

RESEARCH PAPER

Branching the risks: architectural plasticity and bet-hedging in Mediterranean annuals

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Allometric trajectories; architecture; branching; *Emex spinosa*; *Hippocrepis unisiliquosa*; phenotypic plasticity; risk; *Trifolium purpureum*.

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ABSTRACT

It has been suggested that architectural plasticity in shoot size and number allows plants to manage environmental risks. Simpler structures require shorter development times and fewer resources, which secure minimal fitness even under risky and unfavourable conditions. Here we tested the hypothesis that the magnitude of such architectural plasticity depends on the species' developmental strategy. Specifically, species with late reproduction were expected to express the highest levels of architectural plasticity in response to environmental cues predicting high probability of abrupt deterioration in growth conditions. This hypothesis was tested by comparing Mediterranean and semi-arid populations of three species, which differed in growth strategy: *Trifolium purpureum*, a determinate and late flowerer, and *Emex spinosa* and *Hippocrepis unisiliquosa* that flower indeterminately throughout the season. All plants were exposed to varying levels of water availability and competition, but only *T. purpureum* displayed plastic architectural responsiveness to the experimental manipulations. In contrast, the early and extended step-by-step flowering of both *E. spinosa* and *H. unisiliquosa* reflected a relatively deterministic bet-hedging reproductive schedule, whereby minimum fitness is secured even under adverse conditions. These two opposing strategies gave contrasting results, with *E. spinosa* and *H. unisiliquosa* displaying reduced efficiency under favourable conditions under which *T. purpureum* had the highest reproductive efficiency. The evolutionary interplay between deterministic risk-averse and plastic risk-prone growth strategies might reflect contrasts in the probability and severity of environmental risks, and the costs of missed opportunities.

INTRODUCTION

Although phenotypic plasticity helps organisms to buffer fitness losses under environmental adversity and foster growth gains when environmental opportunities arise (Bradshaw 1965; Schlichting 1986; Sultan 1987; DeWitt & Langerhans 2004), it might have significant costs and limitations (DeWitt *et al.* 1998). Specifically, phenotypic plasticity is expected to evolve only in environments of intermediate variability and above minimum levels of environmental predictability (Alpert & Simms 2002).

Among the most dramatic expressions of phenotypic plasticity are changes in plant size under variable growth conditions (Bradshaw 1965; Harper 1985; Tomlinson 1987; Schmid 1992; Clauss & Aarssen 1994; Biere 1995; Hutchings *et al.* 1997). However, not every change in mass can be defined as 'true plasticity' (McConnaughay & Coleman 1999). Plant size or shape may vary due to ontogenetic changes which occur regardless of environmental cues, *i.e.* ontogenetic drift (Evans 1972; Bazzaz 1997; McConnaughay & Coleman 1999). For example, plants must reach a minimum vegetative size before they switch to reproduction (De Jong *et al.* 1998; Jacquemyn *et al.* 2010); this unavoidable ontogenetic constraint might be wrongly interpreted as a manifestation of phenotypic plasticity when

comparing reproductive allocation in plants of different sizes (Fig. 1a and b). However, true plasticity in reproductive allocation can only be demonstrated by comparing similar-sized plants (Fig. 1c and d). Plants have been shown to plastically shift between distinct alternative allometric trajectories in response to competition (Weiner & Thomas 1992; Weiner & Fishman 1994), nutrient availability (Ericsson 1995), light availability (Bonser & Aarssen 1994), water shortage (Huang *et al.* 2010) and photoperiod cues (Shemesh *et al.* 2012).

Size variability is often accompanied by architectural plasticity (McConnaughay & Bazzaz 1992; Weiner & Thomas 1992; Weiner & Fishman 1994; Preston 1999; Sachs 1999; Sultan 2004; Guo *et al.* 2007; Weiner *et al.* 2009). Plants of variable overall sizes not only bear different numbers of constant-size organs but might also express plasticity in both the size and order of their vegetative organs (*e.g.* Schmid & Bazzaz 1990; Gruntman & Novoplansky 2011; Shemesh *et al.* 2012). Regardless of their plastic attributes, branching patterns have important implications for plant performance.

Generally, branched plants are expected to be more efficient than long and un-branched plants for two main reasons: lateral branches that emerge from existing larger branches of lower order may require less resources and time before switching to reproduction (*e.g.* Sachs 1999). Additionally, under resource

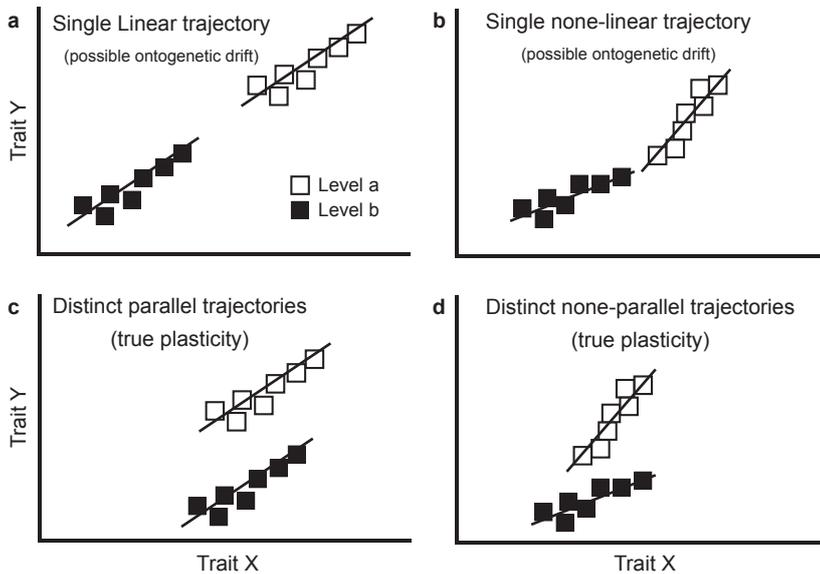


Fig. 1. Schematic depiction of linear (a,c) and non-linear (b,d) scenarios of ontogenetic drift and true plasticity (after Weiner 2004). Levels 'a' and 'b' are generic and can refer to any treatment group.

abundance, multiple simultaneously-growing tips are expected to enable higher total growth rates (e.g. Huhta *et al.* 2000). Accordingly, under improved conditions, highly branched canopies, where a large number of high-order laterals branch from a few large infrastructural branches, are expected to be more efficient and ultimately produce more seeds, compared to plants that allocate the same initial amount of resources to fewer growth axes (Novoplansky 1998; Shemesh *et al.* 2012). However, developing large infrastructural branches might be risky when resource or time availabilities and predictabilities are limited or where abrupt environmental stress might curtail growth or cause total failure (e.g. Siddique & Sedgley 1985).

The effect of branching on seed production efficiency has been studied mostly in agricultural settings (e.g. Beuerlein *et al.* 1971). For example, non-irrigated, field-grown soy plants, which were allowed to maintain only their seminal shoot and first basal branch, produced significantly more seeds than intact control plants, which developed a larger number of infrastructural branches (Siddique & Sedgley 1985). The higher seed production was attained in the pruned plants by regenerative branching of the remaining intact shoots. The fact that the pruned soy plants outperformed their intact controls suggests that allocation to large vegetative branches may only be adaptive under abundant resources and development time, but such a developmental scheme might incur significant costs under limiting growth conditions (Cohen 1971; Shemesh *et al.* 2012).

Here, we tested the general hypothesis that the branching architecture of Mediterranean annual plants is plastically tuned to fit inter-seasonal variability in growth conditions. Specifically, plants perceiving cues informative of benign or improved future growth conditions were expected to develop more complex canopies, in anticipation of increased final size. In contrast, when expecting poor growth conditions, plants were expected to develop canopies with simpler architecture, which would ensure minimum fitness before termination.

In a previous study, *Trifolium purpureum* showed significant effects of photoperiod and germination timing on shoot architecture. Plants perceiving photoperiod cues typical of the season's end and plants that germinated late developed fewer branches and reduced their allocation to large infrastructural

branches (Shemesh *et al.* 2012). In plants with a deterministic flowering pattern, such as *T. purpureum*, development of the inflorescence terminates branch growth. Flowering in such plants usually occurs late in the season, when inflorescence number is limited by the number of already existing branches. Late flowering is typical of plants of relatively mesic Mediterranean environments, where the variable timing of the season's end renders late blooming risky (Aronson *et al.* 1992, 1993). These risks are expected to select for high levels of plasticity in branch size and positioning, enabling the plant to fine-tune its growth to the time left until the end of the season and limit the risk of failure of large branches before they complete their reproduction (Shemesh *et al.* 2012). Under even more precarious conditions, such as in arid and semi-arid environments, where the end of the season is even less predictable and early catastrophic termination is more imminent, plants are expected to demonstrate increasingly cautious and thus less plastic architectural schemes, with early transition to reproduction and continuous translation of biomass gains into reproduction throughout the season. Such bet-hedging, step-by-step development is expected to curtail fitness losses due to early catastrophes. However, such risk-averse development schemes are also prone to significant missed-opportunity costs under benign or improved growth conditions (Novoplansky 1998).

In order to test the hypothesis that anticipated future conditions affect branching order and complexity irrespective of canopy size, plant development was observed in plants from Mediterranean (MED) and semi-arid (SAR) populations of three annual plants, which differ in their natural distribution and growth habits under variable water availability and competition levels.

Water availability and competition were manipulated as both are known to have compelling effects on the length and quality of growth conditions in Mediterranean and semi-arid environments (Noy-Meir *et al.* 1973; Sher *et al.* 2004). As competition is expected to impose water deficiency and other growth limitations, we expected competition and water availability to have additive effects; however, due to the ability of plants to detect neighbours and pre-empt their competitive effects (Aphalo & Ballare 1995; Smith 2000; Pierik *et al.* 2003),

we also expected that plants would demonstrate more pronounced architectural responses to competition than to resource limitations alone (Novoplansky *et al.* 1990; Aphalo *et al.* 1999; Moreno *et al.* 2009; Novoplansky 2009; Shemesh *et al.* 2011).

Plants were predicted to have higher allocation to large infrastructural branches under high water availability and low competition, or if from a Mediterranean population, due to their anticipated better growth conditions compared to their SAR counterparts. The relatively mesic *T. purpureum*, which has a deterministic flowering scheme (Fig. 2a), was expected to display greater architectural plasticity compared to the more xeric *Emex spinosa*, which has an indeterminate growth habit (Fig. 2b). The variable growth habits and plastic behaviours were expected to bestow relative advantages under different growth conditions. For example, the increased architectural plasticity was expected to allow *T. purpureum* higher ability to take advantage of abundant growth conditions. However, increased allocation to large infrastructural branches was also predicted to be risky under unfavourable growth conditions, such as drought or competition. In contrast, *E. spinosa* was expected to be better adapted to stressful growth conditions, but to incur missed-opportunity costs, *i.e.* reduced reproductive efficiency, under improved growth conditions. Finally, it was predicted that *Hippocrepis unisiliquosa*, which has an intermediate growth habit, would have intermediate levels of branching plasticity and missed-opportunity costs.

MATERIAL AND METHODS

The plants

Trifolium purpureum (Papilionaceae) is a Mediterranean annual legume, occurring mostly in undisturbed grasslands throughout the Mediterranean and semi-arid parts of Israel. This species has a deterministic flowering pattern and it blooms towards the end of the growing season (Zohary & Feinbrun-Dothan 1966; Fig. 2a). Seeds were collected from

two populations: a MED population at Achihud (32°54' N, 35°10' E; 600 mm annual rain fall (a.r.f.)), located in a typical Mediterranean habitat patchily dominated by *Quercus calliprinos*, *Pinus halepensis* and open grasslands, growing on Terra-rosa and Rendzina soils. The SAR population was located next to Pura (31°29' N, 34°46' E; 320 mm a.r.f) in semi-arid, loess soil shrubland dominated by sparse perennial shrubs such as *Retama raetam* and *Atriplex halimus*, annual plants or exposed biological crust.

H. unisiliquosa (Papilionaceae) is an annual Mediterranean legume, common to undisturbed shrublands throughout Israel. This species has indeterminate flowering, with variable proportions of the nodes flowering throughout the growing season. Seeds were collected from MED shrubland near the city of Jerusalem, (31°46' N, 35°13' E; 554 mm a.r.f.), dominated by *Sarcopoterium spinosum* on Terra-rosa soil. The SAR population was situated near Ofakim (31°16' N, 34°49' E; 198 mm a.r.f.) and dominated by perennial shrubs such as *Thymelaea hirsuta*, *Noaea mucronata* and *Atractylis serratuloides*, patches of annual grassland and biological crust (Boeken & Shachak 1994). *E. spinosa* (Polygonaceae) is a Mediterranean annual plant typical of disturbed habitats, with large populations in semi-arid and arid regions of Israel. *E. spinosa* has an indeterminate flowering (Weiss 1980), with flowers continuously emerging from all nodes throughout the growing season (Fig. 2b). Young field-germinated transplants were collected from sandy Mediterranean grassland near Hadera, (32°26' N, 34°53' E; 517 mm a.r.f.) and from a semi-arid population near Ofakim (31°16' N, 34°49' E; 198 mm, see site description above).

Growth conditions

Plants were grown in 1.5-L plastic pots with a top diameter of 15 cm. The pots were filled with washed, seedless top sandy soil (Rhodoxeralf; Goldshleger *et al.* 2009) and 2.5 g of Osmocote controlled release fertiliser (15% N, 9% P₂O₅, 10% K₂O; Scotts, Geldermalsen, The Netherlands) were thoroughly mixed into the top 5 cm of soil of each pot.

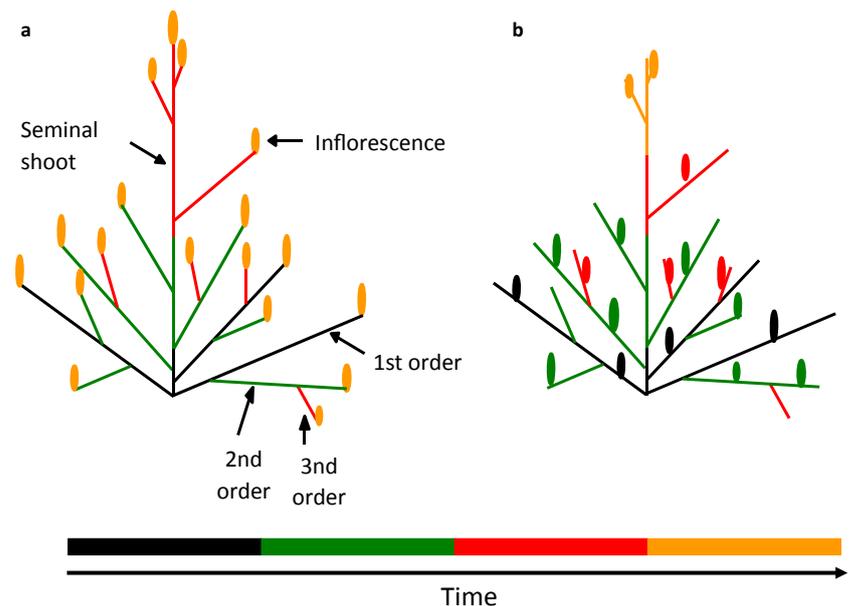


Fig. 2. Schematic growth trajectories of a late-blooming species (*T. purpureum*; a) and of an indeterminate-blooming species (e.g. *E. spinosa*; b).

Seeds of *T. purpureum* and *H. unisiliquosa* were sown in November 2006, which is their natural germination time in Israel. For *E. spinosa*, field-germinated seedlings were used due to the lack of available seeds. Similar-sized 7–14-day-old seedlings with one true leaf were collected from the field and planted in the growth facility, 2 weeks after sowing the *T. purpureum* and *H. unisiliquosa*. All pots were watered with tap water daily for 1 week, to maximise germination and ensure establishment. Germination of the *T. purpureum* and *H. unisiliquosa* began after 5 days, at which time the seedlings were thinned to the desired densities. Following seedling thinning, plants were watered daily to field capacity with tap water for 14 days, after which they were assigned to their experimental treatments.

Plants were assigned to either low density (one plant per pot for all species) or high density (six plants per pot in *T. purpureum* and *H. unisiliquosa*, and four plants per pot in *E. spinosa*) treatments. The different densities in *E. spinosa* resulted from the limited number of seedlings that could be fitted into a single pot. Individual pots were assigned to either high (H) or low (L) water availability. Plants in the H water treatment were irrigated to field capacity daily, while ensuring proper drainage and root aeration. Low water plants were kept just above wilting point by simultaneously irrigating all pots with 250 ml water, when over 10% of the plants showed signs of wilting. In most cases, signs of wilting appeared almost simultaneously in all pots. Each treatment combination had an average of 14 replicates for *T. purpureum* and *E. spinosa* and 25 replicates for *H. unisiliquosa*. The variable replication levels resulted from large differences in germination rates. In order to control for the effect of positioning within the growth facility, similar-sized seedlings were grouped into experimental blocks. Due to variability in germination, not all blocks included all eight treatment combinations.

The experiment was conducted at the Ecological Growth Facility, Sede Boker Campus (30°51' N, 34°46' E) under quasi-ambient conditions but protected from frost, rain and strong winds. Pots were spaced 20 cm apart on wovenmesh benches.

Data collection

The plants were harvested on 15 April 2007, 152 days after germination in *T. purpureum* and *H. unisiliquosa*, and 140 days after planting in *E. spinosa*. Harvest time fitted the natural end of the growing season, when MED annual plants ripen fruits and rapidly senesce. All plants, including the SAR plants, were alive at harvest. The architecture of each shoot system was analysed, recording branch size and order, including the number of leaves on each branch. The roots were carefully washed and both shoots and roots were dried in a ventilated oven at 60 °C for 48 h. The biomass of roots, vegetative and reproductive parts of each plant was weighed using an analytical balance. The biomass of intact pods and inflorescences were found to be highly correlated with seed biomass in both *H. unisiliquosa* ($R^2 = 0.91$, $P < 0.001$) and *T. purpureum* ($R^2 = 0.74$, $P = 0.001$) and were therefore used as a proxy for fitness. Fitness of *E. spinosa* was estimated using achene biomass.

The roots of neighbouring plants sharing the same pot could not be untangled and thus root biomass was recorded per pot and later averaged per plant.

Statistical analysis

In order to ensure that the variances of variable scores in different treatment combinations were symmetrical and not proportional to their means, all ANOVAS were conducted on $\ln(x + 1)$ transformed data (Zar 1999). In such analyses, significant interactions in ANOVAS on log-transformed data do not necessarily indicate that the experimental effects were not additive, but rather that they were not multiplicative on the original, untransformed, scale. Data presented in the figures are untransformed. All response variables were analysed using full factorial ANOVAS, with competition (competition, no competition), water (high, low) and origin (MED, SAR) as fixed factors. Replication blocking was included as a covariate to depict positional variation across the growth facility.

Reproductive allocation was calculated as the ratio between reproductive biomass and total plant biomass. As the main focus here was shoot development and reproductive allocation, the results regarding reproductive and root biomass are presented in the supplementary material (Tables S1–S2, Figs S1–S6).

In order to test whether the observed architectural responses expressed true plasticity rather than ontogenetic drift (Evans 1972), allometric comparisons were conducted (Weiner & Thomas 1992). Because there were no significant overlaps in total plant biomasses between plants belonging to different treatments (<10% of data overlapped between the two treatment levels that had the strongest effect on the dependent variable in each species; data not shown), leaf and branch numbers were compared instead, where more overlap was found (Fig. 3). The relationships between number of leaves on the seminal shoot and number of second-order branches were compared, enabling estimation of the proportion of nodes on the seminal shoot that developed lateral branches. Additionally, in order to estimate the proportion of nodes that developed lateral branches at the level of the entire shoot system, treatment effects were tested on total leaf number/total branch number allometries. For the sake of clarity, the allometric data are separated according to the treatment that had the strongest effect on the dependent variable in each species. While water best divided the data in *T. purpureum* (Fig. 3a and b, Table 1) and *H. unisiliquosa* (Fig. 3c and d, Table 2), competition most sharply separated the data in *E. spinosa* (Fig. 3e and f, Table 3). Complete analysis of the effects of all treatment combinations is presented in the supplementary material (Figs S7–S9).

All analyses were conducted using SYSTAT v. 11 (Systat Software, Inc. IL, USA.)

RESULTS

The experimental treatments affected both plant size and architecture, with patterns varying between the three species. The following sections describe the specific effects of water availability, competition and origin on size and branching patterns of the studied species.

Trifolium purpureum

The number of leaves on the seminal shoot was negatively affected by both water availability and competition, and this effect was stronger in plants experiencing competition (significant water \times competition interaction; Fig. 4a). The

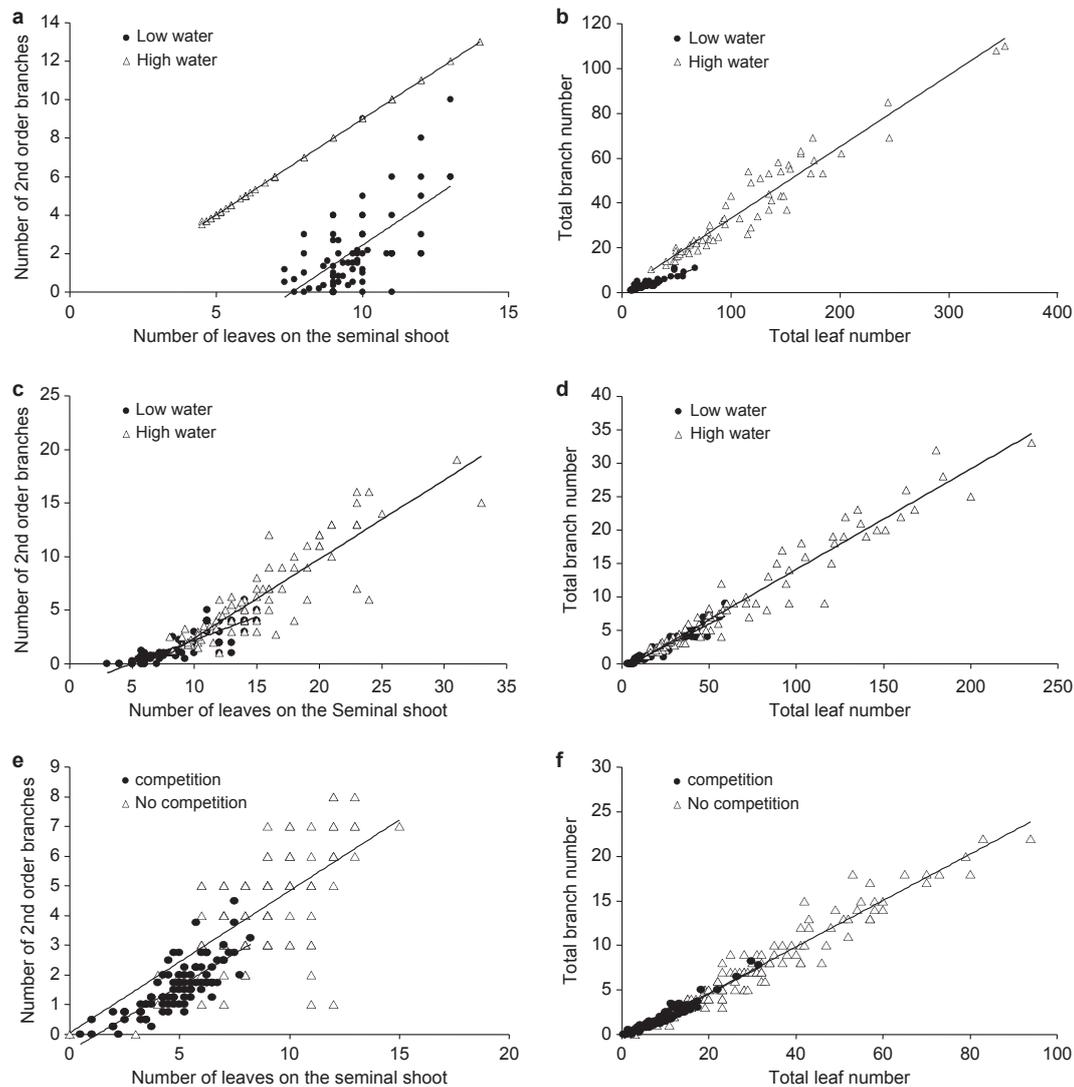


Fig. 3. Number of second-order branches as a function of the number of leaves on the seminal shoot (a,c,e) and total branch number as a function of total leaf number (b,d,f) for *T. purpureum* (a,b) *H. unisiliquosa* (c,d) *E. spinosa* (e,f; see Methods for more information).

number of second-order branches was positively affected by water availability and negatively affected by competition (Fig. 4b). While water availability caused a clear allometric shift in the ratio between the number of leaves on the seminal shoot and the number of second-order branches (Fig. 3a), both competition and origin affected this relationship along the same ontogenetic trajectories ($F_{3,133} = 258.45$, $P < 0.001$; see Table S3 and Fig. S7 for a complete separation of treatment effects). Total leaf number was positively affected by water availability and negatively affected by competition (Fig. 4c). Total branch number was positively affected by water availability and negatively affected by competition. The positive effect of water was higher in plants growing alone (significant water \times competition interaction; Fig. 4d). While water availability caused a clear allometric shift in the ratio between total leaf and branch numbers (Fig. 3b), both competition and origin affected this relationship along the same ontogenetic trajectories (Fig. S7). The relationship between total leaf number and total branch number was affected by water availability. Specifically, under high water availability plants were more branched,

with more branches per leaf number (Fig. 3b; significant water \times total leaf number interaction; $F_{3,133} = 1311.10$, $P < 0.001$; see Table S3 and Fig. S7 for a complete separation of treatment effects). Total vegetative shoot biomass was positively affected by water availability and negatively affected by competition. The positive effect of water was higher in plants growing alone (significant water \times competition interaction). SAR plants were more responsive to competition than the MED plants (significant origin \times competition interaction; Fig. 4e). Regardless of origin, reproductive allocation was positively affected by water availability and negatively affected by competition (Fig. 4f).

Hippocrepis unisiliquosa

The number of leaves on the seminal shoot was positively affected by water availability and negatively affected by competition. MED plants developed more leaves on the seminal shoot and were more responsive to competition compared to SAR plants (significant origin \times competition interaction; Fig. 5a).

Table 1. The effects of origin (MED, SAR), water (High, Low) and competition (with, without) on size and architectural variables in *T. purpureum*.

<i>T. purpureum</i>	df	vegetative shoot biomass		no. seminal shoot leaf		no. second-order branch		no. total leaf		no. total branch		reproductive allocation	
		F	P	F	P	F	P	F	P	F	P	F	P
block	25	1.96	*	1.42	n.s.	1.31	n.s.	1.13	n.s.	0.97	n.s.	1.26	n.s.
origin	1	0.36	n.s.	1.35	n.s.	2.17	n.s.	0.18	n.s.	0.52	n.s.	0.14	n.s.
competition	1	222.12	***	81.38	**	37.94	**	79.35	**	80.79	**	11.86	**
water	1	889.54	***	90.13	**	108.56	**	373.98	**	1099.01	**	238.55	**
origin × competition	1	4.41	*	0.32	n.s.	1.08	n.s.	2.92	n.s.	1.86	n.s.	1.98	n.s.
origin × water	1	0.05	n.s.	0.30	n.s.	4.00	n.s.	1.32	n.s.	0.97	n.s.	0.01	n.s.
competition × water	1	91.47	***	29.02	**	0.55	n.s.	3.74	n.s.	27.09	**	4.72	n.s.
competition × water × Origin	1	1.62	n.s.	1.42	n.s.	0.10	n.s.	0.01	n.s.	0.57	n.s.	0.04	n.s.
error	98												

Replicate block included as a covariate in the ANOVA. n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The significance values for the seminal shoot leaf number, second-order branch number, total leaf number and total branch number were corrected using Bonferroni correction.

Table 2. The effects of origin (MED, SAR), water (High, Low) and competition (with, without) on various size and architectural variables in *H. unisiliquosa*.

<i>H. unisiliquosa</i>	df	vegetative shoot biomass		no. seminal shoot leaf		no. second-order branch		no. total leaf		no. total branch		reproductive allocation	
		F	P	F	P	F	P	F	P	F	P	F	P
block	15	1.45	n.s.	2.56	**	1.96	n.s.	2.64	**	1.07	n.s.	0.68	n.s.
origin	1	56.83	***	19.42	**	103.01	**	62.05	**	85.29	**	18.97	**
competition	1	119.59	***	90.96	**	87.14	**	124.86	**	84.92	**	0.03	n.s.
water	1	332.15	***	177.71	**	282.56	**	281.81	**	251.06	**	56.19	**
origin × competition	1	12.10	**	14.62	**	16.15	**	17.10	**	16.67	**	5.72	*
origin × water	1	25.00	***	0.59	n.s.	1.67	n.s.	2.13	n.s.	16.05	**	0.11	n.s.
competition × water	1	57.25	***	2.72	n.s.	0.85	n.s.	5.91	*	18.81	**	1.76	n.s.
competition × Water × Origin	1	0.97	n.s.	3.33	n.s.	4.59	n.s.	5.40	*	0.03	n.s.	4.32	n.s.
error	96												

Replicate block included as a covariate in the ANOVA. n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The significance levels for the seminal shoot leaf number, second order branch number, total leaf number and total branch number were corrected using a Bonferroni correction.

Table 3. The effects of origin (MED, SAR), water (High, Low) and competition (with, without) on various size and architectural variables in *E. spinosa*.

<i>E. spinosa</i>	df	vegetative shoot biomass		no. seminal shoot leaf		no. second-order branch		no. total leaf		no. total branch		no. reproductive allocation	
		F	P	F	P	F	P	F	P	F	P	F	P
block	28	1.33	n.s.	1.059	n.s.	1.05	n.s.	0.82	n.s.	1.46	n.s.	2.53	**
origin	1	0.01	n.s.	9.57	**	7.70	*	36.13	**	44.75	**	11.59	**
competition	1	480.48	***	265.28	**	283.08	**	429.57	**	331.13	**	0.46	n.s.
water	1	223.82	***	62.97	**	41.75	**	125.39	**	126.01	**	20.40	**
origin × competition	1	0.24	n.s.	8.23	*	3.53	n.s.	0.98	n.s.	6.58	*	0.65	n.s.
origin × water	1	0.07	n.s.	5.24	*	7.03	*	6.04	*	0.14	n.s.	1.55	n.s.
competition × water	1	25.81	***	8.81	**	17.27	**	1.74	n.s.	7.89	*	4.87	n.s.
competition × water × origin	1	0.34	n.s.	5.65	*	0.11	n.s.	1.44	n.s.	0.09	n.s.	2.54	n.s.
error	176												

Replicate block included as a covariate in the ANOVA. n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The significance levels for the seminal shoot leaf number, second-order branch number, total leaf number and total branch number were corrected using a Bonferroni correction.

The number of second-order branches was positively affected by water availability and negatively affected by competition. MED plants developed more second-order branches and were

more responsive to competition compared to SAR plants (significant origin × competition interaction; Fig. 5b). The relationship between number of leaves on the seminal sheet and

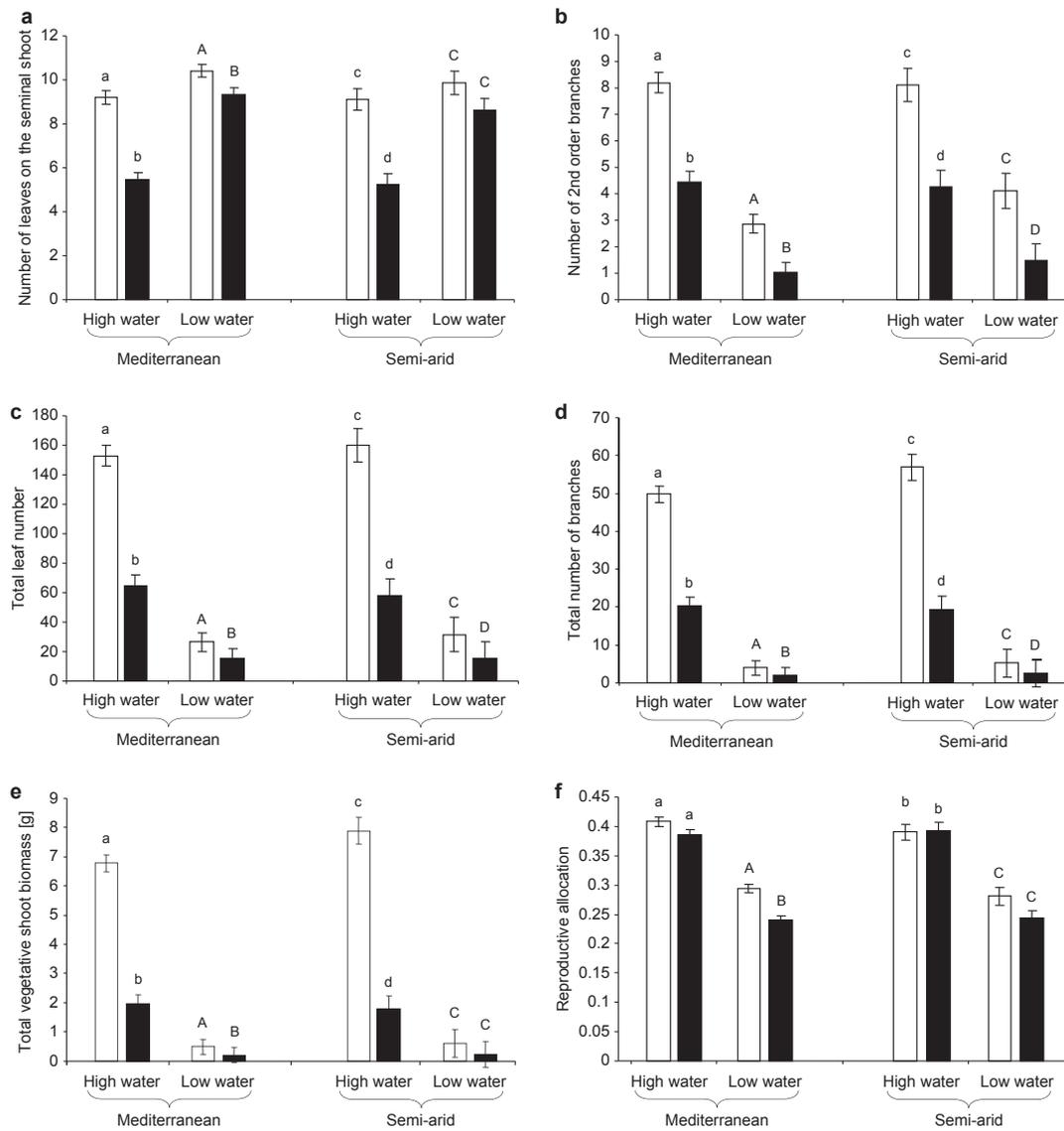


Fig. 4. *T. purpureum*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on number of leaves on the seminal shoot (a), number of second-order branches (b), total leaf number (c), total branch number (d), total vegetative shoot biomass (e) and reproductive allocation (f). Different letters represent Tukey *post-hoc* comparisons within each of the four water \times origin combinations ($P < 0.05$, following Bonferroni correction). Bars represent mean \pm 1 SE (See Table 1 for additional statistical information).

number of second order branches was affected by water availability. Specifically, plants experiencing high water availability produced more branches per leaf number (Fig. 3c; significant water \times number of leaves on the seminal sheet interaction; $F_{3,165} = 332.23$, $P < 0.001$; see Table S4 and Fig. S8 for a complete separation of treatment effects). Total leaf number was positively affected by water availability and negatively affected by competition. MED plants developed more leaves and were more responsive to competition compared to SAR plants (significant origin \times competition interaction). The positive effect of water was higher in the no-neighbour treatment (significant water \times competition interaction; Fig. 5c). Total branch number was positively affected by water availability and negatively affected by competition. MED plants developed more branches and were more responsive to both competition and water compared to SAR plants (significant origin \times competition and

origin \times water interactions). The positive effect of water was higher in the no-neighbour treatment (significant water \times competition interaction; Fig. 5d). The allometric relationships between total number of leaves and branches demonstrated changes along fixed ontogenetic trajectories (Fig. 3d; $F_{3,165} = 1229.138$, $P < 0.001$; see Table S4 and Fig. S8 for a complete separation of treatment effects). Total vegetative shoot biomass was positively affected by water availability and negatively affected by competition. MED plants developed more vegetative shoot biomass and were more responsive to both competition and water, compared to SAR plants (significant origin \times competition; origin \times water interactions). The positive effect of water was more prominent in the no-neighbour treatment (significant water \times competition interaction; Fig. 5e). Reproductive allocation was significantly higher under low water and in SAR plants. Competition had opposite effects

on plants from the two origins; it increased and decreased reproductive allocation in MED and SAR plants, respectively (significant origin \times competition interaction; Fig. 5f).

Emex spinosa

Seminal shoot leaf number was positively affected by water availability and negatively affected by competition. SAR plants developed more leaves on the seminal shoot but were less responsive to competition and water availability, compared to MED plants (significant origin \times competition and origin \times water interactions). The positive effect of water was more prominent in plants experiencing competition (significant water \times competition interaction; Fig. 6a). The number of second-order branches was positively affected by water availability

and negatively affected by competition. SAR plants developed more second-order branches but displayed weaker response to water, compared to MED plants (significant origin \times water interaction). The positive effect of water was more prominent in plants experiencing competition (significant water \times competition interaction; Fig. 6b). The effects of all three factors resulted in changes along fixed ontogenetic trajectories, as demonstrated by the allometric relationship between number of leaves on the seminal shoot and number of second-order branches (Fig. 3e; $F_{3,185} = 153.70$, $P < 0.001$; see Table S5 and Fig. S9 for a complete separation of treatment effects). Total leaf number was positively affected by water availability and negatively affected by competition. MED plants developed more leaves and were more responsive to water, compared to SAR plants (significant origin \times water interaction; Fig. 6c). Total branch number was

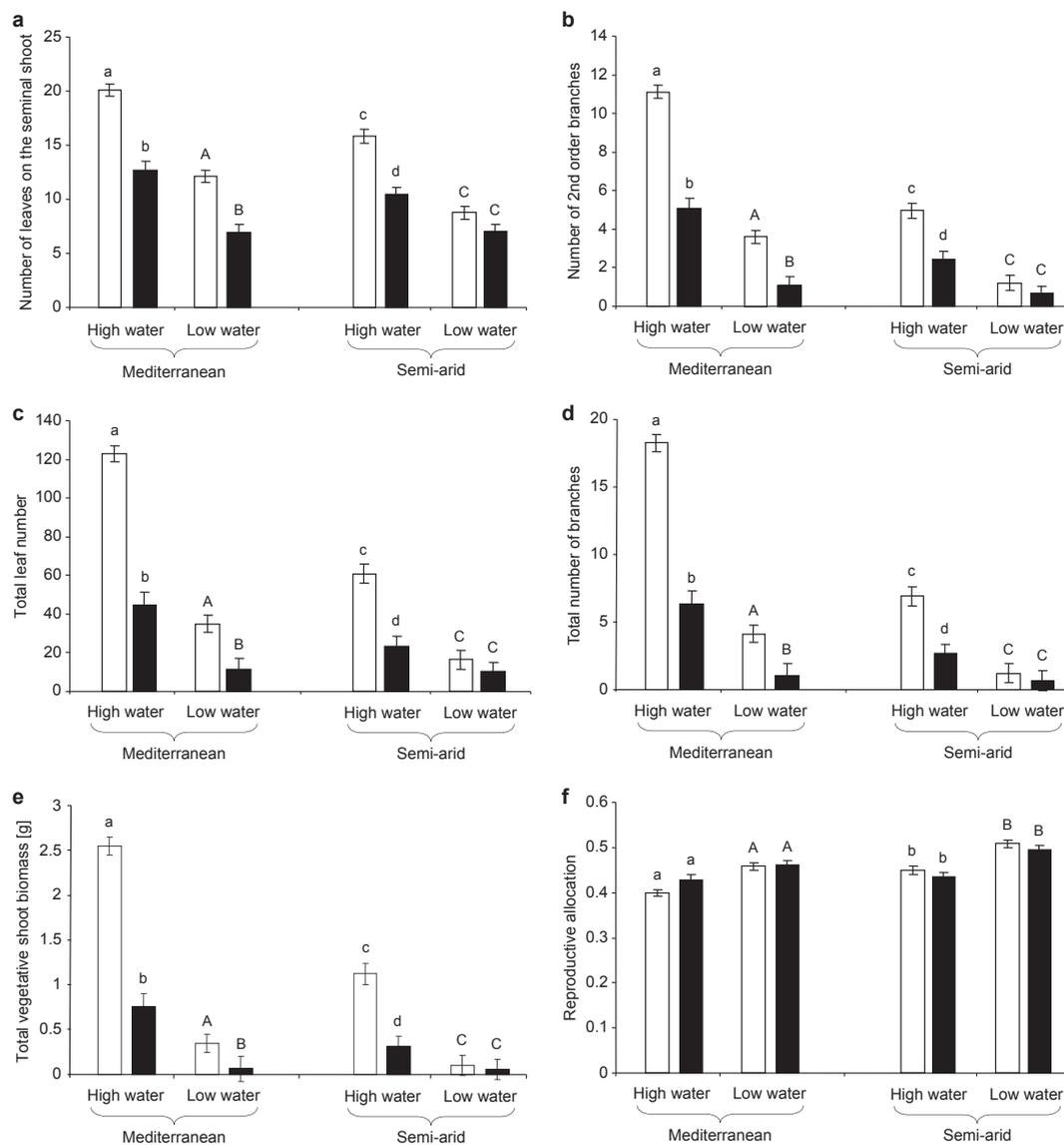


Fig. 5. *H. unisiliquosa*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on number of leaves on the seminal shoot (a), number of second-order branches (b), total leaf number (c), total branch number (d), total vegetative shoot biomass (e) and reproductive allocation (f). Different letters represent Tukey post-hoc comparisons within each of the four water \times origin combinations ($P < 0.05$ following Bonferroni correction). Bars represent mean \pm 1 SE (See Table 2 for additional statistical information).

positively affected by water availability and negatively affected by competition. MED plants developed more branches and had a weaker response to competition, compared to SAR plants (significant origin \times competition interaction). The positive effect of water was higher in the no-neighbour treatment (significant water \times competition interaction; Fig. 6d). The effects of all three factors resulted in changes along ontogenetic trajectories, as demonstrated by the allometric relationship between the total number of leaves and branches (Fig. 3f; $F_{3,185} = 1333.65$, $P < 0.001$; see Table S5 and Fig. S9 for a complete separation of treatment effects). Total vegetative shoot biomass was positively affected by water availability and negatively affected by competition. The positive effect of water was more prominent in the no-neighbour treatment (significant water \times competition interaction; Fig. 6e). Reproductive allocation was higher in plants experiencing water shortage or in SAR plants (Fig. 6f).

DISCUSSION

The operative rationale of natural selection is related to the ways in which organisms negotiate various risks and opportunities. Both genetic differentiation and adaptive phenotypic plasticity are largely dependent on the amount and quality of both evolutionary and ecological information regarding anticipated conditions (Aphalo & Ballare 1995; Alpert & Simms 2002; Novoplansky 2009). When environmental information is sufficient at fine scales, organisms may largely depend on phenotypic plasticity (Bradshaw 1965; Levins 1968; Alpert & Simms 2002), but when such information is limited, organisms are expected to rely on deterministic solutions, which require little or no environmental responsiveness (Cohen 1966). Due to their structural simplicity, continuous juvenility and highly modular structure (Sachs 1991), plants are able to demonstrate high degrees of phenotypic plasticity in both size (e.g.

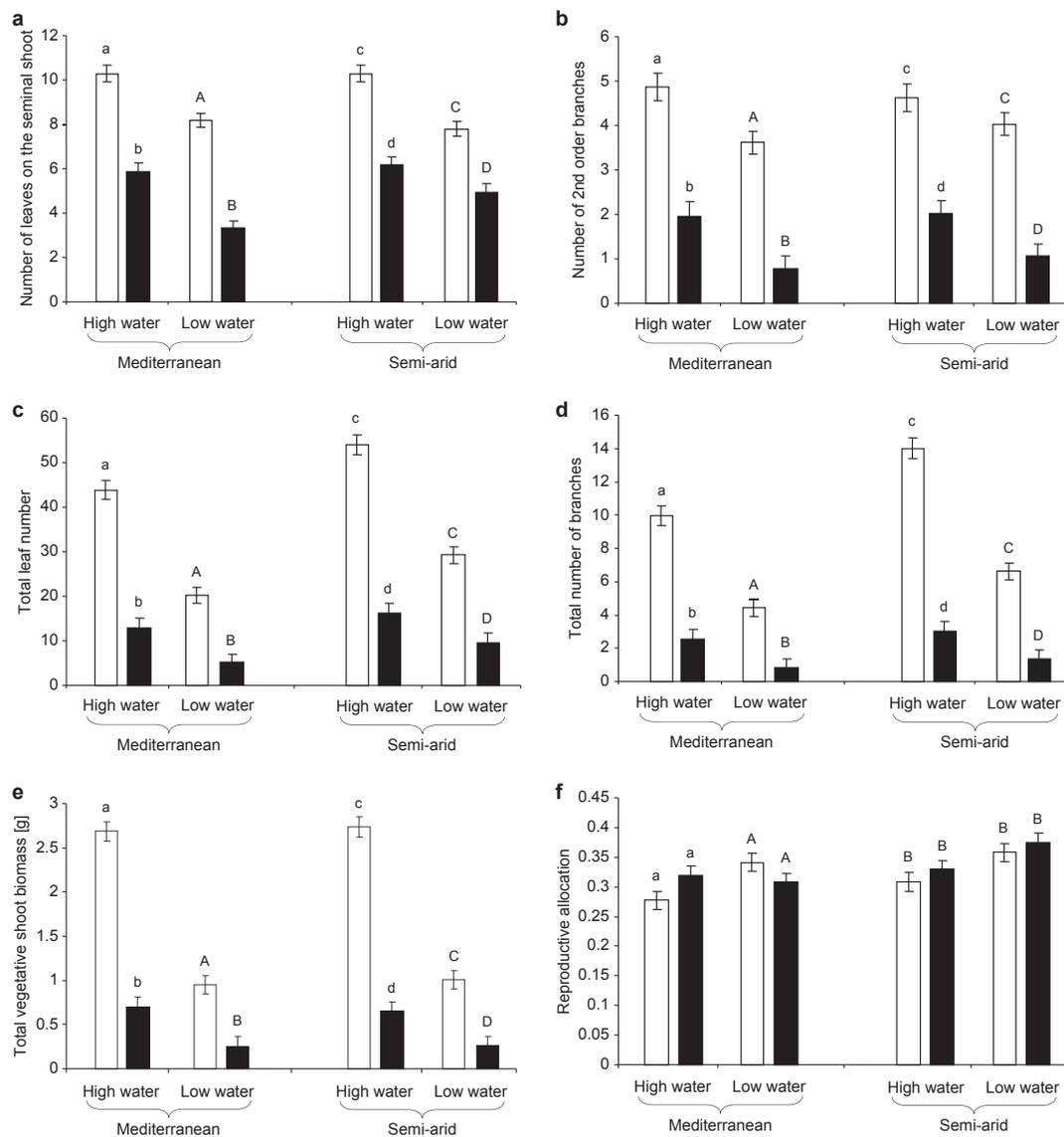


Fig. 6. *E. spinosa*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on number of leaves on the seminal shoot (a), number of second-order branches (b), total leaf number (c), total branch number (d), total vegetative shoot biomass (e) and reproductive allocation (f). Different letters represent Tukey *post-hoc* comparisons within each of the four water \times origin combinations ($P < 0.05$ following Bonferroni correction). Bars represent mean ± 1 SE (See Table 3 for additional statistical information).

Delagrange *et al.* 2004; Harder & Johnson 2005) and architecture (e.g. Alpert 1991; Hutchings & de Kroon 1994; Weiner & Fishman 1994; Herben *et al.* 1997; Herben & Novoplansky 2010; Karkanis *et al.* 2011); however, phenotypic plasticity might be rendered less effective when the environmental heterogeneity is coarse-scaled (Levins 1968) or overly chaotic (Novoplansky 1996; DeWitt *et al.* 1998). Consequently, dependence on phenotypic plasticity is expected to depend on the magnitude of the costs and opportunities caused by environmental heterogeneity.

Plastic shoot architecture

The results demonstrate that the more mesic *T. purpureum* relies on architectural plasticity to take advantage of resource abundance and curtail fitness losses due to potential abrupt deteriorations in growth conditions. Under severe water stress, these plants expressed increased apical dominance, with more leaves on the seminal shoot and fewer first-order lateral branches, compared to well-watered plants (Fig. 4a and b). This plastic switching between two distinct developmental trajectories (Weiner 2004; Fig. 3a and b) enables *T. purpureum* to shift between alternative architectural modes: on the one hand, a simpler, less branched canopy, which develops under resource limitation, allows minimal fitness even under stressful conditions, decreasing the probability of total failure given abrupt termination, while reducing efficiency to some extent (Fig. 4f). On the other hand, a highly branched canopy, typical of well-watered plants, enables greater reproductive efficiency under resource abundance (Aarssen 1995; Fig. 4f).

In a previous experiment, *T. purpureum* plants were shown to plastically alter their architecture in response to late-season photoperiod cues, but not in response to water stress (Shemesh *et al.* 2012). It was suggested that this difference was caused by the high reliability of photoperiod cues compared to water availability. In order to increase reliability of the water availability cues in the current study, more severe water limitation was used in the low-water treatment. It is possible that this increase in severity resulted in increased cue reliability and therefore led to a plastic reaction.

Bet-hedging

As expected, the relatively xeric *E. spinosa* and *H. unisiliquosa* presented significant size responses to both resource availability and competition (Figs 5a,e and 6a,e); however, neither species displayed any noteworthy architectural plasticity (Fig. 3c–f). Although the branch architecture of *H. unisiliquosa* apparently demonstrated a significant response to water (Table S4), this was only a result of the nonlinearity of the ontogenetic trajectory (Figs 1b and 3c) and not a result of true plasticity (Fig. 1c and d). As hypothesised, the more xeric opportunistic *E. spinosa* and, to some extent, the intermediate *H. unisiliquosa* demonstrated that these species mainly rely on deterministic bet-hedging (*sensu* Cohen 1966), step-by-step developmental schemes, whereby vegetative growth and reproduction are tightly coupled in time. Such continuous flowering schemes ensure minimum fitness at the earliest possible time in the growing season; in some cases *E. spinosa* can flower a mere two weeks after germination (Shemesh, unpublished data), which is expected to substantially minimise the risks of total failure due to sudden deterioration in growth conditions, typical of disturbed (e.g. Grime 2001) and arid environments (Evenari *et al.* 1982; for a

review see Seger & Brockmann 1987). Previous studies have demonstrated similar bet-hedging strategies with regard to a variety of ecological phenomena, such as seed dormancy (Siewert & Tielborger 2010), seed dimorphism (e.g. Sadeh *et al.* 2009) and reproductive behaviour in insects (Hopper 1999). For example, a fixed proportion of dormant seeds might limit short-term performance in favourable years while maximising long-term fitness by minimising the risk of total failure in poor years (Cohen 1966). However, deterministic risk-averse development schemes such as those presented in *E. spinosa* and *H. unisiliquosa* are also expected to incur significant missed opportunity costs (*sensu* Brown 1988), expressed as reduced reproductive efficiency under favourable conditions (Figs 5f and 6f). Here too, a reduction in mean fitness under improved conditions is traded off with reduced risk of total failure, fostered by early and stepped flowering (Fig. 2b), therefore minimising the long-term variance and maximising the geometric mean of the fitness (Cohen 1966; Seger & Brockmann 1987).

Evolutionary background

The clear differences in ontogenetic schemes presented by *T. purpureum* compared with *E. spinosa* and *H. unisiliquosa* may be related to the evolutionary background of these plants (Weberling 1989; Prusinkiewicz *et al.* 2007). On the one hand, the late and determinate flowering of *T. purpureum* is expected to be favoured in relatively stable and mesic conditions typical of the northern Mediterranean habitats of this species (Zohary & Feinbrun-Dothan 1966). On the other hand, the step-by-step developmental scenarios presented by *E. spinosa* and *H. unisiliquosa* are expected to be favoured in more disturbed and stressful xeric ecosystems, where a swift and risky deterioration in growth conditions is common (Grime 2001). Regardless of its evolutionary rationale, the relationship between flowering pattern (determinate *versus* indeterminate) and timing (step-by-step *versus* sudden and late) is inevitably more complex than exemplified by the species studied here (Prusinkiewicz *et al.* 2007). For example, many members of the Boraginaceae display terminal blooming but do so in a step-by-step manner over long periods (Zohary & Feinbrun-Dothan 1966; Prusinkiewicz *et al.* 2007). The lack of a strict correlation between the ecological challenge and the developmental characteristics suggests that step-by-step development schemes can be attained by both determinate and indeterminate ontogenetic flowering modes. However, the opposite theoretical scenario, of an indeterminate flowerer with delayed flowering until the end of the season, is less likely to occur, as such blooming behaviour would be less efficient (Cohen 1971; Figs 5f and 6f) without conferring any risk aversion. The complex relationship between flowering schedules, developmental plasticity and environmental conditions calls for a detailed meta-analysis, where the growth strategies in plants from different origins, taxonomic groups and ontogenetic schemes are compared. Such an analysis is expected to elucidate the relationship between environmental variability and reproductive risks, and the interplay between their evolutionary solutions.

Unlike the clear differences in shoot architectural plasticity between species, the differences between ecotypes were mainly evident in size responses to resource availability and competition. The fact that no origin effect could be found on shoot architecture might suggest that ecotypic differentiation in these traits has not yet occurred, either due to the short geographic distances between the field populations (100–200 km), or due

to the weaker effects of environmental differences between the MED and SAR sources compared to the larger effects of the evolutionary history of these species.

Response to competition

Because plant current competition is highly correlated with continued competition, it is unlikely that the observed lack of architectural plasticity in branching in response to competition resulted from limited cue reliability. It seems more plausible that the experimental setup did not emulate the correct levels of light competition typical to dense stands in the field. In their natural habitat, *T. purpureum* plants typically encounter high densities (often more than one plant 1 cm^{-2} ; Novoplansky unpublished data), resulting in severe light competition. Therefore, it is possible that the relatively low canopy densities dictated by the experimental design and pot spacing, which were required to prevent canopy interactions between neighbouring pots belonging to different treatments, competition for light did not reach sufficient levels required for the initiation of architectural plasticity under competition in *T. purpureum*.

CONCLUSIONS

The results demonstrate alternative means used by plants from different backgrounds to mitigate risks of fitness loss imposed by limited environmental predictability and possible catastrophes. Further comparative studies of the ecological implications of changing growth, size and architectural responses under various growth scenarios for a larger number of taxa from differing environmental and taxonomic backgrounds is expected to shed more light on the neglected field of developmental risk management in plants.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Fig. S1. *T. purpureum*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on root biomass.

Fig. S2. *H. unisiliquosa*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on root biomass.

Fig. S3. *E. spinosa*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on root biomass.

Fig. S4. *T. purpureum*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on reproductive biomass.

Fig. S5. *H. unisiliquosa*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on reproductive biomass.

Fig. S6. *E. spinosa*: effects of competition (competition – black bars, no competition – white bars), water availability and plant origin on reproductive biomass.

Fig. S7. *T. purpureum*: complete separation of seminal shoot and total plant data into the different treatment combinations.

Fig. S8. *H. unisiliquosa*: complete separation of seminal shoot and total plant data into the different treatment combinations.

Fig. S9. *E. spinosa*: complete separation of seminal shoot and total plant data into the different treatment combinations.

Table S1. The effects of origin (MED, SAR), water (High, Low) and competition (with, without) on the root biomasses of the three species.

Table S2. The effects of origin (MED, SAR), water (High, Low) and competition (with, without) on the reproductive biomasses of the three species.

Table S3. *T. purpureum*: results of a multiple regression of the number of second-order branches and total branch number (n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Table S4. *H. unisiliquosa*: results of a multiple regression of the number of second-order branches and total branch number (n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Table S5. *E. spinosa*: results of a multiple regression of the number of second-order branches and total branch number (n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

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