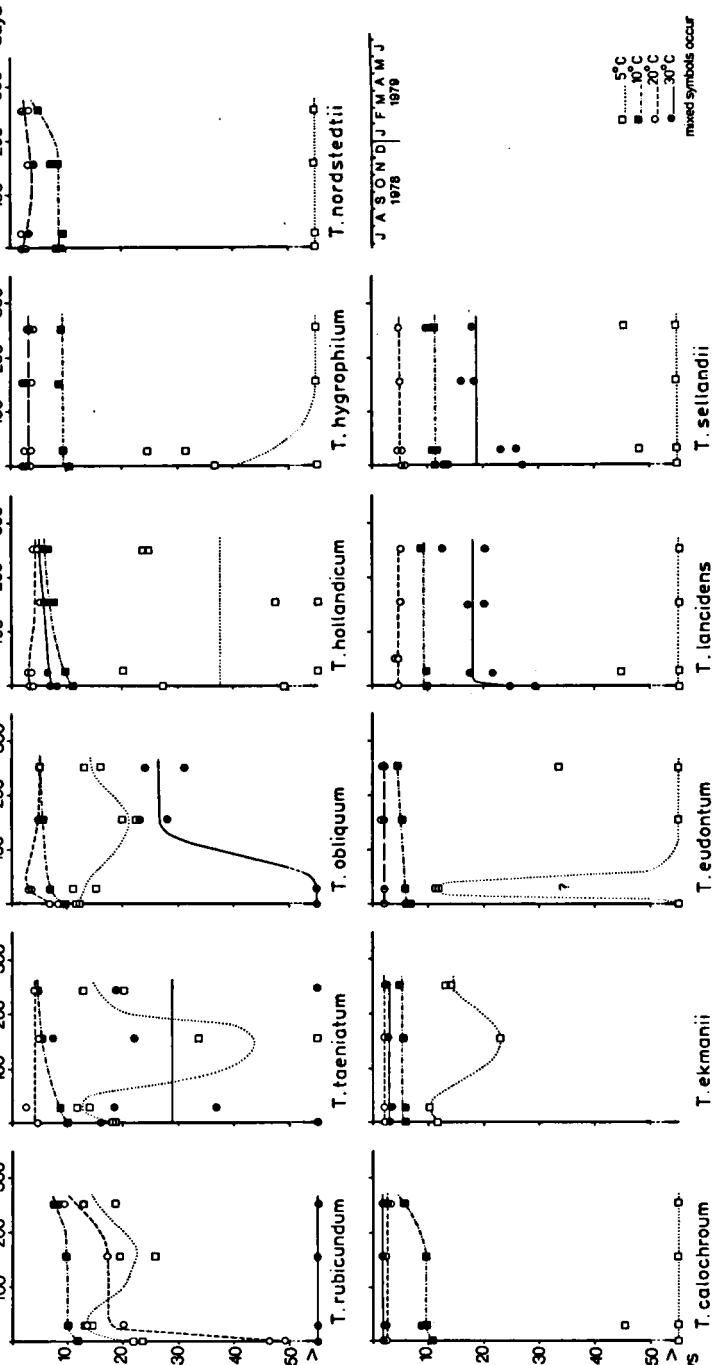

Fig. 2. Changes in MGTs at various temperatures in days in the course of time after dry storage (t = 0: fresh achenes). See also note under *fig. 1.*

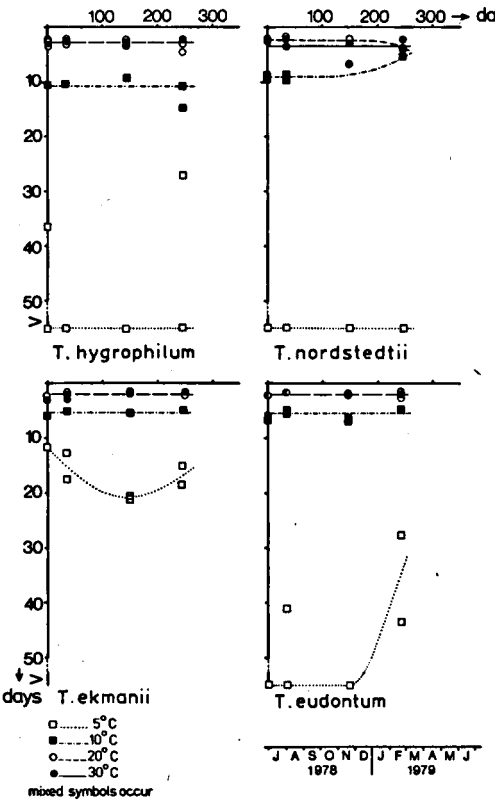

Fig. 3. Changes in MGTs at various temperatures in days in the course of time after outside storage (t = o: fresh achenes). See also note under *fig. 1.*

behaviour of *T. ekmanii* and *T. eudontum* at 5 °C is subject to alteration, the most striking phenomenon is that achenes of *T. eudontum* after outdoor storage for eight months can germinate (albeit at a very slow rate) at 5 °C, which they did not, or hardly, do so before.

After soil storage (*fig. 4*) manifest changes occur, however. After the cold season (eight months of storage time) germination of all species is accelerated at all temperatures as compared to the germination time of fresh achenes, and the differences in MGT between the temperatures tested are clearly smaller. It is, furthermore, striking that the various taxa react in different ways: the inhibiting action of an incubation temperature of 30 °C in germination. for instance, is immediately undone by soil burial in *T. taeniatum*, but not in *T. rubicundum* and *T. obliquum*. The soil storage induces a germination inhibition at 10 °C in *T. nordstedtii* and *T. calochroum*, but this was not noted in other species.

3.2. Effect of illumination

Table 2a shows the mean percentages of "darkness germination" of the various species and demonstrates an inhibiting effect of darkness in all taxa investigated. The one-way ANOVA indicates a significant diffference between the germi-

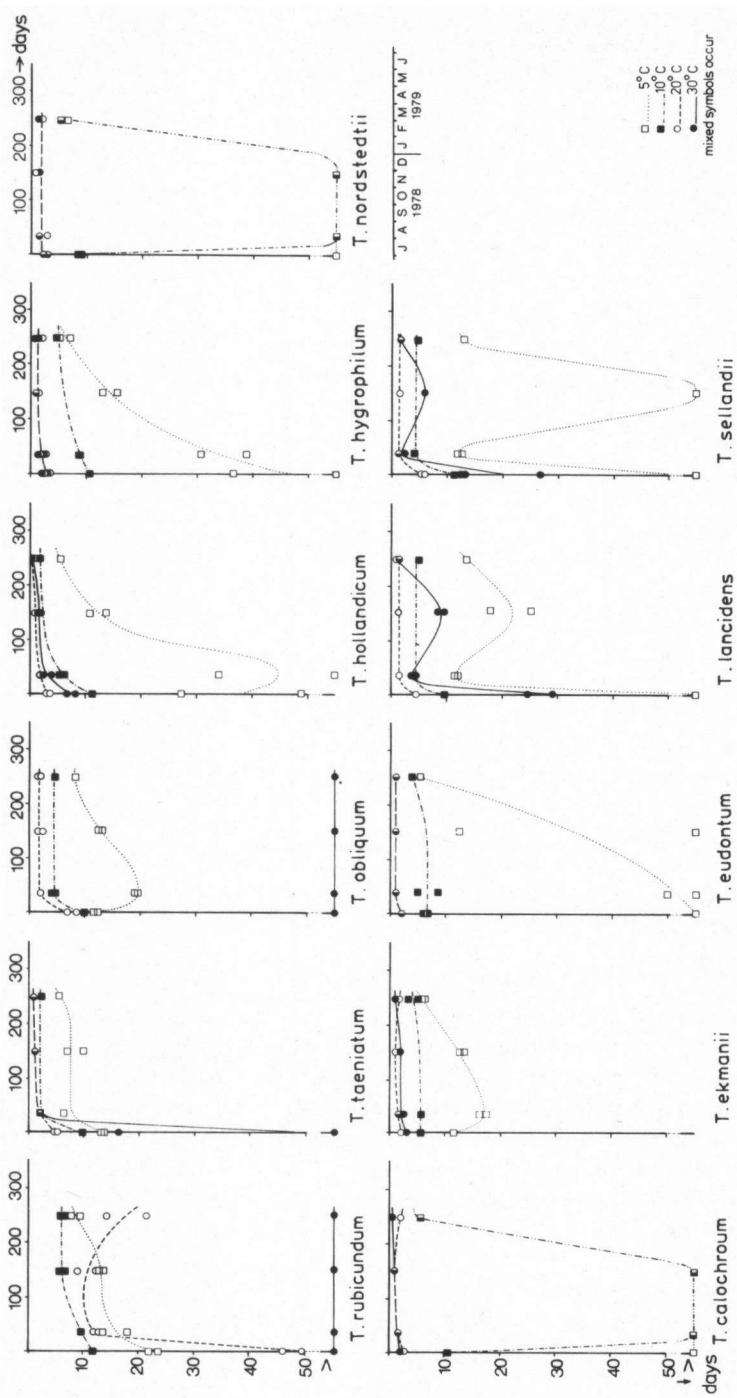

Fig. 4. Changes in MGTs at various temperatures in days in the course of time after starage in garden soil (t = o: fresh achenes). See also note under *fig. 1*.

Table 2.
a. Mean germination percentages in light and in the dark under otherwise equal conditions; significance of the differences (as one-way Anova), and calculated mean percentage of "darkness germination" (see text).

Species	Germination (%) light	dark	Significance	"Darkness germination" (%)
T. rubicundum	21.8	0.0	$p < 0.01$	0.0
T. taeniatum	97.9	56.4	n.s.	57.7
T. obliquum	99.0	11.4	$p < 0.001$	11.5
T. hollandicum	98.1	37.5	$p < 0.001$	38.3
T. hygrophillum	96.7	29.4	$p < 0.05$	30.4
T. nordstedtii	93.2	5.7	$p < 0.01$	6.1
T. calochroum	99.5	91.7	n.s.	92.2
T. ekmanii	100.0	76.3	$p < 0.01$	76.3
T. eudontum	100.0	97.9	n.s.	97.9
T. lancidens	95.2	51.5	$p < 0.05$	54.1
T. sellandii	76.3	19.5	$p < 0.05$	25.5

b. One-way Anova of differences in percentages of "darkness germination" between species tested.

Source of Variation	d.f.	S.S.	M.S.	F ratio	Significance
Between species	10	23,078	2307.8	30.44	$p < 0.001$
Within species	11	834	75.8		
Total	21	23,912			

nation rates in light and in the dark, in most species; in *T. taeniatum*, *T. calochroum* and *T. eudontum* this could not be established. The percentages in question differ from species to species: the germination of achenes of *T. rubicundum*, for instance, is completely inhibited in the dark, whereas in *T. eudontum* there is only a small difference between the germination rates in light and those in the dark. A oneway ANOVA of these percentages indicates that, at least partly, these differences between species are significant (*table 2b*).

Possible changes in the light requirements for germination have only been studied in four species stored for 5 months (*table 3*). Although the two-way ANOVA (NIE et al. 1975) of these data shows that not all species react in the same way, as can be deduced from the significance of the interaction term in the ANOVA (see *table 3b*), in *table 3a* a number of corresponding changes can be observed. After dry indoor storage, but particularly after outside storage the rate of inhibition of germination by darkness decreases, except in *T. eudontum*, in which species also the germination of freshly harvested achenes is hardly inhibited. After a soil burial period of five months all species exhibit a much stronger inhibition than when fresh achenes are tested, however. This is especially manifest in the *Spectabilia T. hygrophilum* and *T. nordstedtii* which

Table 3.
a. Changes in mean percentages of "darkness germination" after 5 months storage of four species of *Taraxacum*.

Species	fresh	dry	Stored for 5 months: outside	in soil
T. hygrophilum	30.4	62.1	97.5	1.7
T. nordstedtii	6.1	12.9	68.2	0.6
T. ekmanii	76.3	83.7	98.1	50.6
T. eudontum	97.9	89.6	95.2	76.2

b. Two-way Anova of 3a.

Source of variation	d.f.	S.S.	M.S.	F ratio	Significance
Main effects					
Species	3	22,174	7,391	107.2	$p < 0.001$
Storage	3	13,679	4,560	66.1	$p < 0.001$
2-way interaction	9	5,332	592	8.6	$p < 0.001$
Residual	16	1,103	69		
Total	31	42,288			

hardly show any germination in the dark. How the inhibition changes after longer periods of storage could unfortunately not be ascertained owing to lack of time and insufficient quantities of achenes.

3.3. Survival after storage

Since the number of all non-viable (decayed) achenes per petri dish was always recorded, the percentage of viable achenes in fresh lots and in stored samples could easily be computed. There are no indications of the effect of any experimental conditions (especially of the temperature) on the viability of the achenes. The percentage of viable achenes in fresh lots ranges from 78% to 93%; these percentages differ significantly within the group of microspecies tested, see *table 4*.

In order to assess the mortality during storage of all taxa and after all forms of storage the logaritm of the recorded percentage of viable achenes was plotted against the storage time. After dry (indoor) storage any relation – if present – appeared to be linear, so that regression lines through the points of observations could be computed. Only the regression lines of *T. obliquum* and *T. hollandicum* proved to be significant (see *table 5a*); the mortality in these species averages 0.01% and 0.03% respectively per day, which corresponds with half-time values of 5.5 and 2.8 years, respectively. In all other species no statistically significant mortality after dry storage could be demonstrated. Also in achenes stored outside the relation between the logarithm of the percentage and the time proved to be a linear one. For all four species included in the experiment the regression was significant (see *table 5b*). The mortality was high in especially *T. hygro-*

Table 4.
a. Mean percentage of viable achenes immediately after harvesting.

Species	Viability (%)
T. rubicundum	88.6
T. taeniatum	94.7
T. obliquum	90.2
T. hollandicum	78.6
T. hygrophilum	81.8
T. nordstedtii	90.1
T. calochroum	91.4
T. ekmanii	91.5
T. eudontum	93.1
T. lancidens	85.3
T. sellandii	89.2

b. One-way Anova of the differences in the 4a percentages between species tested.

Source of variation	d.f.	S.S.	M.S.	F ratio	Significance
Between species	10	0.172	0.017	20.33	$p < 0.001$
Within species	413	0.350	0.001		
Total	423	0.522			

Table 5. Regression analysis of the relation between the logarithm of the percentage of viable achenes and the time in days, and the half-time values calculated from it.

Species	Regression coeff. (per day)	Significance	Half-life
a. After dry (indoor) storage: 4 analysis dates, 48 recordings.			
T. rubicundum	0.0000	n.s.	–
T. taeniatum	0.0000	n.s.	–
T. obliquum	–0.0001	$p < 0.05$	5.5 yr
T. hollandicum	–0.0003	$p < 0.05$	2.8 yr
T. hygrophilum	0.0000	n.s.	–
T. nordstedtii	0.0000	n.s.	–
T. calochroum	–0.0001	n.s.	–
T. ekmanii	0.0000	n.s.	–
T. eudontum	0.0000	n.s.	–
T. lancidens	0.0001	n.s.	–
T. sellandii	0.0000	n.s.	–
b. After storage outside: 6 analysis dates, 54 recordings.			
T. hygrophilum	–0.0019	$p < 0.001$	155 days
T. nordstedtii	–0.0002	$p < 0.001$	3.4 yr
T. ekmanii	–0.0005	$p < 0.001$	1.6 yr
T. eudontum	–0.0003	$p < 0.05$	2.7 yr

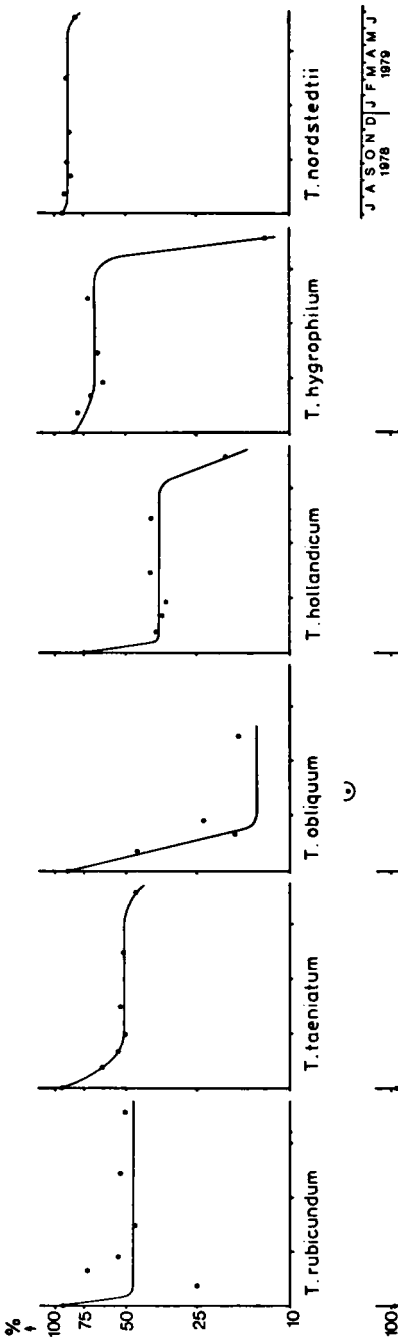

Fig. 5. Relation between percentage of achenes surviving after soil storage (log scale) and time in days. Each point represents the value obtained from one bag containing 500 achenes. Curves drawn through these points are personal interpretations.

philum, viz., 0.19% per day, corresponding with a half time of survival of 155 days.

The situation is altogether different in samples stored in soil, because no such linear relation between the logarithms of percentages and the time was found, so that no regression lines and half-time values could be computed. The course of the changes of survival numbers in soil-stored lots is shown in the diagrams of *fig. 5*. By and large the course of the curves is rather consistent throughout: immediately after having been buried, the samples show a decrease in the percentage of surviving achenes until a certain level is attained, and from that time onward this percentage remains practically constant during the following cold season and the spring, after which period in some species the percentage may start decreasing again during the next summer. The levelling off of the percentages after burial varies appreciably, however: from 86.9% of surviving achenes in *T. nordstedtii* to 22.0% in *T. eudontum*, whilst the data of *T. obliquum* are rather inconsistent: it seems as if this species is hardly capable of surviving in the form of a seed bank. The decrease during the following summer is not very evident in such species as *T. rubicundum* and *T. ekmanii*, but manifest in other ones such as *T. hygrophilum* in which the percentage fell off suddenly from 67.3% to 10.2%.

It must be borne in mind, however, that – in contrast to the other samples stored differently – the decrease in number of viable seeds recovered from buried samples is not only attributable to mortality but also to subterranean germination. The experimental procedure does not distinguish between these two causes because seedlings quickly decay underground: the germinated achenes were scored as "non-viable" ones; presumably the incidence of subterranean germination is an important factor, since in the samples of all species studied, especially in the first lots dug up after burial and again in samples dug up in the following spring and summer, regularly living seedlings were encountered. Also in other published reports (for references, see COOK 1980) the great importance of seed losses by subterranean germination from the seed bank has been emphasized.

4. DISCUSSION

4.1. Differentiation in germination ecology

One of the more prominent results of the present investigation is the manifest differentiation between the micro-species studied. Not two of these taxa behaved in an identical fashion. *T. nordstedtii*, *T. calochroum* and *T. eudontum*, for instance, are rather similar as regards the effect of the temperature on the germination of newly collected achenes (*fig. 1*), but *T. nordstedtii* differs from the other two in the effect of light (*table 2*), and *T. eudontum* distinguishes itself by the behaviour of the achenes after soil burial (*fig. 4*); all three species differ in their rates of survival of achenes in the seed bank (*fig. 5*). The greatest resemblance in germination ecology appears to exist between *T. lancidens* and *T. sellandii*, which differ, however, markedly in their morphology and habitat (*table*

1). There are no consistent differences between the various sections studied. The species belonging to the sections *Erythrosperma* and *Obliqua* differ from the other ones in that their achenes can germinate at somewhat lower temperatures, but it remains to be seen if one may generalise such findings after a study of so few species. It is clear, however, that even closely affined taxa may exhibit appreciable differences, as is evident from the variation within the section *Vulgaria* (the lowermost 5 species in the *figs. 1, 4, 5* and in *table 2a*).

These results render it quite clear that publication of ecological data relating to dandelions is of very limited significance unless one states quite clearly which microspecies was (were) included in the investigation. MEZYNSKI & COLE (1974), for instance, reported that "seeds" of "*Taraxacum officinale Weber*" (presumably species of the section *Vulgaria*) show an optimum germination at temperatures alternatingly changing from 20°C (for 16 hrs.) to 10°C (during eight hrs.); they were astonished as regards the great discrepancies between their findings and data from the older literature, and attempted an explanation by means of a "post-harvest dormancy" and "shifts in temperature specificity", but it is more than likely that different microspecies were involved. In other (unpublished) experiments, the present authors did not find any stimulation of the germination by changing temperatures, for that matter; however, one cannot preclude the possibility that the plants studied by the above-cited workers belonged to microspecies which do indeed exhibit this peculiarity.

4.2. Adaptations to the habitat

Before an attempt can be made to relate the recorded data to the natural habitats of the respective microspecies studied, one has to ascertain whether the MGT established and used in our present report has indeed some ecological relevance. Germination experiments yield a number of different results which may well have a certain ecological significance, such as the duration of the "lag"phase between the time of sowing and the acual beginning of germination, the rapidity of progress of subsequent germination, the ultimate percentage of successful germinations, and the time required to attain that maximum percentage. In our opinion the progression of the germination rate is a more cogent measure than the ultimate percentage recorded, considering for instance that Ross and Harper (ROSS 1968, ROSS & HARPER 1972, see also HARPER 1977: ch. 6) have shown that early germinated seeds produce seedlings which capture an indisproportionally large share of the available environmental resources, compared to seedlings germinated later. On the other hand, in unstable environments also a tardy and in time extended germination may have selective advantages in connection with a spreading of risks and hazards acting against incidental destruction of a whole cohort of seedlings.

As pointed out already in section 2.2., in our experiments we decided to compare species and temperatures on the basis of the rapidity of germination recorded as the MGT. Although this is an arbitrary measure, and we are well aware of the possibility of one choosing and studying other parameters, we are of the opinion that the germination patterns of dandelions can be satisfactorily

characterised this way. Since the ecological relevance of small differences in MGT is not quite clear, we took into account especially the more manifest differences in the ecological interpretation of our experimental findings. The ensuing deductions are, therefore, in our opinion indeed of ecological significance. In the following paragraphs an attempt is made to compare the experimentally recorded particulars of the germination ecology of the species studied with the germination strategy in their natural habitats.

Most of the microspecies of *Taraxacum* can only be identified by specialists, and only when they are flowering. This is the principal reason why the habitat of each individual microspecies is only superficially known, so that attempts to relate the recorded data concerning the germination ecology can only give an overall picture of the situation. The Dutch dandelions occur mainly in grassland, those belonging to the sections *Erythrosperma* and *Obliqua* especially in dunal grass vegetation, those of the sections *Palustria* and *Spectabilia* in mesotrophic, moist hayfields, and those belonging to the section *Vulgaria* in eutrophic pastures and other anthropogenous types of grassy vegetation (HAGENDIJK et al. 1975), Their principal flowering period falls in May and achene shedding follows in June. In the dunes most of the achenes germinate during October, and in the other habitats in August. The recorded germination particulars give some insight into the differences in principal germination time. In the summer the arid dune habitat is not favourable for the settlement of seedlings but moister, i.e., for germination more clement, conditions prevail in the autumn, and the life cycle of many dune plants is adapted accordingly (PEMADASA & LOVELL 1974). Germination during brief periods of rainy weather in the summer would be too hazardous. The germination of the three dune dandelions included in our investigation, *T. rubicundum*, *T. taeniatum* and *T. obliquum*, appears to be strongly inhibited by temperatures above 20°C (*fig. 1*). When the temperature tends to become lower, in September and October, germination may take place and – owing to the still relatively fast rate of germination at 5°C – continues till late in the autumn. The other taxa, all from much wetter grasslands, exhibit exactly the opposite strategy: their achenes are capable of germinating at temperatures as high as 30°C, so that summer germination occurs as soon as the local conditions permit, *i.e.*, after hay-making, because before the grass is moved germination is inhibited by lack of light (see 3.2), or perhaps on account of a change in the specific wave-length distribution of the light (through the filtering action of the stand of vegetation before it is mowed), as was demonstrated for a great many grassland species (GRIME 1979: 92–95). In the autumn the grasslands are often very wet, which is very unfavourable for the establishment of seedlings (by an oxygen deficiency in the soil, among other things): germination does not take place, because the germination of all dandelions studied (*T. ekmanii* excepted) appears to be strongly inhibited when the temperature is below 10°C (*fig. 1*). More detailed examples of the adaptive nature of the germination ecology require more exhaustive studies.

4.3. Ecological differentiation within a single habitat

It is evident from the preceding subchapter that on account of differences in their germination ecology, germination is prevented in seasonal periods when the physical factors are unfavourable for local settlement. Biotic conditions may also hamper the establishment of seedlings, however. An example is the presence of a dense vegetation cover before mowing, mentioned above: growth is inhibited through a too limited supply of light (see 3.2) and germination only commences after the hay-making season. Another unfavourable environmental bio-factor interfering with a successful settlement might be the presence of competing seedlings of other microspecies of dandelion. Differences in the germination strategy may prevent such situations, since, as GRUBB (1977) says: "very many of the differences between species are effective in ensuring that their seeds germinate in sites that differ in time and space". In this way a form of niche differentiation between the various microspecies is brought about, which enables their cohabitation. Relevant indications are also provided by our data: the most rapidly proceeding germination was found at 20°C in *T. taeniatum*, and at 10°C in the affined and sympatrical *T. rubicundum* (*fig. 1*). This means that the former can germinate earlier in the autumn than the latter and/or in warmer micro-habitats within their environments. A second example is found in the related and sympatrical *T. hygrophilum* and *T. nordstedtii*: the germination pattern of their fresh achenes is very similar (*fig. 1* and *table 2a*), but when they become covered by soil there are manifest differences (*fig. 4*), because the inhibition of germination at lower temperatures of achenes of *T. hygrophilum* soon diminishes, whereas in the other species an inhibition at 10°C is induced, so that buried seeds of *T. hygrophilum* coming to the surface in the autumn after having been buried in the soil (*e.g.*, in mole hills) are able to germinate, whereas those of *T. nordstedtii* cannot do so. These examples may demonstrate that differences in germination strategies offer several possibilities of niche differentiation.

4.4. Germination patterns

Although it is clear that there are appreciable ecological differences between microspecies of *Taraxacum*, a recording of similarities may also be worthwhile, because in this way one may arrive at a more general cognisance of the germination patterns of dandelions as a part of their life cycles. In the Netherlands, the majority of the achenes of dandelions are shed at the beginning of June. Although they appear to be completely capable of immediate germination under laboratory conditions and there is obviously no "innate dormancy" (HARPER 1977: 65), they do not usually germinate at once in nature on account of aridity, high temperatures (in the dunes) and/or lack of light (in dense stands of vegetation) and are in a state of "enforced dormancy" (HARPER 1977). As long as they stay above the soil surface (*e.g.*, among the hay or the stubble) some mortality occurs which is higher according as the conditions are moister and/or more variable (as can be deduced from the fact that the mortality is higher during outdoor storage than during dry indoor storage, cf. *table 5*; compare ROBERTS

1960, see also ROBERTS 1972), but the germination pattern does not change much (*figs. 2, 3*) although the light requirement for germination seems to decrease (*table 3a*). When the environmental conditions subsequently turn more favourable, (often mass) germination starts which is "controlled" by the specific germination ecology of the microspecies involved.

Of the achenes which get buried in the soil and become water-imbibed a certain (and in different species different) percentage germinates at once (see 3.3). The remainder forms an addition to the seed bank and stays in a state of enforced dormancy, since achenes recovered from soil appear to germinate almost instantly. The light requirements presumably play an important part: *Table 3a* shows that achenes of *T. hygrophilum* and *T. nordstedtii*, also after having been dug up, can hardly germinate without light. Since achenes of *T. ekmanii* and *T. eudontum* do germinate – albeit rather poorly – in such circumstances, it seems that other factors than light alone inhibit subterranean germination (compare WESSON & WAREING 1969b). It is noteworthy that the light requirements of achenes after soil-burial in these two taxa, and also in *T. hygrophilum* and *T. nordstedtii* is greater than that of freshly harvested ones or of achenes stored indoors or outdoors (see *table 3a*). A sojourn in soil appears to increase the light requirements, as is also found in other plant taxa (WESSON & WAREING 1969 a, b). A selective process of germination (the not light-dependent achenes germinating in the soil and disappearing from the seed bank) may also play a role in this connection for that matter.

The temperature dependence of achene germination in the seed bank is also subject to changes (*fig. 4*). Some taxa (*T. nordstedtii, T. calochroum*) exhibit germination inhibition at low temperature (10°C) after soil storage of the achenes, which prevents subterraneous germination during the autumn and winter seasons, but in other species the temperature dependence falls off rapidly (*T. taeniatum*) or more gradually (*T. hygrophilum*), so that their achenes can germinate more and more easily in a whole range of conditions. A third group of species (*e.g., T. lancidens* and *T. sellandii*) exhibit after an initial decrease of the temperature dependence a germination inhibition at winter temperatures. Such phenomena decide whether or not a given species can germinate in the cold season after having been brought to the surface.

The achenes which remain in the seed bank do not germinate nor do they exhibit any appreciable mortality, so that the seed bank remains constant during the autumn and winter (*fig. 5*). However, in the following spring a marked decrease of the temperature dependency was noted: experiments at different temperatures do not or hardly show any difference in the progression of germination, and the germination may occur at all temperatures tested (*fig. 4*). It is also apparent from *fig. 5* that consequently the seed bank diminishes, presumably as the result of subterranean germination. Also in the field new seedlings emerge (unpublished demographic data). Apparently the dormancy of a part of the achenes in the seed bank is broken in spring and germination follows; whether also changes in light dependency play a role is still unknown, and neither is known whether the subsequent germination pattern of the remaining achenes in

the seed bank is subject to alteration. Only further relevant studies can elucidate this point.

5. CONCLUSIONS

The results of a study of the germination ecology of a random selection from the 5 Dutch sections of *Taraxacum*, representing about five per cent of all the Dutch dandelion microspecies, reveal that each species investigated has its own germination strategy. In some respects these strategies appear to be adaptations to the specific habitats of the species in question by the inhibition of germination at times when the conditions in these habitats are unfavourable for the establishment of seedlings. Other phenomena differing in sympatrically occurring taxa indicate niche differentiation between these microspecies: by the different strategies their achenes may germinate at (partly) different sites and/or times of the year.

Although all microspecies included in the investigation prove to differ in their germination patterns this does not imply that *all* 199 recorded Dutch dandelions differ in their ecology. Ecologically equivalent species may be present, but the present study suggests that this is not often the case. We do not claim either that it is precisely the germination ecology which is the decisive factor in the ecological differentiation within and between the different habitats of Dutch dandelions. The present report rather gives an example of possible strategies leading towards an ecological differentiation between the various microspecies, which is presumably also present in other phases of the total life cycle.

The ecological differences between microspecies of *Taraxacum* and the fact that they can be related to the respective habitats, strongly suggest that each micrspecies is fine-tuned to its own specific environment and that not all species are specialised on the exploitation of the resources of "the same 6 square inches of new mud" (JANZEN 1979). ABBOTT's (1979) vision that each microspecies exploits it own resource, and thus maintains the genetic diversity within the genus *Taraxacum*, appears to be much more realistic.

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