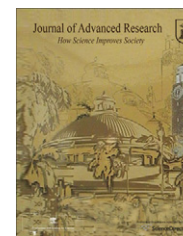




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ORIGINAL ARTICLE

Size-class structure and growth traits of *Anastatica hierochuntica* L. populations as rainfall indicators in aridlands

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KEYWORDS

Rain gauge;
Resource allocation;
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Specific leaf area;
Leaf area index

Abstract Field data verified by green house experiment were used to evaluate the response of *Anastatica hierochuntica* L. to the amount of rainfall. Field study of the populations was carried out in the runnel and depression microhabitats of gravel and sand sites. Four water treatments, equivalent to 100, 200, 500 and 1000 mm rainfall, were used to simulate different levels of water availability. Under 500 and 1000 mm rainfall, the size-class structure of *A. hierochuntica* populations consists of a high proportion of large size-class individuals, while a higher proportion of small size-class individuals was obtained under 100 and 200 mm rainfall. The dry skeletons of *A. hierochuntica* can be used as a “rain gauge” to predict the amount of rain or water received. The dominance of small size-classes (from < 1 to 8 cm³) gives a prediction of less than 200 mm rainfall received. Intermediate size-classes (8–64 cm³) characterize habitats with 200–500 mm rainfall, while habitats with > 500 mm rainfall produce large size-classes (> 64 cm³). Small size-class individuals produced under low amounts of rainfall allocated up to 60% of their phytomass to the reproductive organs. Allocation to reproductive organs decreased with the increase in the amount of rainfall, while allocation to the stem increased in large size-class individuals produced under the highest amount of rainfall (1000 mm) reaching 54%. Increased allocation to stem in large-sized individuals favours the hygrochastic seed dispersal role in the plant. The root/shoot ratio decreased with the increase of the individual size-class, i.e. under high rainfall treatments. Higher values of relative growth rate, net assimilation rate

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and leaf area index were obtained under high water treatments. Conversely, less expanded leaves, i.e. lower specific leaf area, were manifested in the lowest water treatments.

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Introduction

Variation in life history traits is influenced by ecological and evolutionary factors [1]. In desert environments, survival of plant species depends on their adaptive strategies that permit higher reproductive output accompanied by an efficient dispersal mechanism [2,3]. The way in which organisms allocate their energy supplies to vegetative and reproductive structures has been investigated by several authors [1,4–8].

Ecological data support the abundance of annuals rather than that of perennials in disturbed habitats [3,9,10]. Under water stress prevailing in deserts, annuals with short life-spans and greater reproductive allocation (r-strategists) are more favoured than perennials (k-strategists) with long life-spans and smaller reproductive allocation [11,12], especially in unpredictable environments [13]. An annual plant living in a desert environment has to grow rapidly and to convert the energetic and mineral resources obtained during the vegetative phase into seeds [14]. Several studies demonstrated that annuals have higher seedling growth rates [15] and higher allocation to reproductive structures [16]. The early attempt at flowering and the gradual shift of phytomass to reproductive structures may constitute an adaptation to an uncertain environment [17].

Phenotypic diversity and the capacity of a species to adapt its life history traits according to the environmental conditions possibly exist among annual species. A single species exhibits an annual, biennial or perennial life cycle in response to arid unpredictable environmental conditions [8,18]. In this case, the plant may shift from an r- to a k-strategy when a high amount of rainfall is received in wet years and live as an r-strategist in dry years to ensure yearly seed production [8].

Anastatica hierochuntica L. (family: Brassicaceae) is a desert annual, widespread in the Egyptian deserts, characterized by an efficient mechanism of seed dispersal [3,19,20]. This mechanism depends on the hygrochastic nature of the dead curled branches. After senescence, the dry lignified stem branches curl around the enclosed fruits, and then uncurl hygrochastically when wetted by rainfall. Seeds on the uncurled dry plants (skeletons) are released by the force of rain drops on the fruit valves. It is likely that the species may be an effective predictor for water availability in the plant's habitat as rainfall availability and volume are the main limiting factors for seed release and germination. The species is phenotypically plastic in response to the water conditions of the environment [5,21]. The species is subject to over collection for medicinal uses since the infusion of the skeletons was reported to reduce pain and facilitate childbirth and is used as an emmenagogue and for epilepsy [22]. The present work aims at undertaking field and experimental study to investigate the relationship between the amount of rainfall and the crown volume of *A. hierochuntica* skeletons and the possible use of the species as a "rain gauge"; and the plasticity of life history traits as affected by the amount of rainfall.

Material and methods

Field data

The populations of *A. hierochuntica* are associated with habitats collecting runoff water such as runnels and depressions. Depression microhabitats accumulate greater amounts of runoff water producing richer growth of the species. Even in desert environments with as low an annual rainfall as 80 mm or less, some microhabitat types such as depressions may receive amounts of water several times the actual rain in the region due to active runoff and catchment areas. The size-class structure of *A. hierochuntica* populations was studied in the runnel and depression microhabitats of gravel and sand sites during the late spring-early summer seasons of 2003–2005. The gravel site is located in Wadi Hagoul (around 70 km east of Cairo), and the sand site is located in the desert of the Bahareya Oasis (around 300 km south-west of Cairo). The mean annual rainfall in both study sites is less than 80 mm [23].

The number of individuals belonging to each size-class was recorded and the percent of contribution relative to the total number of individuals was estimated in the different microhabitats. All individuals in $5 \times 5 \text{ m}^2$ quadrants were uprooted, sorted into size-classes and measured. Five replicates were used. Dry skeletons of *A. hierochuntica* were allotted into different size-classes (Table 1), according to crown volume. The crown of the skeleton has a spherical shape so the volume (cm^3) was measured by the equation: $4/3\pi d^3$, where d is the mean radius of the crown [2,3]. For each of the differentiated size-classes, growth and dry matter allocation traits were taken. These measurements included: root depth and shoot height, root/shoot ratio, mean diameter and number of fruits per individual skeleton. Each plant was separated into root, stem, and reproductive organs, and then oven-dried and weighed to estimate the pattern of phytomass allocation across different organs.

Greenhouse experiment

Dry skeletons of *A. hierochuntica* were collected from naturally growing populations in Wadi Hagoul. Seeds were liberated

Table 1 Volume range of *A. hierochuntica* size-classes.

Size-class	Volume range (cm^3)
1	< 1
2	1–2
3	2–4
4	4–8
5	8–16
6	16–32
7	32–64
8	64–128
9	128–256
10	> 256

from fruits in the sowing day. The experiment was conducted in the Cairo University greenhouse in natural environmental conditions during March to August 2003. Soil used for the experiment was collected from sites where *A. hierochuntica* populations grow in Wadi Hagoul. The soil was not sieved; only large stones were discarded. Seeds were sown in four sets of plastic pots. A total of 20 pots per set, five replicates for each of the four harvest growth stages (seedling, juvenile, flowering–fruiting and fruiting–senescence), represented the four water treatments.

The simulated rainfall treatments were chosen to represent habitats with low water income such as runnels, and habitats with high water income such as depressions, which receive several times (up to 1000 mm) of the actual rainfall due to accumulation of runoff water. The simulated rainfall treatments were 100, 200, 500 and 1000 mm rainfall corresponding to the amounts of irrigation water (tap water). These amounts of simulated rainfall were scheduled for every water treatment in order to prevent leakage of water from pots. Seedlings were thinned to five plants per pot at the seedling stage.

In each growth stage, individuals of *A. hierochuntica* were harvested. The root depth and shoot height, root/shoot ratio, mean shoot diameter, leaf area per plant, and number of flowers and fruits per individual were measured or counted. The volume, percent resource (dry phytomass) allocated across different organs, and the number of seeds per individual were calculated. The leaf phytomass of individuals from the green house experiment was ignored in the calculation of the dry matter allocation, so that the data would be comparable with field data where leaves are shed from dry skeletons.

Data analysis

Analysis of variance was used to test the significance of differences between means of the measured characters for plants raised under the four water treatments in different growth stages or growth intervals. Regression was made between the crown volume of *A. hierochuntica* skeletons and the amount of simulated rainfall (greenhouse experiment), and the size-classes (field data). The leaf area index (total leaf area of individual per pot area) and the reproductive effort (dry phytomass allocated to seeds) were calculated. Relative growth rate, net assimilation ratio, leaf area ratio, leaf weight rate and specific leaf area were calculated according to [24].

Results

Size-class structure

Variation of size-class structure of *A. hierochuntica* in the different microhabitats is shown in Table 2. Smaller size-classes characterize the microhabitats receiving lower amounts of rainfall. In this context, *A. hierochuntica* populations grown in the runnel microhabitat constitutes mostly smaller size-classes as compared to those grown in the depression microhabitat of the same site. The highest proportion of the small size-classes was in the runnel and the gravel-depression microhabitats, where up to 87% of individuals belonging to the smallest size-class were recorded. As a higher amount of runoff water accumulates in the sand-depression microhabitat, larger size-classes increased their representation in the population.

Table 2 Demographic variation of size-class structure of *A. hierochuntica* populations in the runnel and depression microhabitats of the gravel and sand habitat types. Values are means \pm standard deviations. See Table 1 for the volume range of size-classes.

Size-class	Gravel		Sand	
	Runnel	Depression	Runnel	Depression
1	87.61 \pm 9.20	47.04 \pm 10.60	32.49 \pm 4.24	–
2	7.51 \pm 1.30	38.22 \pm 7.60	42.83 \pm 6.60	1.69 \pm 1.41
3	3.75 \pm 0.70	10.29 \pm 2.20	12.70 \pm 1.50	3.94 \pm 3.52
4	1.13 \pm 0.40	–	8.27 \pm 2.56	6.19 \pm 4.2
5	–	4.44 \pm 1.00	–	8.44 \pm 4.6
6	–	–	–	20.25 \pm 8.99
7	–	–	3.69 \pm 0.71	22.49 \pm 7.5
8	–	–	–	31.10 \pm 5.9
9	–	–	–	3.88 \pm 2.3
10	–	–	–	2.02 \pm 1.19

Table 3 Demographic variation of size-class structure and percentage contribution in *A. hierochuntica* populations raised under different water treatments equivalent to 100, 200, 500 and 1000 mm rainfall. Values are means \pm standard deviations. See Table 1 for the volume range of size-classes.

Size-class	Treatment (mm rainfall)			
	100	200	500	1000
1	72.50 \pm 12.30	18.90 \pm 5.20	–	–
2	27.50 \pm 6.30	39.40 \pm 7.30	–	–
3	–	33.50 \pm 6.10	4.50 \pm 0.50	1.20 \pm 0.30
4	–	8.20 \pm 2.50	7.20 \pm 1.60	2.10 \pm 0.50
5	–	–	16.40 \pm 3.10	3.40 \pm 0.90
6	–	–	36.20 \pm 7.80	–
7	–	–	24.30 \pm 5.20	27.20 \pm 4.70
8	–	–	11.40 \pm 2.60	36.50 \pm 5.20
9	–	–	–	22.90 \pm 3.20
10	–	–	–	6.70 \pm 1.10

The influence of the amount of rainfall on *A. hierochuntica* size-class structure (size hierarchy) was tested in the greenhouse experiment as shown in Table 3. The size-classes obtained were 1–2 under 100 mm rainfall, 1–4 under 200 mm rainfall, 3–8 under 500 mm rainfall and 3–10 under 1000 mm rainfall. The representative size-classes with a higher contribution to the populations ranged from small size-classes in the first two rainfall treatments (size-class 1 under 100 mm rainfall and 2–3 under 200 mm rainfall) to intermediate size-classes in the third rainfall treatment (size-classes 5–7 under 500 mm rainfall) and large size-classes in the fourth rainfall treatment (size-classes 7–9 under 1000 mm rainfall).

The regression between the amount of simulated rainfall and the obtained crown volume (as a measure of plant size) outlined the overall relationship between these two variables as in Fig. 1a, and a strong correlation ($R^2 = 0.92$) was obtained. In lower amounts of rainfall (100 and 200 mm), the crown volume increased slowly, then more rapidly at higher amounts of rainfall (500 and 1000 mm). The same trend is observed between the size-class and the crown volume in natural populations in field conditions as shown in Fig. 1b, indicating

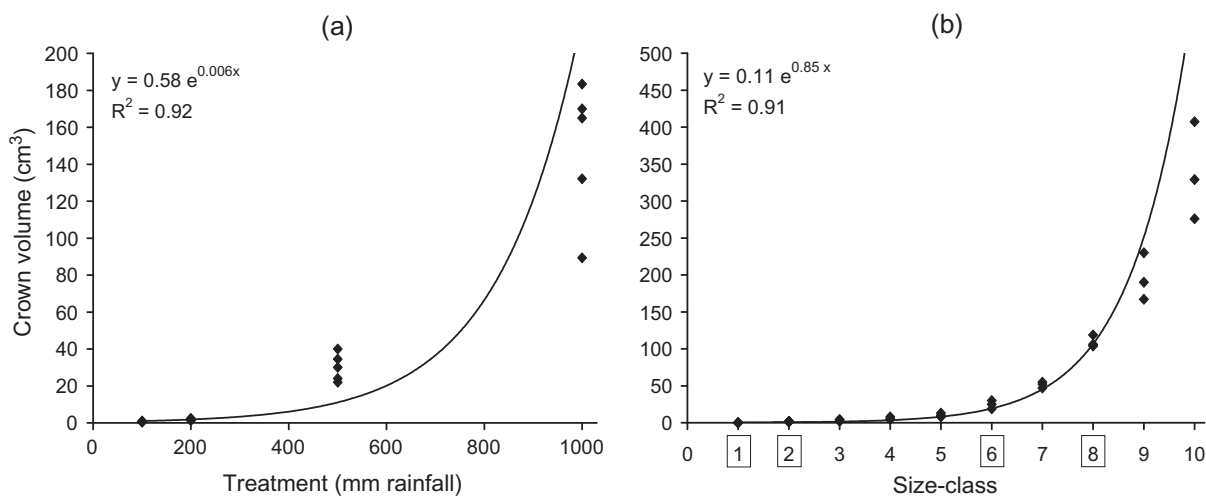


Fig. 1 Relationships between (a) the amount of simulated rainfall treatment and the obtained crown volume and (b) the size-class and the crown volume of *A. hierochuntica* populations growing naturally under field conditions. The size-classes of plants occurring naturally which nearly match the highest proportion of size-classes obtained from populations raised under the simulated rainfall treatments are framed: 1, 2, 6 and 8 corresponding to 100, 200, 500 and 1000 mm rainfall, respectively. See Table 1 for the volume range of size-classes.

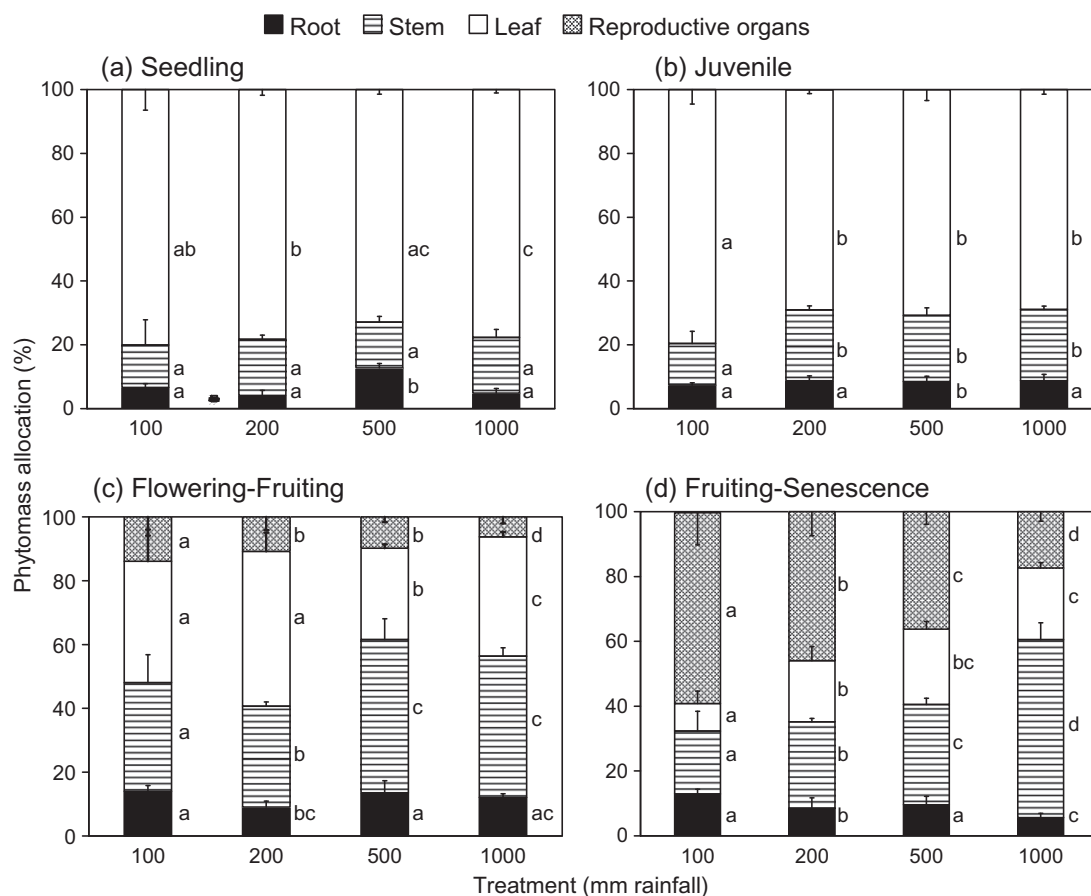


Fig. 2 Phytomass allocation (%) of *A. hierochuntica* raised under simulated rainfall treatments in different growth stages. Values are means \pm standard deviations, different letters within the same series indicate significant difference at ($P < 0.05$).

that higher amounts of rainfall are needed for the production of larger size-classes. Variation of the crown volume in natural

populations and in the water treatment experiment attained J-shaped curves indicating their similarity and the possibility of

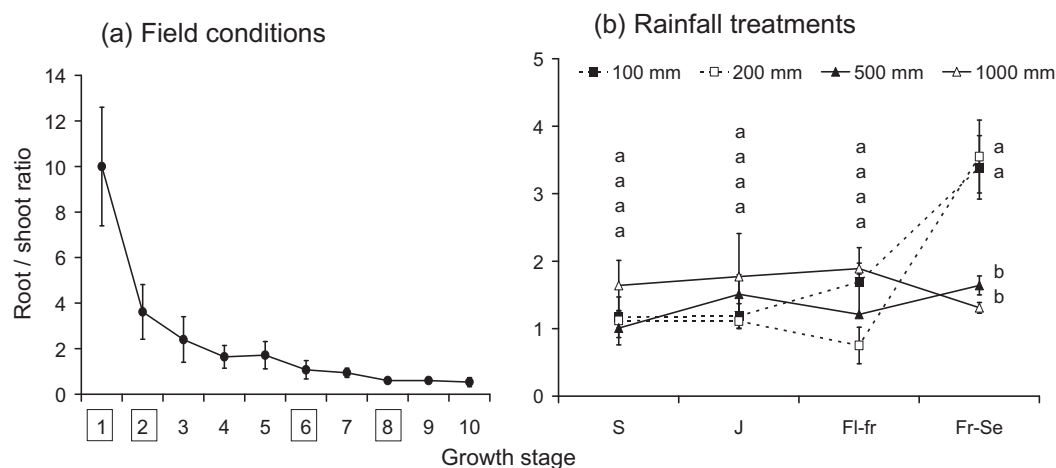


Fig. 3 Root/shoot ratios in different growth stages of *A. hierochuntica* growing naturally under field conditions (a) and raised under different simulated rainfall treatments (b). The size-classes that nearly match the highest proportion of size-classes obtained from populations raised under the water treatments are framed: 1, 2, 6 and 8 corresponding to 100, 200, 500 and 1000 mm rainfall, respectively. S = seedling, J = juvenile, Fl-Fr = flowering-fruiting, and Fr-Se = fruiting-senescence. Values are means \pm standard deviations. Different letters within the same growth stage indicate significant difference at ($P < 0.05$).

prediction of field populations from the experimental simulation of rainfall treatments.

Resource allocation

The percent resource (dry phytomass) allocation to root is generally not affected by water treatment except in the fruiting-senescence growth stage where the percent dry phytomass allocated to root in individuals raised under 1000 mm rainfall was significantly lower than that in the case of individuals raised under the other treatments (Fig. 2).

Variation of dry phytomass allocation to stem increased at the expense of the allocation to leaves (Fig. 2a and b) in the seedling and juvenile growth stages. Percentage allocation to stems increased in the flowering-fruiting growth stage as in Fig. 2c, for all water treatments. However, in the fruiting-senescence growth stage as in Fig. 2d, the percent dry phytomass allocation to stem decreased in favour of the increase in dry phytomass allocation to the reproductive organs. The percent allocation to leaves decreased throughout the growth stages and attained its minimum at the fruiting-senescence growth stage where the percent dry phytomass allocated to leaves increased with the increase in the amount of water applied.

The root/shoot ratio varied with the differences in water treatments. Field data in Fig. 3a reveal a decreased root/shoot ratio as the size-class increased. These results are in accordance with experimental data in Fig. 3b where low water treatments (100 and 200 mm rainfall) have higher root/shoot ratios than high water treatments (500 and 1000 mm rainfall) at the fruiting-senescence growth stage.

At the fruiting-senescence growth stage, a trade-off exists between the percent of phytomass allocated to vegetative and reproductive organs in both the field and the greenhouse experiment Fig. 4a and b. The percent of phytomass allocated to stem varied from 21.34% under 100 mm rainfall treatment to 70.65% for 1000 mm rainfall treatment. This contrasts with

the percent of phytomass allocated to the reproductive organs, which varied from 64.42% under 100 mm rainfall treatment to 22.02% for 1000 mm rainfall treatment. On the other hand, the percent of phytomass allocated to root seems not to be greatly affected by variation of water treatment. A decreased percent of phytomass allocation to root was observed as the size-class increases in the case of naturally grown field populations.

In accordance with field data, trade-offs also exist in the fruiting-senescence growth stage between the number of seeds and the reproductive effort in treated individuals, where the number of seeds increased from 10.7 seeds per individual under 100 mm rainfall treatment to 1344 seeds per individual for 1000 mm rainfall treatment in Fig. 4c and d. This increment in the number of seeds corresponds to a decline in the reproductive effort from 0.19 under 100 mm rainfall treatment to 0.06 for 1000 mm rainfall treatment. The number of fruits increased with the increase in the crown volume and the amount of water received as in Fig. 4e and f. Alternatively, the dry phytomass of 100 seeds increased from the low/intermediate size-classes (1-6), and then decreased in larger size-classes (7-10). Similarly, the dry phytomass of 100 seeds significantly increased under 100-500 mm rainfall treatments, and then significantly decreased for 1000 mm rainfall treatment, where values reached 122 mg as compared to 141.2 mg in the case of 500 mm rainfall treatment.

Growth traits

Slower relative growth rate (RGR) in the seedling/juvenile growth interval was observed in the 200, 500 and 1000 mm simulated rainfall treatments as compared to the 100 mm simulated rainfall treatment, which had the highest RGR as in Fig. 5a. This slow RGR is compensated for in the juvenile/flowering-fruiting growth interval, where 500 and 1000 mm rainfall treatments showed significantly higher values of

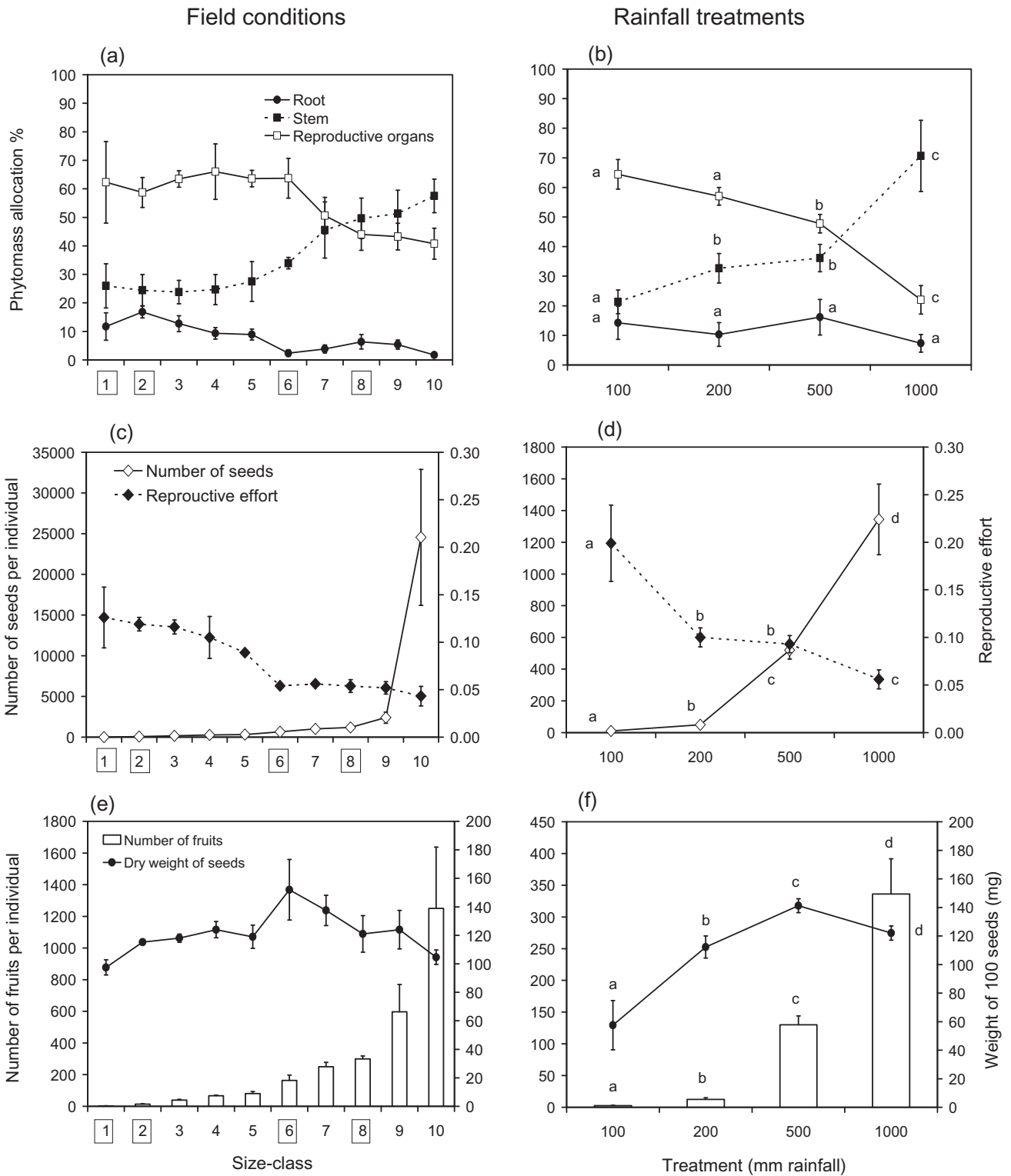


Fig. 4 Trade-offs between some reproductive traits of *A. hierochuntica* individuals belonging to different size-classes in field populations and populations raised under the simulated rainfall treatments in the senescence stage; (a and b) phytomass allocation% to reproductive organs, stem and root (leaf phytomass was neglected here for experimental data to be comparable with field data where leaves are shed from dry skeletons), (c and d) the number of seeds per individual and the corresponding reproductive effort, and (e and f) number of fruits and dry weight of 100 seeds. The size-classes that nearly match the highest proportion of size-classes obtained from populations raised under the rainfall treatments are framed: 1, 2, 6 and 8 corresponding to 100, 200, 500 and 1000 mm rainfall, respectively. Values are means \pm standard deviations, different letters within the same series indicate significant difference at ($P < 0.05$) for water-treated populations.

RGR than 100 and 200 mm rainfall treatments. At the last growth interval, i.e. flowering to senescence, RGR greatly decreased to its lowest values. The net assimilation rate (NAR), as shown in Fig. 5b, followed the same trend as that

of RGR: increasing from the seedling/juvenile to the juvenile/flowering–fruiting growth interval for all water treatments, with significantly higher values in the 500 and 1000 mm rainfall treatments.

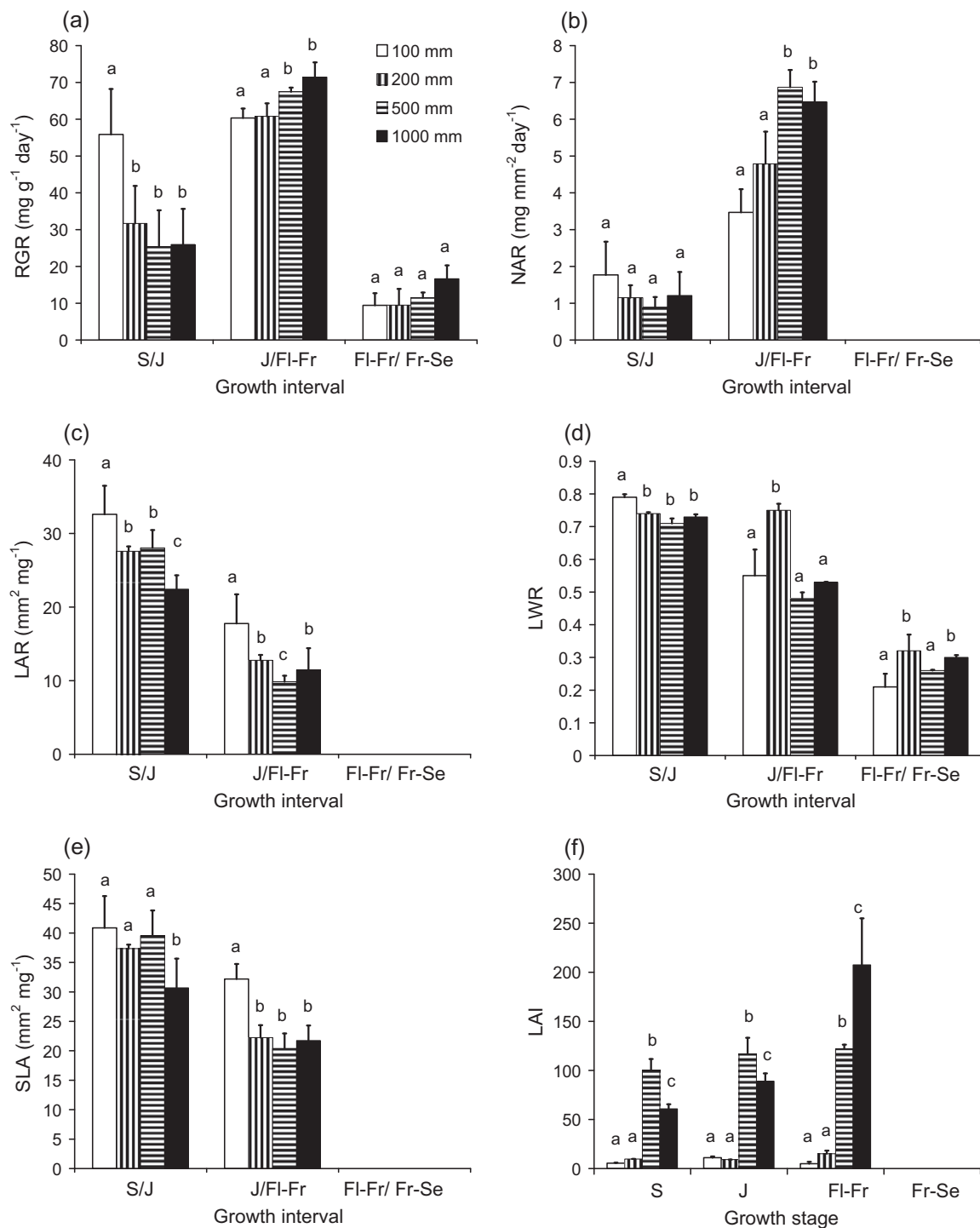


Fig. 5 Growth traits of *A. hierochuntica* populations raised under different simulated rainfall treatments: (a) Relative growth rate (RGR), (b) net assimilation rate (NAR), (c) leaf area ratio (LAR), (d) leaf weight ratio (LWR) and (e) specific leaf area (SLA) in different growth intervals and (f) leaf area ratio (LAI) in different growth stages. S = seedling, J = juvenile, FI-Fr = flowering–fruiting, and Fr-Se = fruiting–senescence. Bars topped by different letters are significantly different at ($P < 0.05$) within the same growth interval (growth stage in the case of LAI). Note that in the Fr-Se stage, dry leaves did not provide data for leaf area so no data are shown for LAI in this stage and in the FI-Fr/ Fr-Se growth interval for NAR, LAR and SLA.

A higher leaf area ratio (LAR) and leaf weight ratio (LWR) at the seedling/juvenile growth interval (Fig. 5c and d) in the four water treatments reflect the allocation of the highest percent of phytomass to leaf in the seedling and juvenile growth stages. The specific leaf area (SLA) also decreased as in Fig. 5e, from the seedling/juvenile to the juvenile/flowering–fruiting growth interval, with the highest values obtained in the 100 mm rainfall treatment. Generally, the SLA and LAR decreased with the increase in water treatment. The same trend was observed in the case of LWR, except for higher values recorded under 200 mm rainfall treatments at the juvenile/flowering–fruiting and flowering–fruiting/flowering–senescence growth intervals.

The LAI (mm² leaf area per mm² pot area) attained significantly higher values under 500 and 1000 mm rainfall treatments than under lower water treatments as in Fig. 5f. LAI values were significantly higher under 500 than under 1000 mm rainfall treatment in the seedling and juvenile growth stages. In the flowering/fruiting growth stage, LAI becomes greater under the 1000 than under the 500 mm rainfall treatment.

Discussion

Simulated rainfall and size-class structure

Among the adaptations of desert annuals, one of those is their ability to regulate their body size according to water availability [11,21,25–27]. In the present work, *A. hierochuntica* demonstrated a highly plastic adjustment mechanism in response to changes in simulated rainfall treatment. This response is verified by the strong relationship between the amount of rainfall and the resulted crown volume of skeletons. Small size of *A. hierochuntica* (2–3 mm height, 2–3 branches, few small leaves and 1–5 fruits) was recorded by Evenari et al. [21] in extremely arid localities. In high soil moisture, the plant may reach 15–20 cm height, 25–30 cm crown diameter, possess tens of branches and have hundreds of fruits.

Experimentally, raising *A. hierochuntica* under different water treatments resulted in different size-class structures. As the amount of the available water increased, the contribution of individuals belonging to larger size-classes increased. The size-class variation within single populations and habitats

was observed by Obeid et al. [28] and Ogden [29]. This change in size-class structure was attributed to the spatial heterogeneity in soil water availability. In this view, plants in microhabitats with a higher amount of soil water (e.g. depressions) have a size-class structure that is dominated by larger size-classes, reflecting higher reproductive output than those in microhabitats with lower amounts of soil water (e.g. runnels) [21,30]. This spatial heterogeneity of soil water is caused by the redistribution of rain water through run off. Accordingly, the size-class structure of *A. hierochuntica* populations under field conditions consists of a higher proportion of larger size-classes in the depression microhabitats as compared to the runnel microhabitats. Similarly, the proportion of larger size-classes increased in the sand habitat type, which receives higher annual rainfall water than does the gravel habitat type.

Matching the field and experimental data, one may deduce that the amount of rainfall is the most important factor in controlling the crown volume of *A. hierochuntica* individuals. Moreover, the highly plastic response of the species to soil water resulted in different size-class structures in different microhabitats of the same site. Generally, single individuals can-not be used as a measure (rain gauge) of the amount of rain fallen or water received in a habitat. One can, however, infer from the standing dry skeletons of *A. hierochuntica* the amount of rainfall possibly fallen and/or the amount of soil water in a specific habitat from the size-class structure of the populations in that habitat. In this context, the dominance of individuals belonging to larger size-classes in a microhabitat indicates a higher amount of rainfall and/or soil water in this microhabitat and vice versa.

The percentage of size-classes contribution to the *A. hierochuntica* populations raised under different rainfall treatments, shown in the optimal prediction curves as in Fig. 6, could be used for the prediction of water income in a particular microhabitat type. By comparing the field data with the experimental results of simulated rainfall treatment, three predictions are deduced: (1) the dominance of small size-classes (from < 1 to 8 cm³) in the population indicates that the site received rainfall amounts equivalent to less than 200 mm rainfall; (2) the dominance of intermediate size-classes (8–64 cm³) indicates rainfall amounts equivalent to 200–500 mm; and (3) the dominance of large size-classes (> 64 cm³) reflects rainfall amounts equivalent to more than 500 mm. Therefore, studying the population structure of the species in a specific microhabitat type and comparing it to the optimal curves could be used as a rough predictor for the amount of water received in a microhabitat.

Resource allocation trade-offs and growth analysis

Plant species allocate nutritional and energetic resources in a strategic manner that maximizes fitness under the prevailing environmental conditions [16]. Therefore, trade-offs exist in the allocation of resources to organs that differ in life history functions [4]. *A. hierochuntica* possesses a high capacity to allocate phytomass flexibly according to water availability. Under low amounts of rainfall (small size-classes), e.g. under 100 and 200 mm rainfall treatments, plants allocate most of their phytomass to reproductive organs that may reach up to 60% of the total phytomass. Under high amounts of rainfall (large size-classes), e.g. under 1000 mm rainfall treatments, only up

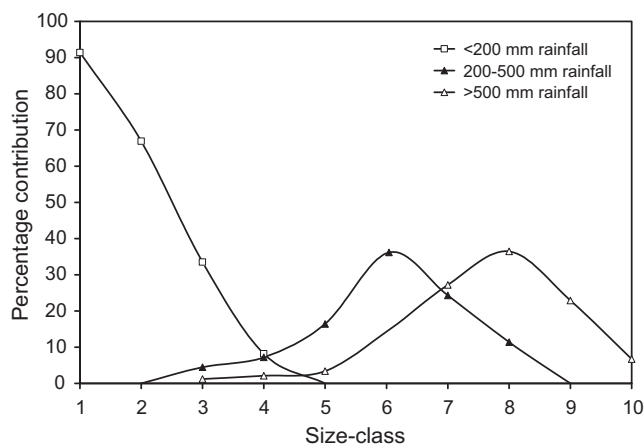


Fig. 6 The expected optimal curve of size-class distribution under different amounts of rainfall.

to 20% of phytomass is allocated to reproductive organs while 55% is allocated to stem, compared to 19% of phytomass allocated to stem under 100 mm rainfall treatment. The species may produce one fruit as quickly as possible, and many more fruits and seeds over a prolonged period in favourable soil moisture conditions. This tactic is a key element in understanding the species population dynamics and is thought to ensure the production of seeds even in dry years when only small-sized individual plants can be attained [31–33].

The increase of the percent of phytomass allocated to stem at high amounts of rainfall was reported by Hickman [31] in the case of *Polygonum cascadense* to maximize the competitive ability of the species in a moist environment with richer plant cover. It is noticed by Hegazy [5] that *A. hierochuntica* invested a relatively large proportion of phytomass in stem under high water treatments and deduced that this expenditure on stem brings rewards in terms of increased seed dispersal through repeated curling and uncurling, and avoidance of predation through minimizing seed exposure. From this point of view, the increase in the percent phytomass allocation to stem may be considered an adaptive behavior supporting the hygrochastic feature of *A. hierochuntica*. The difference in the allocation of the reproductive phytomass between seeds and the structures protecting and dispersing them was reported for other annuals [32] in deserts.

With the increase of the amount of rainfall, the reproductive output (represented by the number of fruits and seeds) increased; however, the amount of phytomass devoted to seed production decreased. Negative relationships between seed size and number have been reported by Werner [34] for a single species growing in different habitats, and by Primack [35] for various species of the same genus. Furthermore, a higher reproductive allocation was reported for plant communities in dry conditions [36] and in disturbed environments [31,37].

The root/shoot ratio was found to decrease as the size-class of *A. hierochuntica* increased. This trend was observed in field populations but was less pronounced in populations raised under simulated rainfall treatments. Ideally, increased phytomass allocated to root is supposed to increase the ability to compete for below-ground resources at low nutrient supply [38]. Also, the allocation of less resource to the root systems in nutrient rich conditions was also reported [39]. For *A. hierochuntica* the resource allocation to sexual and hygrochastic organs usually comes at the expense of root.

The significantly higher RGR and NAR in the juvenile/flowering–fruiting growth stage, which was not coupled with increased LAR, may be partly attributable to the ability of the reproductive structures, including the fruits of *A. hierochuntica*, to photosynthesize. The contribution of the green reproductive structures to the energetic cost of their own production is recorded by Bazzaz and Reekie [40]. Moreover, Gedroc et al. [39] reported the increase in RGR in nutrient rich conditions, which may hold for the significantly greater RGR and NAR in the juvenile/flowering–fruiting growth interval, and LAI in all growth stages under the high water treatments (500 and 1000 mm rainfall). It is noticeable that the increase of the amount of simulated rainfall caused a decrease in SLA coupled with an increase of LAI, i.e. the production of few more expanded leaves in low rainfall treatments and many small leaves in high rainfall treatments. The life span of small size-classes is short and may extend from one to a few weeks. The large size-classes, having longer life spans, may be obliged

to produce more leaves to fulfill the plant's photosynthetic needs. In this case, small leaves are produced to endure the harsh desert conditions [41].

Conclusions

Anastatica hierochuntica possesses a high flexibility to adjust its size and life history traits in accordance with the amount of water in the habitat. Hence, the occurrence of different size-class structures of *A. hierochuntica* populations reflected different microhabitats receiving different amounts of rainfall. In spite of the strong correlation between the amount of rainfall and the obtained crown volume, the size-class structure rather than single individuals can be used as “rain gauge” due to: (1) soil water heterogeneity that may support population individuals of variable size-classes even if the amount of rainfall is low; and (2) size-class hierarchy that can be attained by the species even under different amounts of rainfall.

The percent of phytomass allocated to the reproductive organs of *A. hierochuntica* individuals increased with the decreased amount of rainfall (in small size-classes) to ensure reproductive output in dry years. In large size-classes, the percent of phytomass allocated to stem increased with the increase in the amount of rainfall. This also favours the reproduction process of the species because the increased allocation to stem in the large individuals helps in the dispersal of a large number of seeds and their protection from predation or release at wrong times. The percent of phytomass allocated to root decreased with increasing amounts of rainfall as there is no need for root to occupy large soil volumes. Higher relative growth rate, net assimilation rate and leaf area index in high water treatments (500 and 1000 mm rainfall) suggest higher leaf production and a probable contribution of green fruits to photosynthesis. The high values of the specific leaf area revealed the formation of more expanded leaves in the case of low water treatments (100 and 200 mm rainfall).

The following measures are of great importance for conservation of the species: (1) collection must be prevented from the runnel microhabitats, which receive relatively low rainfall amounts and produce meagre plant growth; (2) collection of skeletons from depressions is recommended instead; and (3) collection of small size-classes is preferred to reduce mass seed loss.

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