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Source: *Ecology*, Vol. 52, No. 3 (May, 1971), pp. 499-506
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1937633
Accessed: 04/12/2010 16:08

ADAPTATION OF GROWTH FORM IN *ECHIUM LEUCOPHAEUM* (BORAGINACEAE)[1]

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Abstract. Ecotype formation in eight populations of *Echium leucophaeum* was studied on La Palma (Canary Islands) at 100-m intervals from sea level to 600 m elevation. Climate varied with altitude, the lower elevation having higher temperatures, evaporation, and wind velocity and lower rainfall. A method for recording growth form of individual plants was developed whereby lateral branch production and branching patterns of woody plants could readily be determined. Height growth, lateral branch production, periodicity, and number of branching cycles of *Echium* were all found to be significantly different in the field, plants from higher elevations having longer branches, more laterals per cycle, fewer cycles, and retarded flowering and fruiting compared with plants near sea level. Two generations of seedlings of the extreme types grown in transplant gardens showed significant differences in inherent rate of growth, indicating genetic adaptation of high and low altitude ecotypes. No significant differences could be shown in the rate of lateral branch formation and periodicity; differences observed in the field with respect to these characteristics may be physiological responses.

INTRODUCTION

Echium leucophaeum Webb is one of the 14 species of branched shrubs of the genus *Echium* endemic to the Canary Islands (Lems and Holzapfel 1968). The species occurs on the four western islands, Tenerife, Gomera, Hierro, and La Palma, between sea level and 800 m. On the latter island particularly dense stands were found near the southern tip below the town of Fuencaliente on coarse volcanic sand. The physiognomy of the plants appeared to vary with altitude (Fig. 1A, B). The purpose of this study was twofold: first, to develop methods of recording the growth form of woody plants quantitatively: and second, to determine to what extent differences in growth form in *Echium* at different altitudes are a matter of genetic adaptation and ecotype formation.

ENVIRONMENTAL MEASUREMENTS

The 600-m slope below Fuencaliente offers a range of environmental conditions. In the Canary Islands the mean annual temperature at sea level is 68°F (Servicio Meteorológico Nacional of Spain 1951–60); it decreases about 0.9°F with every 100-m increase in altitude. Mean annual precipitation at Fuencaliente is 32.7 cm at sea level and 56.3 cm at 600 m.

Air and soil temperatures and evaporation rates were measured on May 19, 1966. Thermometers and white porcelain Livingston evaporation spheres were placed at 10-m, 300-m, and 600-m elevations and read at 1 PM, 3 PM, and 6 PM. Overnight minima were also determined with maximum-minimum thermometers. The drop in temperature with increasing altitude was considerable, and the most pronounced change in soil temperature occurred between 10 m and 300 m (Table 1). Evaporation rates near sea level were about twice as high as at 600 m.

TABLE 1. Temperature and rate of evaporation at different elevations at Fuencaliente, Canary Islands, May 19, 1966

Item	10 m Sand	300 m Sand	600 m Sand	600 m Rocky loam
Evaporation (ml/hr)	4.2	3.0	1.8	2.1
Air temperature (0.5 m above soil) (°F)				
1 PM	78.1	70.1	76.3	74.3
3 PM	76.1	68.3	67.6	66.2
6 PM	68.0	64.4	61.5	62.6
Minimum	62.2	58.7	52.0	52.0
Soil temperature (0.25 m below surface) (°F)				
1 PM	87.0	75.9	75.4	77.2
3 PM	83.0	73.7	74.5	75.9
6 PM	82.1	73.7	73.7	73.1

Eight stations were selected at 100-m intervals of altitude, with two stations at 600 m to test differences in *Echium* growing on sand and on a rocky outcrop with sandy loam soil. Soil samples were collected from the surface and from 25 cm and 50 cm below the surface at four of the stations: 10 m, 300 m, 600 m volcanic sand, and 600 m rocky loam. Hydrogen-ion concentration, percentage of gravel and pebbles (2-mm mesh sieve), and fractions of sand, silt, and clay (Bouyoucos soil hydrometer) were determined. Water content at the time of collection was also de-

[1] Received July 12, 1969; accepted May 15, 1970.

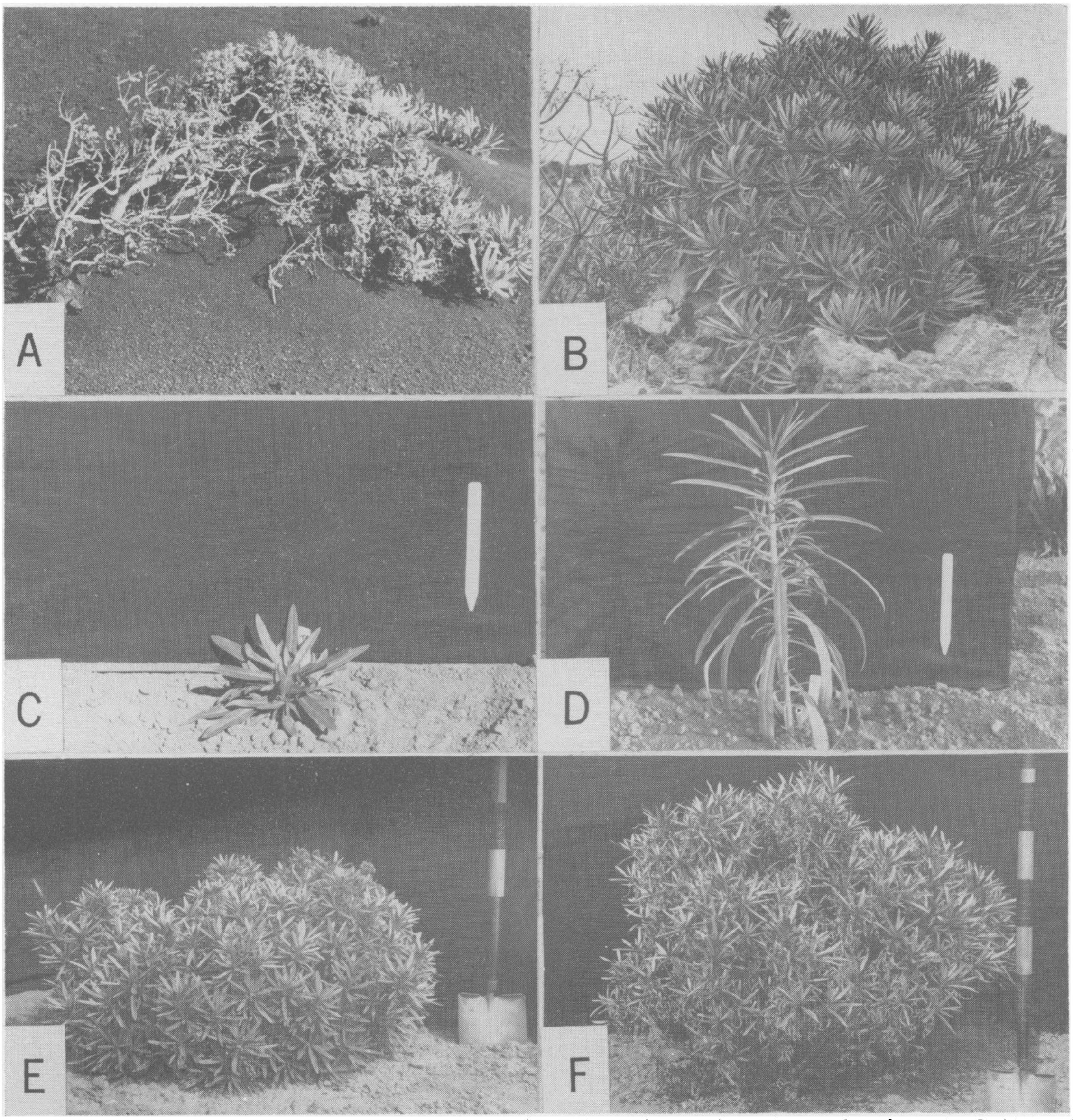

FIG. 1, A–F. Comparison of growth form of *Echium leucophaeum* from 10 m elevation (A, C, E) and from 600 m elevation (B, D, F), Fuencaliente, La Palma. A, B: Appearance of plants in the field; C, D: 2-month-old seedlings growing in transplant garden (scale, 15-cm pot label); E, F: 9-month-old shrubs growing in transplant garden (scale, 10-cm intervals on spade handle).

termined from fresh and ovendry weights. Most of the samples could be classified as sand, with very low clay fractions; only the rocky outcrop area at 500 m had enough silt to fall in the category of sandy loam (Table 2). The sandy loam samples had pH values below 7.0, whereas pH of the volcanic sand varied from 7.2 to 7.9.

Zonation of Vegetation

The town of Fuencaliente (700 m) is on the lower fringes of the pine woodland (*Pinus canariensis*). Below, on the slope down to sea level, we found representative species of the subtropical scrub zone rich in succulents (Crassulaceae, Euphorbiaceae, Asclepiadaceae). At each station a list of species was compiled, and species coverage was estimated according to a scale proposed by Braun-Blanquet (1932) (Table 3). Two factors affect the apparent change in species composition. Near 600 m there is more disturbance because of attempts at agriculture (grapes, sweet potatoes) especially on ash fields; this influence extends to about 300 m. The change in climate and the increased salt spray near sea level encourage the presence of halophytes and bring about the shift from a community of *Euphorbia regis-jubae, Kleinia neriifolia,* and *Rumex lunaria* to a community dom-

TABLE 2. Soil data from three depths (surface, 25 cm below surface, 50 cm below surface) and different elevations at Fuencaliente, Canary Islands

Item	10 m			300 m			600 m (sand)			600 m (rock)	
	Surface	25 cm	50 cm	Surface	25 cm	50 cm	Surface	25 cm	50 cm	Surface	25 cm
pH	7.4	7.9	7.4	7.2	7.4	7.2	7.2	7.5	7.2	5.8	6.7
Gravel and rocks (wt % of total)	13	21	28	19	40	34	8	1	21	20	88
Sand (wt % of fine soil)	94	81	80	94	92	94	96	97	96	67	83
Silt (wt % of fine soil)	6	17	17	5	8	6	3	2	3	32	15
Clay (wt % of fine soil)	0	2	3	1	0	0	1	1	1	1	2
Water present (wt % of total)	0.3	3.8		0.3	6.2		0.3	3.2		4.0	0.9

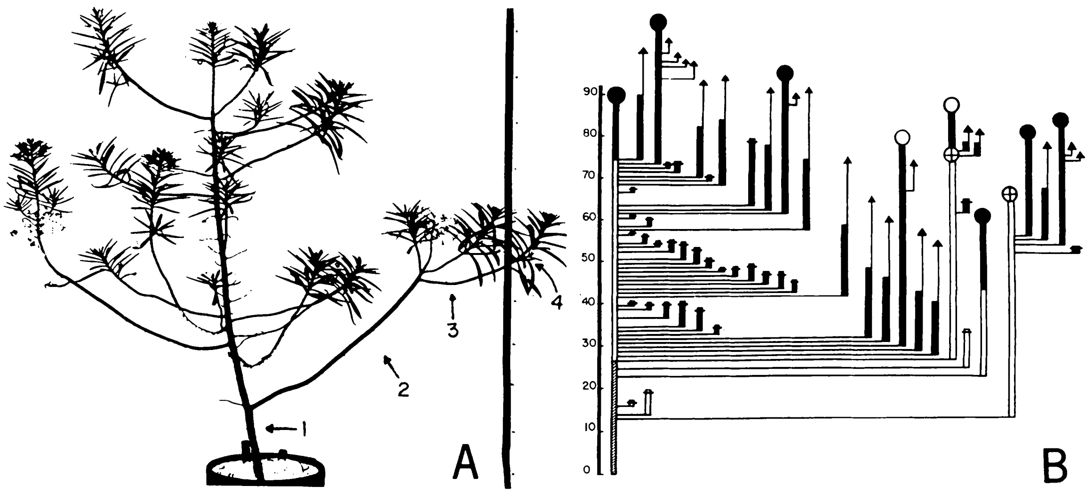

FIG. 2, A, B. Growth form and diagram of *Echium leucophaeum* grown in greenhouse. All branches are plotted vertically, the horizontal lines merely showing points of attachment to main axis. Arrows: leafy vegetative shoots; circles: inflorescences (black—buds, white—flowers, +—fruiting); crossed ends: dead branches. Shading indicates different branching cycles. Material from seed collected at Santa Cruz, La Palma.

inated by *Euphorbia balsamifera, Schizogyne sericea,* and *Astydamia canariensis*. In both of these communities *Echium leucophaeum* plays a dominant or co-dominant role. Table 3 indicates that a fairly abrupt change occurs between 200 m and 300 m.

MEASUREMENT OF *Echium leucophaeum* POPULATIONS IN THE FIELD

To evaluate the growth form of plants growing at different elevations in the field, the following components were measured: height, number of branching cycles, average number of lateral shoots on a branch, and periodicity. At each station the first 50 plants encountered in the center of the local population were analyzed.

The method for determining the number of branching cycles in a plant is illustrated in Fig. 2A, B. The term "branching cycle" is related to the "morphogenetic cycle" mentioned in other papers on growth form (Lems 1962). Ordinarily, a complete morphogenetic cycle in plants with determinate shoots consists of several stages: formation of bud scales around an axillary meristem, vegetative shoot growth and leaf production, formation of inflorescence branches, flowering, and fruiting. The term "branching cycle" is used here because these cycles are not necessarily completed, and several successive shoot generations may be produced before the original shoot flowers. In temperate regions with a well-defined growing season, these cycles are usually correlated with annual weather cycles, a plant completing either one or two, or occasionally a fraction of a cycle per year (Lems 1962). In tropical and subtropical regions, including the Canary Islands, this is much less clear: branching cycles and growth rings in the wood may or may not correspond with

TABLE 3. Vegetation at different stations at Fuencaliente, Canary Islands, in 200-m² areas (combined estimate scale according to Braun-Blanquet (1932))

Species	Plant type[a]	10 m Sand	100 m Sand	200 m Sand	300 m Sand	400 m[b] Sand	500 m[c] Sand	600 m Sand	600 m[d] Rocky loam
Echium leucophaeum (Boraginaceae)	WP	1	2	2	1	2	2	2	2
Euphorbia regis-jubae (Euphorbiaceae)	WP				+				1
Kleinia neriifolia (Compositae)	WP		1	1	+	+			+
Rumex lunaria (Polygonaceae)	WP			1	1	1	1		1
Micromeria sp. (Labiatae)	WP	1	1	1		2		1	1
Lotus glaucus (Leguminosae)	WP			1			+	2	1
Polycarpaea teneriffae (Caryophyllaceae)	HP	1	1	1				1	
Picridium ligulatum (Compositae)	HP		+	1	1				
Aristida adscensionis (Gramineae)	A		1	1		1	1		1
Bromus rubens (Gramineae)	A			1		1		+	1
Wahlenbergia lobelioides (Campanulaceae)	A			+	1	1			
Psoralea bituminosa (Leguminosae)	WP				+			+	1
Lobularia intermedia (Cruciferae)	WP					+		+	+
Tolpis laciniata (Compositae)	HP				1		1	1	1
Ipomoea batatas (Convolvulaceae)	HP				+		1	1	
Hyparrhenia hirta (Gramineae)	HP		1	1					
Pteridium aquilinum (Pteridophyta)	HP				1	1	+	+	1
Notholaena marantae (Pteridophyta)	HP						+		1
Silene gallica (Caryophyllaceae)	A				1	1		1	1
Bidens sp. (Compositae)	A				+	1	1	1	+
Echium plantagineum (Boraginaceae)	A						+	+	
Papaver sp. (Papaveraceae)	A				+			1	
Schizogyne sericea (Compositae)	WP	2	1	1					
Chrysanthemum frutescens (Compositae)	WP			1					
Euphorbia balsamifera (Euphorbiaceae)	WP		1						
Astydamia canariensis (Umbelliferae)	HP	1							
Pennisetum ciliare (Gramineae)	HP			1					
Total number of species		5	9	14	13	18	11	14	23

[a]WP = woody perennial; HP = herbaceous perennial; A = annual.
[b]Additional species only at 400 m: Woody perennial: *Forsskalea angustifolia* (Urtic.) 1; *Inula viscosa* (Compos.) +; *Atriplex* sp. (Chenop.) +; *Phagnalon* sp. (Compos.) +; *Artemisia canariensis* (Comp.) +. Herbaceous perennial: *Agropyron repens* (Gramin.) +. Annual: *Anagallis arvensis* (Prim.) +.
[c]Additional species at 500 m: Annual: *Hordeum vulgare* (Gramin.) 1.
[d]Additional species on rock at 600 m: Woody perennial: *Rubia fruticosa* (Rubiac.) +. Herbaceous perennial: *Tolpis barbata* (Compos.) 1; *Allium* sp. (Amaryl.)1; *Agave americana* (Amaryl.) 1. Annual: *Aira caryophyllea* (Gramin.) 1; *Plantago lagopus* (Plant.) 1; *Tunica prolifera* (Caryoph.) 1; *Vulpia myuros* (Gramin.) 1.

years or rainy seasons in a predictable fashion (Koriba 1958).

In a given population of *Echium,* individuals with a larger number of branching cycles may be assumed to be older than those with small numbers of cycles. We made it a practice to divide the populations into classes according to number of cycles, which may be thought of as an approximation of relative age distribution (Fig. 3). The populations from 300 to 600 m generally had produced no more than six to eight cycles, but as many as 11 and 14 cycles were encountered from 10 to 200 m elevation. Hence these lowland populations were either older or branched more rapidly.

The height measurements of the eight populations were each plotted against the number of cycles on a given plant (Fig. 4). As expected, the taller shrubs in a population have gone through more branching cycles. For each population a regression line may be drawn to show the increase in height per branching cycle. Trends in height increase suggest that the eight populations fall into two groups: short plants which branch close to the ground, growing from sea level to 200 m, and taller plants with more elongated shoot systems found mainly at and above 300 m. Student *t* tests on the regression lines shown in Fig. 4 (lower right) indicate highly significant differences in height growth per cycle, except between 10 and 200 m, between 300 and 400 m, between 500 and 600 m, and between the 600-m rocky loam and the 300-m, 400-m, 500-m, and 600-m sand populations. These tests suggest that the population growing on rocky loam at 600 m was much more variable than the plants on volcanic sand, perhaps indicative of a greater variation in root volumes in soil pockets of different sizes. In general, the regression lines suggest that we are dealing with two different growth patterns: a slow-growing population from sea level to 200 m, and a more rapidly elongating population from 300 m upwards.

Growth in height and number of branching cycles clearly affect the physiognomy of a shrub. To complete the analysis of growth form, we must know the average number of new branches produced by each successive cycle. This will affect the density of the bush; for example, a plant producing an average of two new shoots per branch in each cycle will have two new branches in the second, four in the third, eight in the fourth, etc., resulting in 512 branches after 10 cycles. At the same time, a plant producing

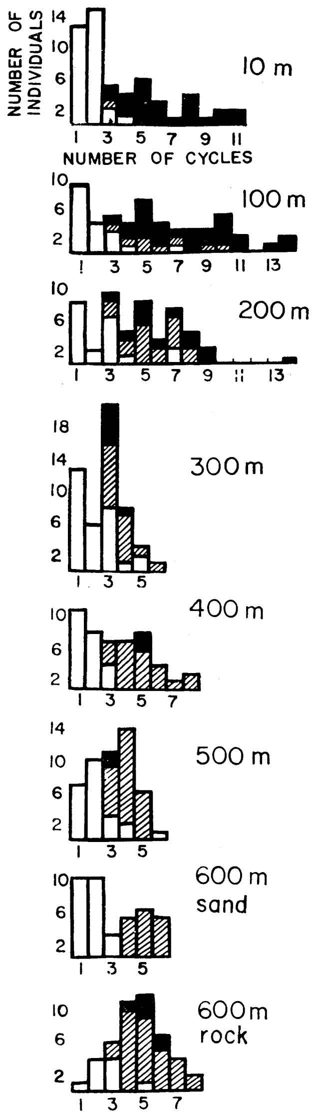

FIG. 3. Periodicity and number of branching cycles of eight populations of *Echium leucophaeum* at Fuencaliente. White: vegetative; black: fruiting; shaded: flowering.

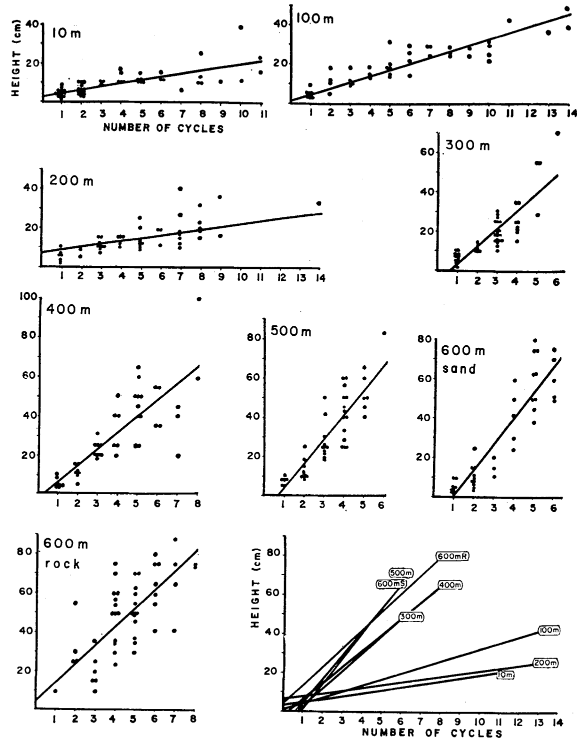

FIG. 4. Heights and numbers of branching cycles of eight populations of *Echium leucophaeum* at Fuencaliente, from 10 m to 600 m elevation. Each dot represents height and number of cycles of a given individual; regression lines show mean increase in height with increase in number of cycles. Last diagram compares all eight populations.

an average of four branches per cycle would have more than 250,000 branches in 10 cycles!

To estimate the mean number of new shoots, four branches of the penultimate cycle were picked haphazardly on each plant and the number of laterals recorded (Table 4). In spite of their apparent density, the lowland plants produced fewer shoots than the plants at and above 300 m. Their dense physiognomy is due to the shortness of the branches, causing crowding around the periphery of the plant; at 600 m the plants are lax enough to accommodate more than six new laterals each successive branching cycle. Differences in branch production were subjected to Student t tests, which showed that there are no significant differences in the mean numbers from 10 m to 300 m, but that above 400 m each successive population differs significantly from those above and below. At 600 m, plants on the rocky outcrop were significantly less branched than those on sandy substrate, resembling most closely the plants from 400 m in shoot production.

The periodicity of each population was recorded by noting whether each of the 50 plants was vegetative, in flower, or fruiting. These observations were made on September 9, 1965, toward the close of the warm, dry season. The first observation to be made from the results (Fig. 3) is that no plant with fewer than three branch cycles had reached reproductive age, that plants with three cycles had started flowering and even fruiting in about 50% of the individuals, but that completely vegetative individuals occurred occasionally even in the class with seven branching cycles. The second observation is that members of each population are well synchronized, and that the lowland populations, especially at 10 m above sea level, are ahead of the ones at higher altitude, having progressed to the fruiting stage.

In summary, the growth-form record of *Echium*

TABLE 4. Mean numbers of lateral branches per branch of *Echium leucophaeum* at different elevations at Fuencaliente, Canary Islands

Elevation (m)	Mean number of branches per branch	*P*	Significance of difference
10	2.35±1.58		
		0.2 –0.1	Not significant
100	2.74±1.29		
		0.3 –0.2	Not significant
200	2.44±1.91		
		0.1 –0.05	Not significant
300	3.02±2.73		
		0.7 –0.5	Not significant
400	3.31±4.12		
		0.05–0.02	Significant
500	4.51±4.00		
		0.01–0.001	Highly significant
600 (sand)	6.61±5.25		
		0.001	Highly significant
600 (rock)	3.40±2.29		

leucophaeum in the field can be stated as follows: significant differences exist between populations near sea level and those above 300 m, with respect to height growth rate, lateral branch formation, and periodicity. Populations at 100 m and 200 m resemble the sea-level group. Plants growing in soil pockets on rock at 600 m resemble those on volcanic sand at 400 m.

MEASUREMENTS OF *Echium leucophaeum* GROWN UNDER UNIFORM CONDITIONS

Seeds were collected from plants near sea level (10 m) and from plants growing in volcanic sand at high altitude (600 m). Growth patterns of 10 seedlings from each group were studied under uniform conditions in an experimental plot at the Santa Ana Botanic Garden in Claremont, California (mean annual temperature 63°F, lat 34° N). Seeds of these adults were then grown under uniform conditions in Maryland for 3 months. Branching and growth trends were indistinguishable for F_1 and F_2 seedlings. In all populations, branching occurred within 2 months, but height growth was much more rapid in both F_1 and F_2 seedlings from 600 m than in those from sea level (Fig. 1C, D). After 9 months of growth, the height and diameter ("spread") of the F_1 bushes were measured. Results were compared by means of Student *t* tests to ascertain whether the observed differences were due to chance (Table 5). The growth rates of the two populations are significantly different, the high altitude form producing longer shoots. Apparently, some genetic selection for height growth has been operative. The differences were not as great under uniform conditions as they were in the Canary Islands, so both genetic adaptation and physiological response must play an important role in height growth.

At the end of 9 months most of the F_1 plants had

TABLE 5. Growth form of *Echium leucophaeum* plants from 10 m and 600 m elevation, grown together in transplant garden

Item	From 10 m elevation	From 600 m elevation	*P*
Mean height (cm)	57.8±7.4	76.1±8.9	0.001
Mean spread (cm)	84.1±7.2	95.3±15.8	0.02–0.05
In flower (%)	11.1	20.0	
In fruit (%)	66.7	50.0	
Vegetative (%)	22.2	30.0	

produced at least some inflorescences. The group from near sea level had two vegetative individuals, one flowering, six fruiting, and one dead; in the 600-m group, three were vegetative, two flowering, and five fruiting. Although these figures are too low for statistical treatment, it is clear that the two groups do not differ in periodicity. Therefore the difference seen in the field, i.e., the greater advancement of the plants near sea level, was probably a physiological response. The uniformity within the populations in the Canaries (Fig. 3) is all the more surprising because of the widely different ages of the plants in the field.

A third aspect of growth form studied in detail was the branching pattern of single individuals from both groups. The method developed for branching-pattern studies resembles that of Nanda (1962) and consists of constructing a complete diagram of the shoot system of the plant (Fig. 2 A, B), in which the vegetative shoots of the most recent branching cycle are represented by thin arrows and the shoots of previous cycles by heavier lines with different shading. The levels at which lateral branches arise and the lengths of the shoots are drawn to scale. In each cycle there are three possible fates of a shoot: the tip may die (indicated by a cross bar in Fig. 2B), or it may produce an inflorescence (indicated by a circle, solid for buds, open for flowers, and with a + for fruits), or it may remain vegetative and continue as an indeterminate shoot into the next branching cycle (indicated as a continuation of the shoot with change of shading). Lines with the same thickness and shading indicate shoots of the same branching cycle and may be presumed to have developed at approximately the same time. A table can now be constructed to show the numbers, types, and average lengths of shoots in each successive cycle. These data are shown in Table 6 for the plant used as an example in Fig. 2A, B. The plants studied in the experimental plot were much more complicated, and diagrams are not shown, to conserve space. Table 6 lists the lengths, types, and numbers of shoots produced in each successive cycle for two individuals grown under uniform conditions representing the sea-level and high-elevation groups. Comparison of these data shows one additional cycle in the plant from 600 m and a

TABLE 6. Average number and length of shoots produced in successive branching cycles by *Echium leucophaeum* plants grown in greenhouse (Fig. 2), and in transplant garden from 10 m and 600 m elevation

Item	1				2				3				4				5			
	Vegetative	Dead	Reproductive	Total	Vegetative	Dead	Reproductive	Total	Vegetative	Dead	Reproductive	Total	Vegetative	Dead	Reproductive	Total	Vegetative	Dead	Reproductive	Total
Greenhouse plant																				
Number of branches	1	0	0	1	2	3	2	7	13	28	8	48	21	0	0	21				
Length (cm)	27	0	0	27	68	16	106	190	163	83	230	476	188	0	0	188				
Mean length per cycle				27				27.1				9.9				9.0				
Mean number of branches per branch of previous cycle				—				7.0				6.9				0.4				
Plant from 10 m elevation																				
Number of branches	1	0	0	1	3	1	15	19	222	131	17	370	628	52	0	680				
Length (cm)	5	0	0	5	41	7	596	644	1294	188	157	1639	1740	46	0	1786				
Mean length per cycle				5				33.9				4.4				2.6				
Mean number of branches per branch of previous cycle				—				19.0				19.5				1.8				
Plant from 600 m elevation																				
Number of branches	1	0	0	1	5	0	0	5	9	1	23	33	256	261	4	521	782	61	0	843
Length (cm)	5	0	0	5	84	0	0	84	180	39	1175	1394	2255	408	66	2729	2551	120	0	2671
Mean length per cycle				5				16.8				42.2				5.2				3.2
Mean number of branches per branch of previous cycle				—				5.0				6.6				15.8				1.6

decline in average shoot length in the last two cycles. When the number of branches of a given cycle is divided by the number in the preceding cycle, it becomes apparent that a decline occurred in new shoot production (although the last cycle may be incomplete, since a number of axillary meristems may not have started development).

The plant from sea level, grown in the transplant garden, had 370 branches in the penultimate cycle, which was complete at the time of the study; the cycle before had 19 branches, hence branch production averaged 19.5 new branches per old one. The plant from 600 m had 521 branches in the penultimate cycle and 33 before that, for an average of 15.8 new branches per old one. A comparison of the original data by means of a Student t test showed that the difference has a probability between 0.1 and 0.2 of being due to chance, and hence is not significant.

In the Canary Islands, plants at higher elevations produced significantly higher numbers of lateral branches than those near sea level. In the transplant garden this is not so: the sea-level plants produced slightly, but insignificantly, higher numbers of laterals than the high elevation ones. Apparently the difference observed in the field was a matter of physiological response.

Acknowledgments

Field work was made possible for this study by a fellowship from the John Simon Guggenheim Memorial Foundation and financial support under Grant GB 38876 from the National Science Foundation. Research on the evolution of plant forms in the Canary Islands continues under grants GB 5246 and GB 13104 to the Museum of Zoology, University of Michigan, by the National Science Foundation. The support of these foundations is gratefully acknowledged.

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