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Growth potentials of *Taraxacum* microspecies from different habitats

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SUMMARY

Various *Taraxacum* microspecies from different fertile habitats were cultured at near optimal conditions in order to study the relationship between growth potential and habitat as a factor in their distribution, taking a high growth rate as essential for the occupation of fertile sites. Differences in relative growth rates between microspecies from fertile and infertile sites were most clear during early vegetative growth and mounted up to approximately 30%. During this stage, the high relative growth rates of microspecies from fertile sites were due to a combined effect of a high leaf area ratio and a high unit leaf rate. Differences in relative growth rates between microspecies from intermediate fertile and infertile sites were small or even absent. In this stage of vegetative growth, growth parameters were rapidly changing: relative growth rate and unit leaf rate declined with age while specific leaf area and/or leaf weight ratio, and thus leaf area ratio, increased; these changes were most pronounced in fast-growing microspecies. During later stages of vegetative growth, differences in relative growth rate between some microspecies occasionally diminished, but microspecies differences in morphology (i.e. leaf weight ratio and specific leaf area) were maintained or even increased. Within the group of the studied slow-growing microspecies, derived from infertile and/or dry sites, the low leaf area ratio was primarily due to a low leaf weight ratio. In microspecies with a high leaf area ratio, with a flat and dense rosette, unit leaf rate was depressed due to effects of self-shading.

Key-words: Fertility, growth analysis, *Taraxacum*.

INTRODUCTION

Microspecies of the genus *Taraxacum* that occur in The Netherlands are classified into six sections (Hagendijk *et al.* 1975, 1982; Øllgaard 1983). The *Taraxacum* section is the largest with 136 microspecies. The other sections are *Erythrosperma* (23 sp.), *Hamata* (17 sp.), *Palustria* (10 sp.), *Spectabilia* (9 sp.) and *Obliqua* (1 sp.). Sections differ in morphology as well as in habitat (Hagendijk *et al.* 1975, 1982; Sterk *et al.* 1983, 1987). Microspecies of the *Taraxacum* section are usually found at sites with a high degree of disturbance, varying in levels of mineral nutrition from low to high fertility. The habitat of the *Hamata* section resembles that of the *Taraxacum* as regards mineral availability but with lower levels

of disturbance. The remaining sections are restricted to more or less undisturbed and infertile sites.

Grime & Hunt (1975) extensively studied the maximum relative growth rate (R_{max}) of a wide range of plant species, growing in various habitats. They found a habitat-related variation in 'growth potential', with values ranging from 0·05 to 0·30 g^{-1} g^{-1} day^{-1}. A high relative growth rate is considered essential for the establishment of plants in productive vegetations, in order to compete for scarce resources such as light and space (Grime 1977). In contrast, at infertile sites, a low growth potential should be advantageous (Chapin 1980; Taylor 1989).

The importance of competition for light in the ecology of *Taraxacum* microspecies has been indicated in various ways. Mowing frequencies affected the floristic composition within a few years (Oomes & Mooi 1981). A lack of safe sites with appropriate light conditions endangered the persistence and spread of low growing plant species like *Taraxacum*. In pot experiments with mixed grass cultures, the low competitive ability of *Taraxacum* for light capture was found as well as differences amongst microspecies in this respect (Sterk *et al.* 1987). The occurrence of *Taraxacum* in early grassland succession, and its growth in early spring and autumn (Cox & Ford 1987; Sterk *et al.* 1987), have been explained as mechanisms to avoid peaks in competition for light (Sterk *et al.* 1987).

To explain the variation in soil preference among *Taraxacum* microspecies, i.e. the presence of a microspecies at fertile sites and its absence at infertile sites or vice versa, studies on differences in nutrient stress tolerance as well as studies on growth at ample nutrient supply are needed. In this study, plants of *Taraxacum* microspecies from different fertile habitats were cultivated under optimized conditions in order to investigate the relationship between 'growth potential' and fertility of the habitat as a factor in the distribution of *Taraxacum* microspecies. By recording leaf area and dry weights of shoots, roots and the (whole) plant, a full growth analysis, including unit leaf rate ($ULR = NAR$, net assimilation rate), specific leaf area (SLA) and leaf weight ratio (LWR) was obtained. In a single experiment, the average leaf shape and the leaf area of the intact rosette were determined. In the evaluation of habitat-related differences in growth among *Taraxacum* microspecies, RGR and some of its components will be discussed.

MATERIALS AND METHODS

The habitats of the studied microspecies vary from fertile and productive sites to dry and infertile sites (briefly summarized in Table 1) after Hagendijk *et al.* 1975, 1982; Sterk *et al.* 1983, 1987). Achenes of the agamospermous and polyploid microspecies were collected from single motherplants and cultivated in the experimental garden of the Vakgroep Bijzondere Plantkunde, University of Amsterdam. Achenes of *T. limburgense*, being the only studied diploid and sexually reproducing microspecies, were collected after cross-pollination. The average weights of achenes and embryos of the studied microspecies are presented in Table 2.

Growth conditions

Achenes were sown either on vermiculite in earthenware pottery, covered with glass, or on tissue paper in Petri dishes. The substrate was moistened with deionized water. Approximately 2 weeks later, seedlings were selected for uniform plant size and placed in 30 litre tanks with an aerated nutrient solution (macronutrients: 10% of a full Hoagland nutrient

Table 1. Summary of taxonomy and habitat of the studied *Taraxacum* microspecies

Microspecies (section)	Habitat
T. sellandii Dahlst. (Taraxacum) *T. ekmanii* Dahlst. (Taraxacum) *T. eudontum* Sahlin (Taraxacum) *T. ancistrolobum* Dahlst. ex. Lindb. (Taraxacum)	Heavily fertilized and grazed grasslands
T. limburgense Hgd., v. Soest & Zbg. (Taraxacum) *T. corynodes* Hgd., v. Soest & Zbg. (Taraxacum)	Moderately fertilized and grazed grasslands
T. adamii Claire (Taraxacum)	Moist peaty and clay-soils; lightly fertilized and grazed
T. raunkiaeri Wiinstedt ex Raunk. (Taraxacum)	Dry and sandy soils, nutrient-poor and lightly grazed
T. lancidens Hgd., v. Soest & Zbg. (Hamata)	Moderately fertilized and grazed grasslands
T. hollandicum v. Soest (Palustria)	Lightly to unfertilized hayfields, periodically flooded, and relative mineral-rich compared with other natural habitats
T. taeniatum Hagl. ex. Holmgr. (Erythrosperma)	Dry, natural dunepastures, with specifically low nitrogen levels
T. nordstedtii Dahlst. (Spectabilia)	Moist, lightly fertilized and grazed grasslands

solution as described by Hoagland & Snijder, 1933; micronutrients: 40% of the concentrations as described by Smakman & Hofstra, 1982). Three to 4 weeks after sowing the plants were again selected for uniform plant size, and the growth experiments were started with the application of a more concentrated nutrient solution (i.e. 25% of a full Hoagland nutrient solution). The nutrient solution was renewed at least once a week; tissue analysis showed that depletion of nutrient was absent. The pH of a fresh solution was 5·7; between renewals, pH increased up to 7·3.

In all growth experiments, mutual shading was avoided by decreasing the number of plants per tank. The development of a flat rosette in some microspecies demanded a considerable increase in cultivation area per plant during development, and thus restricted the number of plants per experiment. Therefore, more than one growth cabinet had to be used, and consequently, environmental conditions amongst the nine series of cultivations varied to some extent, particularly the levels of irradiance (see Table 2). In all experiments, the light period was 12 h; the temperature was 17–18°C during the day, and 12–13°C at night, and the relative humidity was 70–80%. In growth experiments A, B, D, F, and G, Double Flux TL Mf-140 W tubes were used; in experiments E and H, Sylvania Cool White F96T12/CW/VHO tubes; and in experiments C and I, Philips Low Energy No. 84 tubes were used. Irradiance (400–700 nm) was measured at plant height. To facilitate comparisons between the separate experiments, *T. sellandii* and *T. nordstedtii*, as representatives of extreme habitats with regard to mineral nutrition, were included in all experiments.

Table 2. Achene and embryo weights of *Taraxacum* microspecies, collected in 1981 and 1982 from plants growing in an experimental garden. Embryo weight was calculated as the difference between the total achene weight and the weight of the seedcoat. Achene weight is presented in milligrams; embryo weight is presented in milligrams and in percentages of total achene weight

Microspecies	Achene weight	Embryo weight (%)
sellandii	0·831	0·505 (60·8)
eudontum	0·791	—
ekmanii	0·730	0·459 (62·9)
ancistrolobum	0·773	—
corynodes	0·942	0·546 (58·0)
limburgense	0·440	0·278 (63·2)
lancidens	0·565	0·318 (51·3)
adamii	0·461	0·292 (63·3)
raunkiaeri	0·547	0·347 (63·4)
taeniatum	0·294	0·142 (48·3)
hollandicum	0·510	0·324 (63·6)
nordstedtii	0·628	0·366 (58·3)

Table 3. Inventory of the various series of cultivations: studied microspecies, variation in irradiance (PAR) and in harvest characteristics

Experiment	microspecies	Irradiance (μmoles $m^{-2} s^{-1}$)	Number of harvests	Number of days
A	*sellandii, adamii, limburgense, lancidens, taeniatum, hollandicum*	200	4	28
B	*sellandii, eudontum, taeniatum, nordstedtii*	200	5	28
C	*sellandii, adamii, hollandicum, nordstedtii*	180	5	28
D	*sellandii, raunkiaeri, hollandicum, limburgense, nordstedtii*	160	5	27
E	*sellandii, ekmanii, ancistrolobum, corynodes, nordstedtii*	220	5	28
F	*sellandii, lancidens, taeniatum, hollandicum, nordstedtii*	210	12	28
G	*sellandii, ekmanii, adamii, limburgense, nordstedtii*	165	12	28
H	*sellandii, nordstedtii*	220	12	25
I	*sellandii, nordstedtii*	180	16	30–33

Harvest methods

The experimental period ranged from 25 to 33 days, the number of harvests per experiment varied between 4 and 16 (Table 3). Harvesting was done 6 h after the start of the light period. Directly thereafter, fresh weight of shoots and roots were determined. Leaf areas of turgescent leaves were measured with a Licor Areameter Model 3100. In addition, in

Table 4. Denotations and formula used in the growth analysis

Variables	Definition (units)
Basic denotations	
S_f	Shoot fresh weight (g)
S_d, W_d	Shoot and total plant dry weight (g)
LA	Total leaf area (cm^2)
RGR	Relative growth rate [g W_d (g W_d)$^{-1}$ day^{-1}]
ULR	Unit leaf rate (mg W_d cm^{-2} day^{-1})
LAR	Leaf area ratio [cm^2 (g W_d)$^{-1}$]
SLA_f, SLA	Specific leaf area [cm^2 (g S_f)$^{-1}$, cm^2 (g S_d)$^{-1}$]
LWR	Leaf weight ratio
LA_r	Leaf area of intact rosette (cm^2)
Calculated	
$\overline{W_d}$, $\overline{LA}$	Mean values of plant dry weight and total leaf area, calculated as the e-function of ln $\overline{W_d}$ and ln $\overline{LA}$
$W_{d,t}$, LA_t	Fitted values of plant dry weight and total leaf area, obtained by regression analysis using $\overline{W_d}$ and $\overline{LA}$
LAR_t	Fitted values of leaf area ratio
l/b	Length-breadth ratio of leaves
$LA\%$	Ratio of leaf area of intact rosette and total leaf area
Formula	
$LAR = LWR \times SLA$	
$RGR = ULR \times LAR_t = 1/W_{d,t} \times dW_{d,t}/dt$	
$ULR = 1/LA_t \times dW_{d,t}/dt$	

growth experiment I, individual leaves were drawn on graph paper. Plant material was dried for 24 h at 70°C and 30 min at 100°C, and then weighed.

Computation methods

The denotations and formula used in the growth analysis are presented in Table 4. The relative increase in (total plant) dry weight (RGR) was computed by regression through the sample statistics for $\log_e$ transformed (total plant) dry weights, either by a linear regression model with disregard for the actual fitting (for growth experiments with five harvests or less, Table 3), or by regression methods with emphasis on minimizing 'lack of fit', using cubic splines (Parsons & Hunt 1981). In the first case, RGR was derived as the slope of the linear regression equation; it presents an average value over the experimental period (Hunt 1978). Using cubic splines, series of instantaneous RGR-values are obtained as a function of time. In these regression routines, fitted values were also obtained for dry weight of (total) plant ($W_{d,t}$), leaf area (LA_t), leaf area ratio (LAR_t), and unit leaf rate (ULR). Differences between regressed parameter values (e.g. RGR) were tested with a (two-tailed) Student's t-test, using the obtained standard errors and the appropriate degrees of freedom. Differences between sample statistics were tested with an analysis of variance.

RESULTS

Average relative growth rates

In experiments A–E, with a limited number of harvests, average values of RGR were determined for 12 microspecies (Table 5). A 25% difference was found between

Table 5. Average relative growth rates (*RGR*) of total plant dry weight of 12 *Taraxacum* microspecies, during the first stage of vegetative growth, cultured under near optimal conditions. *RGR* was computed as the slope of the linear regression equation through means of ln-transformed dry weights. In each growth experiment, *T. sellandii* and *T. nordstedtii* were included as internal standard

	RGR ($g\,g^{-1}\,day^{-1}$) Experiments				
Microspecies	A	B	C	D	E
sellandii	0·160	0·162	0·167	0·166	0·169
eudontum	—	0·170	—	—	—
ekmanii	—	—	—	—	0·174
ancistrolobum	—	—	—	—	0·167
corynodes	—	—	—	—	0·143
adamii	0·144	—	0·145	—	—
raunkiaeri	—	—	—	0·151	—
limburgense	0·144	—	—	0·151	—
lancidens	0·150	—	—	—	—
taeniatum	0·144	0·150	—	—	—
hollandicum	0·123	—	0·125	0·130	—
nordstedtii	0·138	0·145	0·142	0·144	0·139

T. sellandii, *T. ancistrolobum*, *T. eudontum*, and *T. ekmanii* (microspecies from fertile and productive grasslands) as high extremes, and *T. hollandicum* as low extreme. The time courses of ln W_d-values were curvilinear (data not shown), indicating that *RGR* declined during development. Based on these results, eight microspecies were selected for a detailed growth analysis: *T. sellandii*, *T. ekmanii*, *T. limburgense*, *T. adamii*, *T. taeniatum*, *T. hollandicum*, *T. lancidens*, and *T. nordstedtii*.

Instantaneous relative growth rates

In growth experiments F and G, instantaneous *RGR*-values were obtained for eight microspecies (Fig. 1). The *RGR*-values were presented as a function of plant size (ln $W_{d,t}$) rather than as a function of time. In this way plant size-related differences in *RGR* between microspecies were eliminated. In general, the largest differences in *RGR* ($\simeq 30\%$) occurred during the first period of the experiments, i.e. between small-sized plants. During development, *RGR*-values of some microspecies converged or crossed (in experiment F, *T. sellandii* crossed with *T. lancidens* and *T. nordstedtii*, and in experiment G, *T. sellandii* and *T. ekmanii* converged with *T. adamii* and crossed with *T. nordstedtii*), while for other microspecies the initial differences more or less remained the same (in experiment F, *T. sellandii* versus T. hollandicum and *T. taeniatum*).

Within the range of overlapping plant size, 7–400 mg (approx.) plant dry weight, at a probability level of $P<0{\cdot}05$, the following sequence of *RGR*-values was observed: in experiment F, *T. sellandii* > *T. lancidens* = *T. nordstedtii* and > T. taeniatum, with *T. nordstedtii* = *T. taeniatum* and > *T. hollandicum*, and *T. taeniatum* = *T. hollandicum*; in experiment G, *T. ekmanii* = *T. sellandii* > *T. adamii* > *T. limburgense* = *T. nordstedtii*. These patterns of significant differences in *RGR* were true either for the total plant size

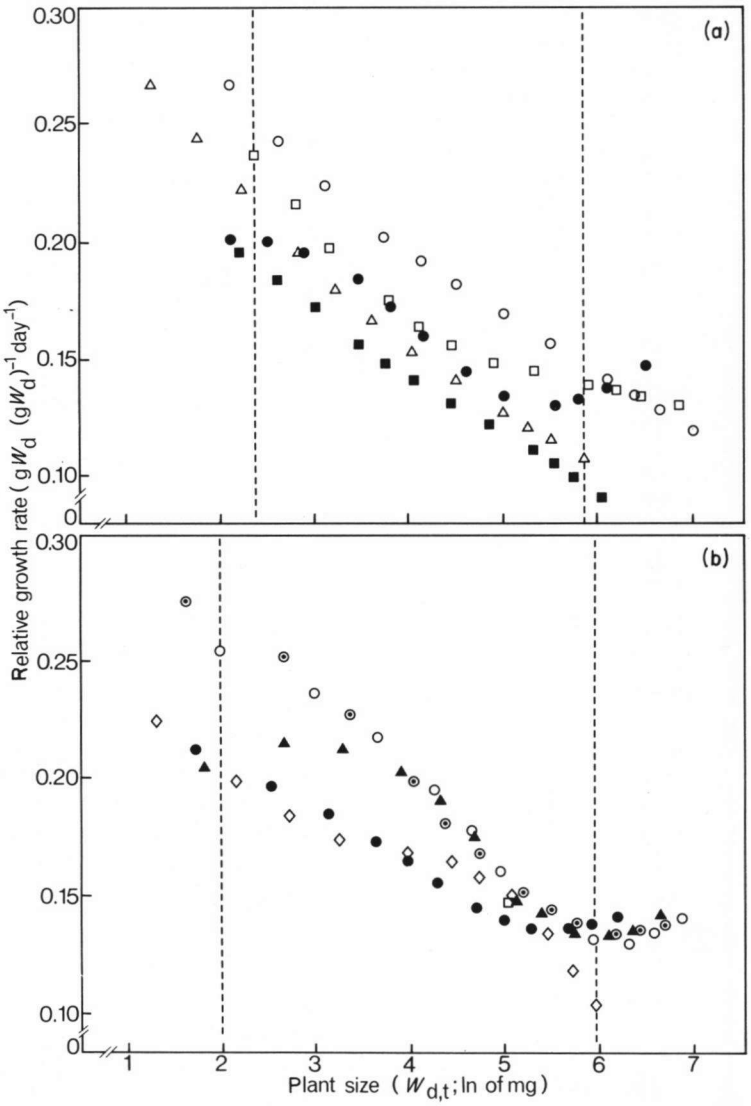

Fig. 1. Instantaneous relative growth rates of total plant dry weight of eight *Taraxacum* microspecies, cultured under near optimal conditions over a period of 28 days, and presented as a function of plant size (i.e. ln of dry weight). Experiment F (Fig. 1a): *T. sellandii* ○, *T. nordstedtii* ●, *T. lancidens* □, *T. taeniatum* △, *T. hollandicum* ■; experiment G (Fig. b): *T. sellandii* ○, *T. nordstedtii* ●, *T. ekmanii* ⊙, *T. limburgense* ◇, *T. adamii* ▲. The vertical lines mark the range of overlapping plant size between the studied microspecies. Relative growth rates were obtained by regression through harvest means, after transformation of individual data to ln-values, using cubic splines. Standard errors were less than 15% of the fitted values located at the ends of the series of data, and less than 4% of the fitted values in the middle section of the series of data.

range (e.g. in experiment F, *T. sellandii* versus *T. taeniatum* and *T. hollandicum*) or for a (substantial) part of the overlapping plant size range (e.g. in experiment F, *T. sellandii* versus *T. lancidens*; in experiment G, *T. sellandii* and *T. ekmanii* versus *T. nordstedtii* and *T. limburgense*). In a few cases, significant differences between *RGR*-values located at the

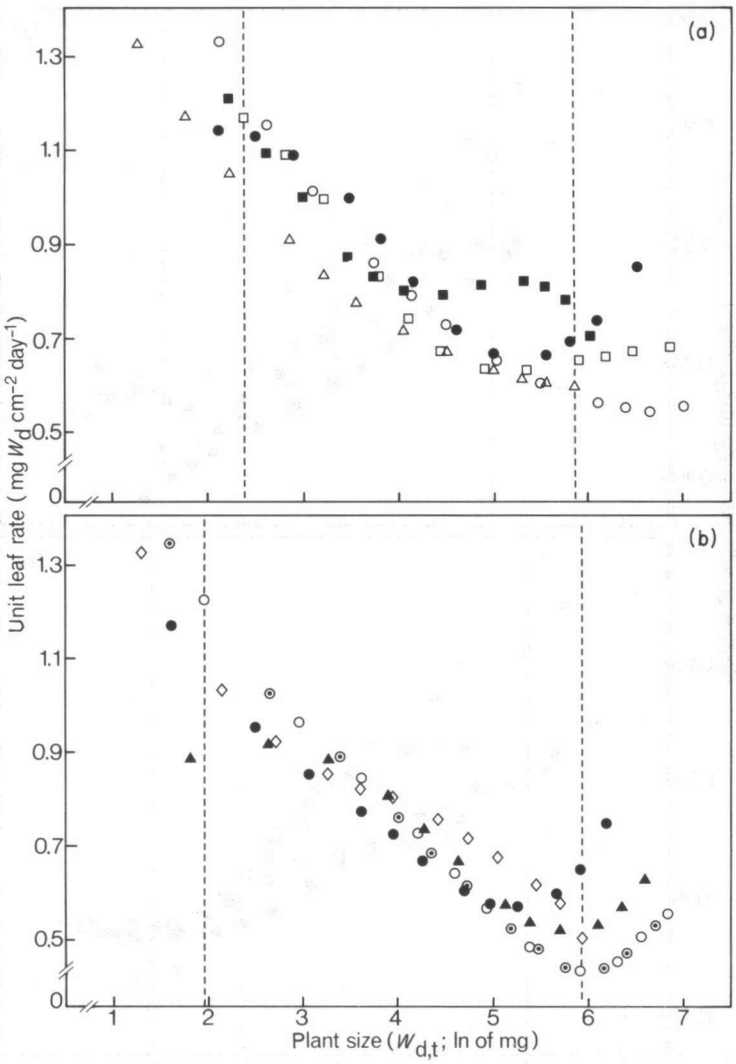

Fig. 2. Instantaneous unit leaf rates of eight *Taraxacum* microspecies, cultured under near optimal conditions over a period of 28 days, and presented as a function of plant size (experiment F: Fig. 2a; experiment G: Fig. 2b). Standard errors were less than 12% of the fitted values located at the ends of the data series, and less than 4% of the fitted values in the middle section of the data series. For details see Fig. 1.

beginning of the series of fitted *RGR*-values were absent because of their high standard errors (e.g. in experiment F, *T. sellandii* versus *T. nordstedtii*).

Instantaneous unit leaf rates

ULR-values fall off steeply during ageing, except for large-sized plants where *ULR* stabilized or even increased (Fig. 2). Within the range of overlapping plant size, differences in *ULR* between the studied microspecies were generally small and not significant. Exceptions were noted: in experiment F, *ULR* of small-sized *T. taeniatum* plants was significantly lower ($0{\cdot}01 > P > 0{\cdot}001$) than that of most other microspecies, the *ULR* of large-sized *T. hollandicum* plants was significantly higher ($P < 0{\cdot}001$) than that of all

other microspecies. Within the small-size plant area, fast-growing microspecies tended to show slightly higher *ULR*-values (e.g. *T. sellandii* and *T. ekmanii* versus *T. nordstedtii, T. adamii*, and *T. taeniatum*). At later stages, microspecies differences in *RGR* and *ULR* sometimes were inversely related (e.g. *T. sellandii* versus *T. hollandicum* and *T. limburgense*).

Morphological growth characteristics

LAR_t was less age-dependent that *RGR* or *ULR* (Fig. 3); most microspecies showed a curvilinear course during development. In both experiments F and G, the range of microspecies' differences in *LAR* increased with plant size from 30 to 100% (approx.) (*T. sellandii* versus *T. hollandicum*) and 65% (approx.) (*T. sellandii* and *T. ekmanii* versus *T. limburgense*) respectively. At a probability level of $0{\cdot}01 > P > 0{\cdot}001$, the pattern of significant differences between fitted as well as average *LAR* values changed during growth in experiment F from *T. sellandii* = *T. taeniatum* > *T. lancidens* > *T. nordstedtii* = *T. hollandicum*, to *T. sellandii* > *T. lancidens* > *T. taeniatum* = *T. nordstedtii* > *T. hollandicum*; in experiment G, the pattern of significant differences changed from *T. sellandii* = *T. ekmanii* = *T. adamii* > *T. nordstedtii* = *T. limburgense*, to *T. sellandii* = *T. ekmanii* > *T. adamii* > *T. nordstedtii* > *T. limburgense*.

In Figs 4 and 5, the components contributing to *LAR, LWR* and *SLA*, are presented as sample statistics. *LWR* was constant (e.g. *T. nordstedtii, T. taeniatum*) or increased (e.g. *T. sellandii, T. ekmanii*) with plant-size (Fig. 4); differences in *LWR* increased by up to 16% (approx.) in both experiments. Except for the smallest-sized plants in experiment F, *LWR* or *T. sellandii* was significantly higher ($P < 0{\cdot}001$) than all other microspecies; in experiment G, *LWR* of *T. nordstedtii* was significantly lower than all other microspecies. *SLA*-values on a dry weight basis showed curvilinear courses with plant size, as was observed for *LAR*. The (steep) decline of *SLA* in large-sized plants coincided with the maturation of the older leaves (data not shown). In this respect, *T. hollandicum* was an exception; *SLA* already started to decrease in intermediate size plants, due to the rapid death of the oldest leaves. Differences between microspecies in *SLA* increased by up to 65% (approx.) (*T. sellandii* versus *T. hollandicum*) and 50% (approx.) (*T. ekmanii* versus *T. limburgense*) in experiments F and G respectively, with *T. hollandicum* (experiment F) and *T. limburgense* (experiment G) showing significantly ($0{\cdot}01 > P > 0{\cdot}001$) lower *SLA*-values than all other microspecies.

Extended growth analysis of T. sellandii *and* T. nordstedtii

Effects of the different levels of irradiance (experiment F, 210 and experiment G, 165 μmole m^{-2} s^{-1}) on the growth parameters of *T. sellandii* and *T. nordstedtii* were (relatively) small: *SLA* was 15–20% higher in experiment F, while *LWR* was virtually unaffected. The higher *LAR* values of the plants in experiment F were counteracted by inverse differences in *ULR*, leaving *RGR* more or less unaltered. Such a lack of response in *RGR* to (even a much wider range of) levels of irradiance was also found for Plantago, at least when seedlings were allowed to adjust to the various light levels during early stages of development (Kuiper & Kuiper 1988).

In order to validate the above conclusion, two additional growth experiments were performed, one at a high level of irradiance (experiment H), and one at a low level of irradiance (experiment I). In experiment I, in addition to the basic measurements, specific leaf area on a fresh weight basis (SLA_f) and the appearance of the shoot were studied as possible factors in *ULR* and subsequently, in *RGR*.

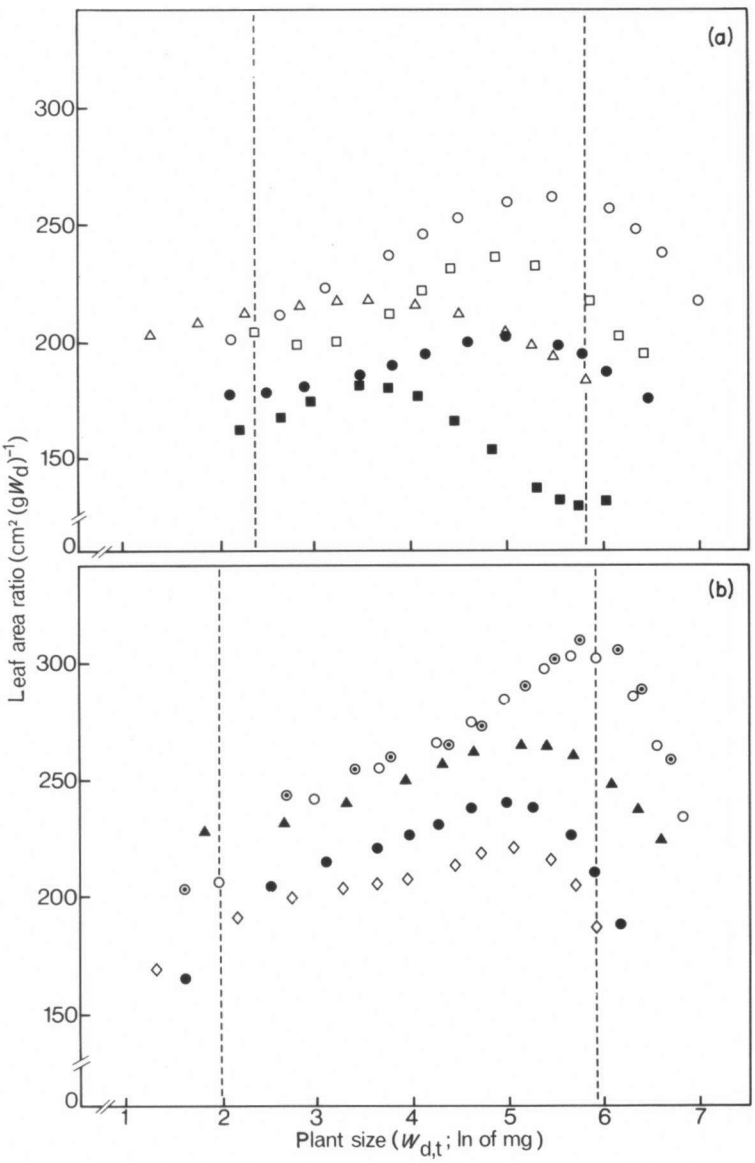

Fig. 3. Leaf area ratio of eight *Taraxacum* microspecies, cultured under near optimal conditions over a period of 28 days, and presented as a function of plant size (experiment F: Fig. 3a; experiment G: Fig. 3b). Standard errors were less than 4% of the fitted values. For details see Fig. 1.

Instantaneous *RGR*-values of *T. sellandii* and *T. nordstedtii*, derived from experiments H and I, resembled those of experiments F and G by showing a gradual diminishment of the initial difference between the two microspecies in *RGR* of $\simeq$25% (Fig. 6). The (small) differences in *RGR* between the separate growth experiments did not correlate with differences in irradiance.

The results for the morphological parameters, as found in H (not shown) and I, agree with earlier findings on *T. sellandii* and *T. nordstedtii* (experiments F and G). Up to an

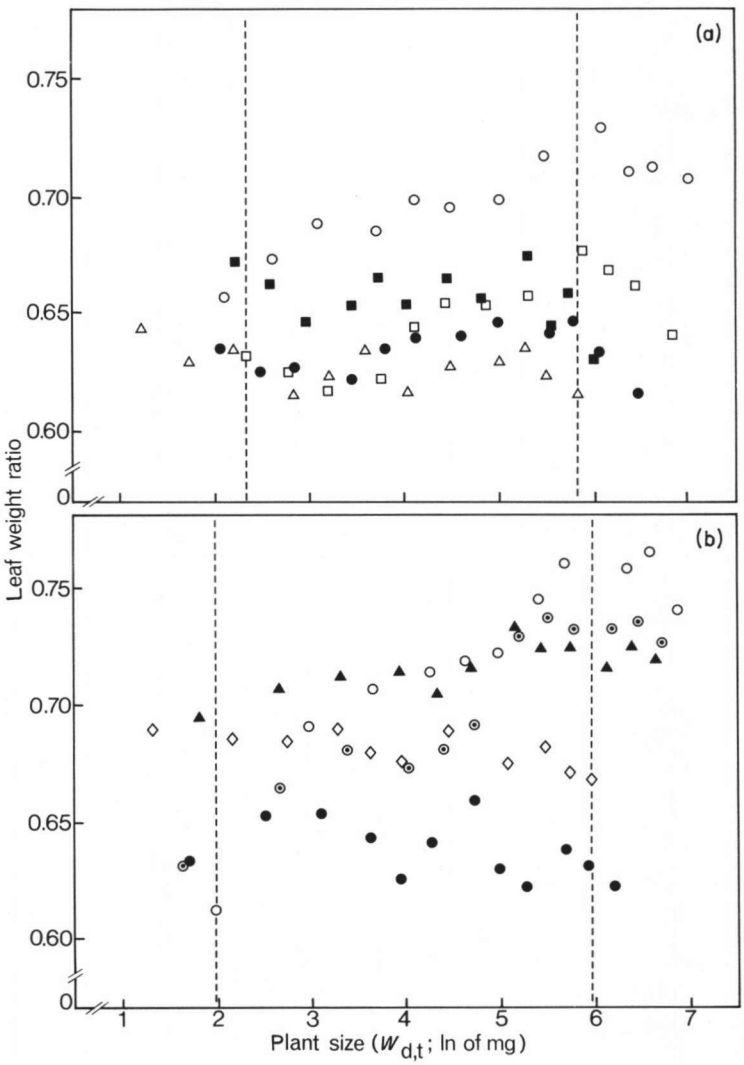

Fig. 4. Leaf weight ratio (on a dry weight basis) of eight *Taraxacum* microspecies, cultured under near optimal conditions over a period of 28 days, and presented as a function of plant size (i.e. ln of dry weight). Leaf weight ratios are the average values of nine plants; mean coefficient of variation in experiment F (Fig. 4a) was 2·6%, and in experiment G (Fig. 4b) 2·7%. Denotations as in Fig. 1.

intermediate plant size, an ≃22% difference in LAR was built up between *T. sellandii* and *T. nordstedtii* (Fig. 7a) due to a gradual increasing difference in *LWR* (≃15%, Fig. 7b) and in *SLA* (on dry weight basis ≃6%, Fig. 7c). This difference in *LAR* was maintained throughout the experiment, but in later stages it was primarily based on differences in *LWR*. During the first period there was a pronounced increase in SLA_f, particularly in *T. sellandii* with an increase of ≃38% during the first stage of development (Fig. 7c). Again, *ULR* of *T. sellandii* declined more steeply with plant size than that of *T. nordstedtii* (Fig. 7d).

There were also noted differences in the shoot appearance between *T. sellandii* and *T. nordstedtii* due to differences in (average) leaf shape and leaf orientation. As indicated

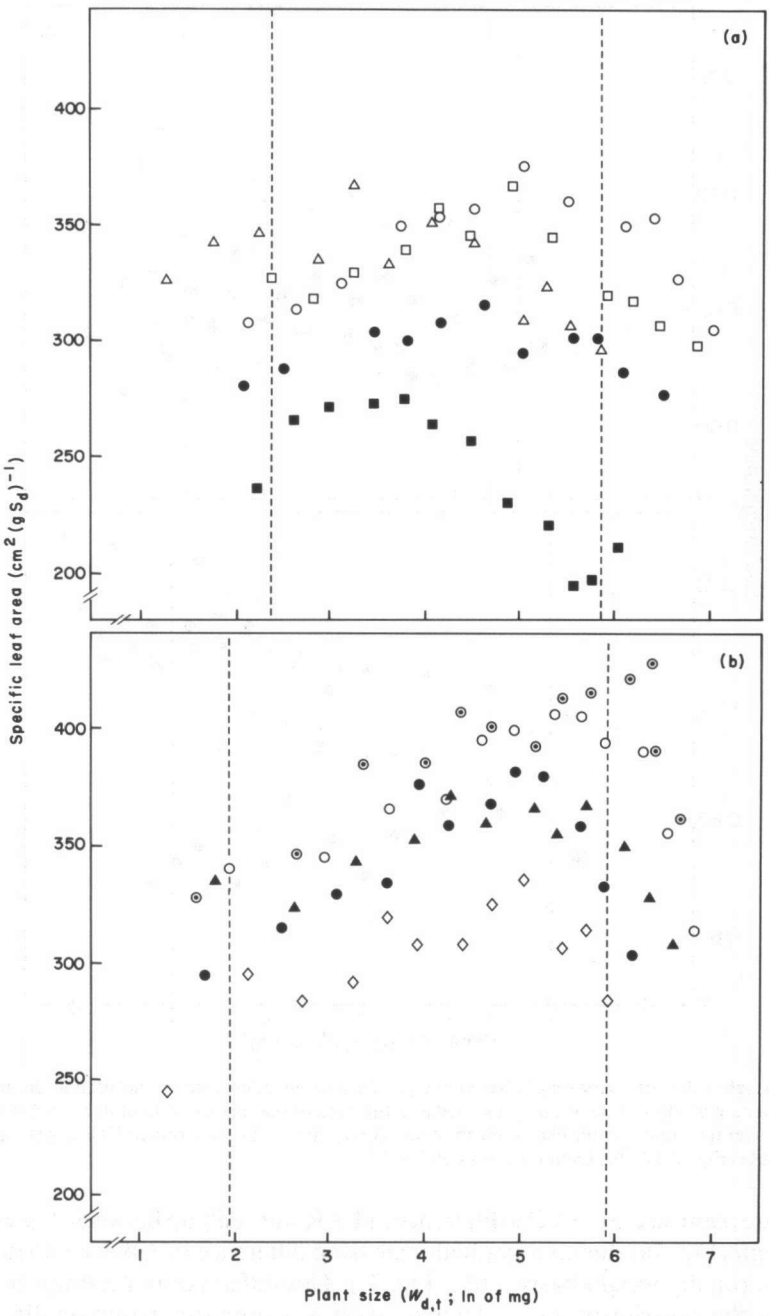

Fig. 5. Specific leaf area on dry weight basis of eight *Taraxacum* microspecies, cultured under near optimal conditions, over a period of 28 days, and presented as a function of plant size (i.e. ln of dry weight). Specific leaf areas are the average values of nine plants; mean coefficient of variation in experiment F (Fig. 5a) was 5·7%, and in experiment G (Fig. 5b) 5·8%. Denotations as in Fig. 1.

by the differences in average length–breadth (l/b) ratios of relevant leaves, with *T. sellandii* having lower l/b ratios at one-third and two-thirds of the leaf length at similar leaf areas

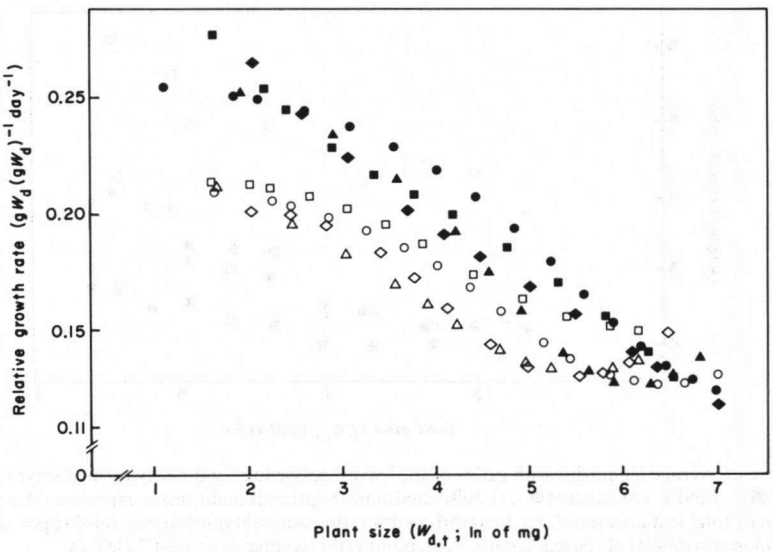

Fig. 6. Relative growth rates of total plant dry weight of *T. sellandii* (filled symbols) and *T. nordstedtii* (open symbols), cultured under near optimal conditions, and presented as a function of plant size (i.e. ln of dry weight). Relative growth rates were derived from four separate series of cultivation (experiment F◆ ◇; G▲ △; H■ □; I● ○), and calculated by regression using cubic splines.

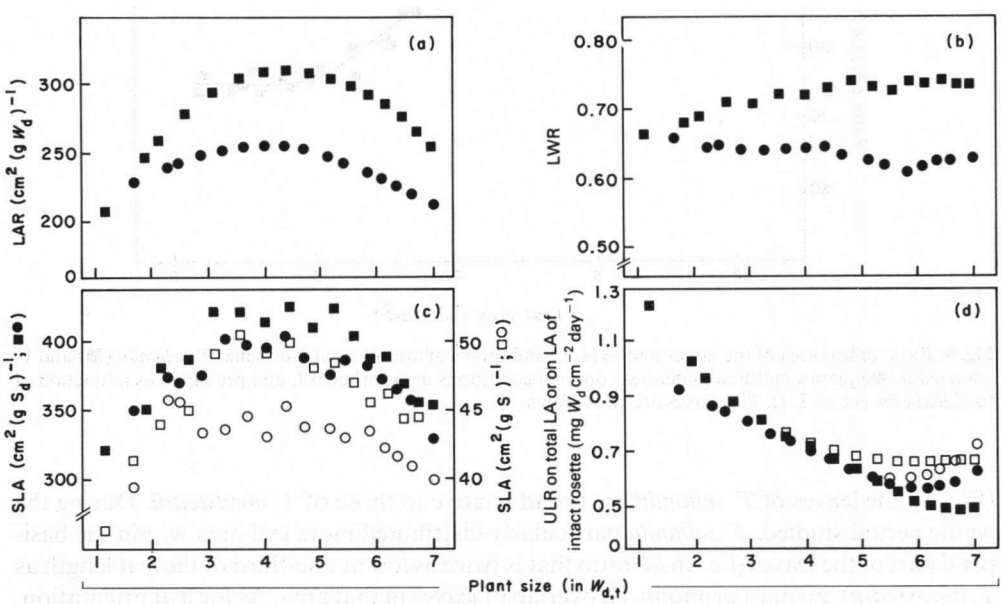

Fig. 7. Average values of leaf weight ratio and specific leaf area, and fitted values of leaf area ratio and unit leaf rate, of *T. sellandii* (■,□) and *T. nordstedtii* (●,○), cultured at near optimal conditions in experiment I, and presented as a function of plant size (i.e. ln of dry weight). In Fig. 7c, closed and open symbols refer to specific leaf area on a dry and fresh weight basis, respectively; in Fig. 7d, closed and open symbols refer to unit leaf rate based on total leaf area and on the leaf area of the intact rosette, respectively.

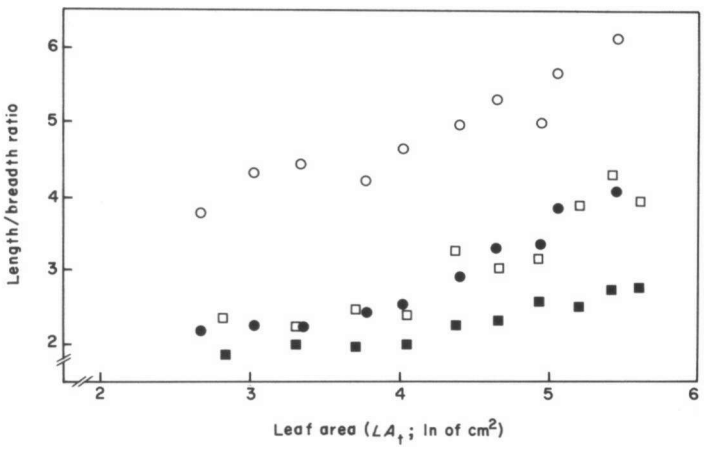

Fig. 8. Course of average length/breadth ratios of the leaves, cotyledons and newly formed leaves excluded, of *T. sellandii* (■,□) and *T. nordstedtii* (●,○), cultivated at near optimal conditions in experiment I, and presented as a function of total leaf area (i.e. LA_t). Length/breadth ratios were obtained at one-third (open symbols) and two-thirds (closed symbols) of the leaf length. Each point is the average of at least 25 leaves.

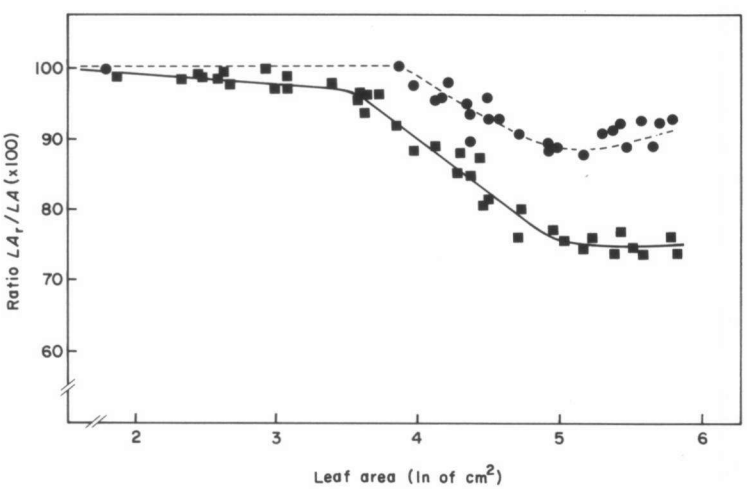

Fig. 9. Ratio of leaf area of the intact rosette (LA_r) and total leaf area (LA) of individual *T. sellandii* (■) and *T. nordstedtii* (●) plants, cultured under near optimal conditions in experiment I, and presented as a function of total leaf area (i.e. ln LA). The curves are handdrawn.

(Fig. 8), the leaves of *T. sellandii* are broad relative to those of *T. nordstedtii*. During the whole period studied, *T. sellandii* particularly distributed more leaf area within the basipetal part of the leaves (i.e. an l/b ratio that is twice as low at one-third of the leaf length as *T. nordstedtii*), giving a pronounced overlap of leaves in that area. As for leaf orientation, the leaves of *T. nordstedtii* were slightly elevated while leaves of *T. sellandii* were lying on the ground, firmly stacked upon each other. As a result, *T. sellandii* had a flat and much denser rosette than *T. nordstedtii*. To quantify these differences in rosette-shape in terms of self-shading, the leaf area of intact rosettes (LA_r) was determined, and compared with

total leaf area (*LA*). In Fig. 9, the ratio of LA_r and *LA* (i.e. *LA*%) is presented as a function of leaf area: a low *LA*%-value represents a high degree of self-shading. *T. sellandii* already showed symptoms of self-shading in small plants; *LA*% decreased to 75% for the maximal leaf area measured. In contrast, *T. nordstedtii* did not suffer from self-shading until an intermediate leaf area was attained. At most, 10% self-shading was observed in this microspecies. Eliminating these effects of self-shading, by using LA_r-values instead of *LA*-values, *ULR*-values, derived from experiment I, were recalculated (Fig. 7d): for *T. sellandii* the decline of *ULR* in large-sized plants could be explained by effects of self-shading.

DISCUSSION

Statistical analysis of RGR

The treatment of growth analysis has evolved from a classical (Blackman 1919) to a functional approach (Hughes & Freeman 1967), and recently, to a synthesis between the two (Poorter 1989a). The value of the classical approach is limited by aspects of random fluctuation (Hunt 1978; Causton & Venus 1981), the restricted possibilities for incorporating all growth parameters into the growth analysis (Evans 1972) and the difficulties in evaluating statistical differences (Poorter & Lewis 1986). The problems linked to the functional approach are located in the selection of the mathematical equation for the description of plant growth data (over- and underfitting), the rigidity of the fitting equations and the limited biological meaning of the estimated errors attached to the derived quantities (Poorter & Lewis 1986). In this study, 'flexible' cubic splines were regressed through harvest means, resulting in the description of the 'path of means' of plant dry weight; differentiation of these values yielded *RGR*. The number of knots was limited to a single one in order to avoid overfitting, not because of its consequences on accuracy (by loss in degrees of freedom), but merely to preserve a means of eliminating random fluctuation.

In view of the limited biological meaning of the (asymmetrically distributed) confidence limits of regressed growth parameters, testing differences should preferentially be based on directly measured variability. Consequently, attempts were made to determine the *RGR* of individual plants by non-destructive measurements. However, this method failed because of its deleterious effects on growth, particularly on that of slow-growing microspecies (data not shown). Another approach is to neglect the derived quantities and their high estimated errors located at both ends of the curve, considering these areas as buffers to the regions of more interest (Hunt 1980; Wickens & Cheeseman 1988). Alternatively, the use of confidence limits in establishing differences in *RGR* could be complemented, or perhaps completely avoided, by repeating frequent harvesting experiments. The consistent results at the beginning of the regressed series of data, in four separate series of cultivation (Fig. 6), may be regarded as (complementary) evidence for differences in *RGR* between small-sized *T. sellandii* and *T. nordstedtii* plants.

The ecological significance of the estimated growth potentials

In preliminary experiments with several microspecies, rough estimates of favourable conditions as regards pH (above a minimal level of 5·0), irradiance (below a maximal level of 240 μmol m^{-2} s^{-1}), and cultivation temperature were established. In view of the results obtained by Roetman & Sterk (1985), the applied cultivation temperature of

17–18/12–13°C (day/night) may be slightly sub-optimal for some microspecies. As far as irradiance (present study) and external nutrient concentrations (Hommels *et al.* 1989a,b) are concerned, optimal conditions appeared to be rather wide, at least for *T. sellandii* and *T. nordstedtii.* On the whole, the presented growth performances of the studied microspecies, cultured in the absence of mutual shading, should be indicative of, and even may approximate to, the actual 'growth potentials'. An exception is *T. hollandicum*; its aberrantly short leaf life, and its deviant mineral status (i.e. the highest levels of internal N, P, and K of all microspecies studied; data not shown), suggested that conditions were not (near) optimal for this particular microspecies.

The present results indicated that the differences in 'growth potential' among *Taraxacum* microspecies may be a factor in their distribution. They agreed with the general conception of a positive correlation between 'growth potential' and fertility of the habitat (Poorter 1989b, and references therein): microspecies from fertile soils, *T. sellandii* and *T. ekmanii* (and also *T. ancistrolobum* and *T. eudontum* in a single experiment) showed higher *RGR*-values than the other microspecies, at least during the early stages of vegetative growth. At later stages, microspecies differences sometimes became smaller. In these experiments, *RGR*-values did not clearly discriminate between microspecies from intermediate fertile soils and from infertile soils (e.g. in experiments F and G: *T. nordstedtii* versus *T. lancidens* and *T. limburgense*).

Strictly speaking, the absolute growth rate rather than the *RGR* determines the competitive ability for capture of light and space (Piggot 1980; Lambers & Dijkstra 1987). Therefore, next to *RGR*, achene weights, or more relevant embryo weights, should be taken into account. Microspecies differences were substantial, with *T. corynodes* showing a four times higher embryo weight than *T. taeniatum* (Table 2). These differences paralleled those observed in *RGR*: achene (embryo) weights of fast-growing microspecies were within the upper half of the observed range (Table 2).

Evaluation of differences in growth potential: LAR, SLA, LWR, *and* ULR

Differences in *RGR* were largely associated with differences in *LAR*. Only during the early stages of vegetative growth, both *LAR* and *ULR* contributed to differences in *RGR*. Later, an increased difference in *LAR* was counteracted by the onset of inverse microspecies differences in *ULR*. Such an association between morphological growth parameters (*LAR*) and 'growth potential' appears to be rather common in plants (Poorter 1989b); in only 10% of the plant species, photosynthetic activity was positively correlated with 'growth potential'. The establishment of morphological features as key factors in the differentiation of 'growth potentials' between *Taraxacum* microspecies agrees with earlier findings in pot experiments (Roetman & Sterk 1985). The situation is more complicated than suggested by these authors due to the (large) ontogenetic changes in the growth parameters. The dramatic decrease in *ULR* with plant size is of particular interest, as *ULR* in general is more stable than *RGR* (Hunt 1982). For example, a decreasing *RGR* in two *Plantago major* L inbred lines went together with an almost constant *ULR* (Dijkstra & Lambers 1989a).

The course of *ULR* cannot be explained in detail, *ULR* being the outcome of a wide variety of physiological processes, e.g. photosynthesis, respiration and loss of plant material by exudation. However, the (small) differences in the declines of *ULR* between fast- and slow-growing *Taraxacum* microspecies, and their effects on the convergence of *RGR*, can be commented upon. Firstly, the sharp decline in *ULR* in

T. sellandii as compared to *T. nordstedtii*, went together with a more drastic increase in *SLA* on a fresh weight basis (SLA_f). Taking the inverse of *SLA* (Hunt 1978) or even better, the inverse of SLA_f (Dijkstra 1989) as an estimate for the thickness of leaves, an increase in *SLA* or SLA_f will be associated with a reduction in photosynthetic machinery per unit area (Bunce 1986), and thus with a reduction in *ULR*. The above trade-off between *ULR* and *SLA*, combined with changes in dry matter composition towards the accumulation of metabolically cheap compounds, could also explain the occasionally observed increases in *ULR* in large-sized plants (Figs 2b, 7d). For example, within the final week of experiment F, *T. nordstedtii* showed an approx. 34% increase in *ULR* (Fig. 2b), together with an approx. 20% decrease in *SLA* on a fresh weight basis, and a 40% increase in level of non-structural carbohydrates in the roots (data not shown).

Secondly, differences in self-shading between *T. sellandii* and *T. nordstedtii* (Fig. 9), due to a variation in rosette shape, contributed to the observed differences in *ULR* declines. For the other microspecies, effects on self shading were not quantified but resemblances were noted, with microspecies from fertile sites (*T. ekmanii, T. eudontum*, and *T. ancistrolobum*) all having a dense and flat rosette.

Although *RGR* proved to be indicative of the habitats of plants (Grime & Hunt 1975), it has recently been suggested that *RGR* itself is not the primary target for natural selection, but rather its components (Lambers & Dijkstra 1987; Poorter 1989b). In this line of reasoning, the adaptive values of the separate growth parameters such as *SLA, LWR* (*LAR*) and *ULR* should be emphasized. In the present study, attention should then be focused on the significance of some basic traits involved in the capture of light and space. Firstly, the high *LWR* of *T. sellandii* and *T. ekmanii* (Fig. 4a,b), which reflects a preferential allocation of dry matter to the shoot, can be interpreted as an adaptation to above ground competition. In contrast, the inherently low *LWR* of *T. nordstedtii* and *T. taeniatum* (Fig. 4a,b) reflects adaptation to dry and/or infertile sites (Chapin 1980; Lambers & Dijkstra 1987). In this context, the relatively high *LWR* of *T. adamii* from infertile sites should be noted as an exception. Secondly, *SLA* could have an adaptive value for the capture of light: a high *SLA*, as displayed by *T. sellandii* and *T. ekmanii* (Fig. 5a,b), represents efficient light utilization per unit shoot weight. However, this interpretation derogates the broad ecological significance of *SLA, SLA* being also involved in adaptations to the light environment, to trampling and, possibly, to herbivory (Lambers & Dijkstra 1987, references therein; Dijkstra & Lambers 1989b). Finally, the high *LAR* in the form of a flat and dense rosette in *T. sellandii*, as in other microspecies from fertile sites, may be advantageous as a means to occupy space at fertile sites because of the exclusion of neighbouring plants, even though it presents a lowering of return of the productive dry matter allocation into a high *LWR* and a high *SLA*, due to effects of self-shading.

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REFERENCES

Blackman, V.H. (1919): The compound interest law and plant growth. *Ann. Bot.* **33:** 353–360.

Bunce, J.A. (1986): Measurement and modelling of photosynthesis in field crops. *CRC Crit. Rev. Plant Sci.* **4:** 44–77.

Causton, D.R. & Venus, J.C. (1981): *The Biometry of Plant Growth.* 16–85. E. Arnold Publishers, London.

Chapin, F.S. (1980): The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* **11:** 223–260.

Cox, T. & Ford, H. (1987): The plastic response of three agamospecies of dandelion to two levels of nutrient. *Ann. Bot.* **59:** 81–91.

Dijkstra, P. (1989): Cause and effect of differences in specific leaf area. In: Lambers, H., Cambridge, M. L., Konings, H. and Pons, T.L. (eds): *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants.* 125–140. SPB Academic Publishing, The Hague.

— & Lambers, H. (1989a): A physiological analysis of genetic variation in relative growth rate within *Plantago major* L. *Funct. Ecol.* **3:** 577–587.

— & — (1989b): Analysis of specific leaf area and photosynthesis of two inbredlines of *Plantago major* differing in relative growth rate. *New Phytol.* **113:** 283–290.

Evans, G.C. (1972): *The Quantitative Analysis of Plant Growth.* Blackwell Scientific Publications, Oxford.

Grime, J. P. (1977): Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Natur.* **111:** 1169–1194.

— & Hunt, R. (1975): Relative growth rate: its range and adaptive significance in a local flora. *J. Ecol.* **63:** 393–422.

Hagendijk, A., van Soest, J.L. & Zevenbergen, H.A. (1975): *Taraxacum* (behalve sectie *Vulgaria*). *Flora Neerl.* **IV**(9): 1–52.

—, — & — (1982): *Taraxacum* sectie *Vulgaria. Flora Neerl.* **1V**(10a): 53–150.

Hoagland, D.R. & Snijder, W.C. (1933): Nutrition of strawberry plants under controlled conditions. *Proc. Am. Soc. Hortic.* **30:** 288–296.

Hommels, C.H., Kuiper, P.J.C. & de Haan, A. (1989b): Responses to internal potassium concentrations of two *Taraxacum* microspecies of contrasting mineral ecology: The role of inorganic ions in growth. *Physiol. Plant.* **77:** 562–568.

—, Tanczos, O.G. & Kuiper, P.J.C. (1989a): Responses to internal nitrogen and phosphorus of two *Taraxacum* microspecies of contrasting mineral ecology: critical N and P concentrations of whole plants. *Physiol. Plant.* **77:** 555–561.

Hughes, A.P. & Freeman, P.R. (1967): Growth analysis using frequent small harvests. *J. Appl. Ecol.* **4:** 553–560.

Hunt, R. (1978): *Plant Growth Analysis.* Studies in Biology No. 96. Edward Arnold, London.

— (1980): Diurnal progressions in dry weight and short-term plant growth studies. *Plant Cell Environ.* **3:** 475–478.

— (1982): *Plant Growth Curves. The Functional Approach to Growth Analysis.* Edward Arnold, London.

Kuiper, D. & Kuiper, P.J.C. (1988): Phenotypic plasticity in a physiological perspective. *Acta Oecol. Oecol. Plant.* **9:** 43–59.

Lambers, H. & Dijkstra, P. (1987): A physiological analysis of genotypic variation in relative growth rate. Can growth rate confer ecological advantage? In: van Andel, J., Bakker, J.P. and Snaydon, R.W. (eds): *Disturbance in Grasslands.* 237–252. W. Junk Publishers, Dordrecht.

Øllgaard, H. (1983): Hamata, a new section of Taraxacum (Asteraceae). *Pl. Syst. Evol.* **141:** 199–217.

Oomes, M.J. & Mooi, H. (1981): The effect of cutting and fertilizing on the floristic composition of an Arrhenatherion elatioris grassland. *Vegetatio* **47:** 233–239.

Parsons, I.T. & Hunt, R. (1981): Plant growth analysis: A program for fitting of lengthy series of data by the method of B-splines. *Ann. Bot.* **48:** 341–352.

Piggot, C.D. (1980): Book review of Grime. *J. Ecol.* **68:** 704–706.

Poorter, H. (1989a): Plant growth analysis: towards a synthesis of the classical and functional approach. *Physiol. Plant.* **75:** 237–244.

— (1989b): Interspecific variation in relative growth rate: On ecological causes and physiological consequences. In: Lambers, H., Cambridge, M.L., Konings, H. and Pons, T.L. (eds): *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants.* 45–68. SPB Academic Publishing, The Hague.

— & Lewis, C. (1986): Testing differences in relative growth rate: a method avoiding curve fitting and pairing. *Physiol. Plant.* **67:** 223–226.

Roetman, E. & Sterk, A.A. (1985): Growth of microspecies of different sections of *Taraxacum* in climatic chambers. *Acta Bot. Neerl.* **35:** 5–22.

Smakman, G. & Hofstra, J.J. (1982): Energy metabolism of *Plantago lanceolata* as affected by changes in root temperature. *Physiol. Plant.* **56:** 33–37.

Sterk, A.A., Groenhart, M.C. & Mooren, J.F.A. (1983): Aspects of the ecology of some microspecies of *Taraxacum* in the Netherlands. *Acta Bot. Neerl.* **32:** 385–415.

—, Hommels, C.H., Jenniskens, M.J.P.J., Neuteboom, J.H., den Nijs, J.C.M., Oosterveld, P. & Segal, S. (1987): *Paardebloemen, planten zonder vader.* Stichting Uitgeverij KNNV, Utrecht.

Taylor, G.J. (1989). Maximum potential growth rate and allocation of respiratory energy as related to stress tolerance in plants. *Plant Physiol. Biochem.* **27:** 605–611.

Wickens, L.K. & Cheeseman, J.M. (1988): Application of growth analysis to physiological studies involving environmental discontinuities. *Physiol. Plant.* **73:** 271–277.