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ROOT TOPOLOGY AND ALLOCATION PATTERNS OF *ATRIPLEX PATULA* SEEDLINGS SUPPLIED WITH DIFFERENT NUTRIENT CONCENTRATIONS

TOPOLOGIA RADICALE E RIPARTIZIONE DELLA SOSTANZA SECCA IN SEMENZALI DI *ATRIPLEX PATULA* IN RISPOSTA A DIVERSE CONCENTRAZIONI DI NUTRIENTI

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Abstract

To test whether sub-optimal available nutrient concentrations would result in a more herringbone root branching pattern, in lower root diameters, and in greater resource allocation to root growth than to above-ground portions, seedlings of *Atriplex patula* were grown under optimal (full), intermediate (1/3 full), and low (1/6 full) nutrient treatments. No significant differences were found between the full and 1/3 nutrient treatments for any of the parameters tested. Root topologies did not show conclusive responses to nutrient availability, however roots treated with 1/6 nutrient concentration showed the tendency to grow in a more herringbone pattern. Total dry weights and shoot dry weights were lower for the plants grown with 1/6 nutrient solution than for the other treatments. Root dry weight, length, and diameter were similar in all treatments. Root/shoot ratios of the 1/6 nutrient treatment were significantly higher than those of the other treatments. Results suggested a nutrient level threshold for *Atriplex patula* located between the intermediate and low nutrient levels provided. The sizes and forms of the roots were fairly conservative among treatments, indicating an allocation strategy towards obtaining their limiting resources.

Keywords: biomass allocation, dichotomous, nutrient supply, root architecture, root system

Riassunto

Allo scopo di testare l'effetto di concentrazioni sub-ottimali di nutrienti sul tipo di ramificazione e sviluppo radicale e sulla ripartizione della biomassa tra apparato aereo e radicale, semenzali di *Atriplex patula* allevati in vaso sono stati sottoposti a trattamenti con concentrazione piena (full), intermedia (1/3 full) e bassa di nutrienti. Non sono state riscontrate differenze significative tra la concentrazione piena e intermedia per tutti i parametri rilevati. La topologia radicale non ha mostrato risposte conclusive alla disponibilità di nutrienti; tuttavia le radici di piante trattate con bassa concentrazione hanno mostrato una crescita tendente al tipo a lisca di pesce. Il peso secco totale e quello della parte aerea è risultato inferiore nelle piante trattate con bassa concentrazione, mentre peso secco, lunghezza e diametro delle radici sono risultati simili in tutti i trattamenti. Il rapporto radici/chioma pertanto si è rivelato maggiore nelle piante trattate con bassa concentrazione di nutrienti. I risultati ottenuti mostrano una soglia di risposta ai livelli di nutrienti per *A. patula* compresa tra la concentrazione intermedia e bassa. Dimensioni e forma degli apparati radicali si sono dimostrate piuttosto conservative, indice di una strategia di ripartizione della biomassa volta a massimizzare l'acquisizione delle risorse limitanti.

Parole chiave: ripartizione della biomassa, dicotomo apporto di nutrienti, architettura radicale, apparato radicale

Introduction

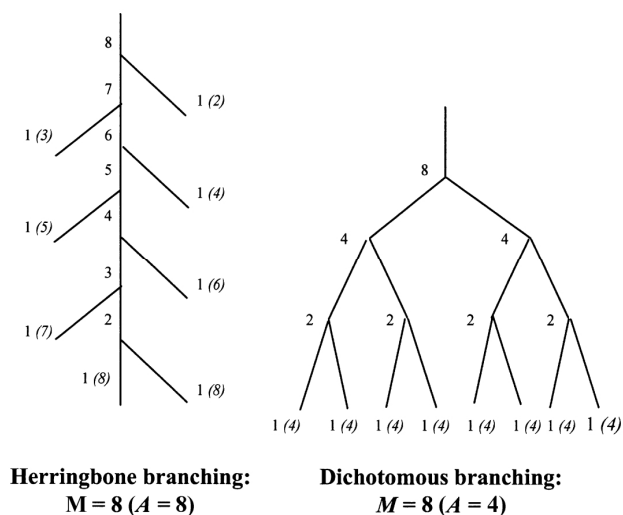
Though the importance of root systems in morphological and physiological studies of plants has long been recognized, most studies of plant ecology have concentrated on the above-ground portions of plants. The major function of roots is the absorption of water and mineral nutrients from the surrounding medium, and in non-agricultural settings, plant growth is typically more limited by nutrient levels than by CO₂ or light (Fitter, 1986). Yet, nutrient and water levels in the soil are strongly influenced by climatic factors and they are the result of dynamic cycles typical of specific environmental settings. Therefore, in studies of natural communities, understanding root systems and root behavior is as critical as understanding above-ground plant functions to evaluate plant response to resource levels (water, nutrients, but also light and CO₂) as well as to climatic parameters both

above- and below-ground. In the past, the intrinsic nature of below-ground plant organs made root research, especially whole system root research, exceedingly difficult. Recent technological and methodological innovations have provided ways of quantifying entire root systems, and have given opportunities for improved understanding of the functioning of plant roots.

Root architecture generally refers to the spatial configuration of the root system, and it encompasses both root topology, or the branching pattern in which individual root axes are connected to each other (Lynch, 1995), and root distribution. The spatial heterogeneity of resource availability in soil (Lynch, 1995), together with the fact that roots demonstrate little morphological variation within a root system, suggest that an ecological analysis of root functions should focus more on parts of the entire

Fig. 1 - The two possible extremes in branching patterns of root systems. Magnitude (M) refers to the number of exterior links (those ending with a meristem); altitude (A) refers to the centrifugal branching order.

Fig. 1 - I due possibili estremi nella tipologia di ramificazione degli apparati radicali. Magnitudo (M) si riferisce al numero di link esterni (ramificazioni che terminano con un meristema); altitudo (A) si riferisce all'ordine di ramificazione in senso centrifugo.



root system (root system architecture) than on the morphology of individual roots (Fitter, 1987). The degree of branching is a feature that greatly determines the overall form of root systems, and it has been known to show wide variation in response to both genetic components and environmental conditions (Fitter, 1987; Fitter, 1991; Fitter and Stickland, 1991).

Plant species differ in the capacity of their roots to respond to soil-nutrient enrichment (Robinson, 1994; Hodge, 2004). Some species display rapid root proliferation, while others, from poor habitats, might exhibit no response to enriched soil sites. It has been suggested that large plasticity in root architecture, together with low relative growth rate are adaptations that allow them to grow well in heterogeneous and poor soil-nutrient conditions (Arredondo and Johnson, 1999). These differences between species in the ability to exploit soil resource heterogeneity may affect their distribution, and could be a mechanism that reduces interspecific root competition (Farley and Fitter, 1999).

In this study we focused on the topological responses of root systems and on the allocation patterns in response to varying levels of nutrient concentrations. The surface area near root tips is the most active in the uptake of water and nutrients (May et al., 1965). Therefore, uptake should be related to the number of root branches and root tips and nutrient availability is expected to have an effect on root length and degree of branching. A more dichotomous pattern of branching, with larger numbers of meristematic root tips per soil volume, should be better suited for taking advantage of high nutrient concentrations (Fig. 1). Fitter (1987) found that root systems

grown under low nutrient conditions, and species adapted to growth under low nutrient conditions tend to demonstrate a “herringbone” type of root architecture, comprised of a root axis and primary laterals. While this pattern is expensive in terms of production and maintenance costs per meristem, it is efficient for exploring a large volume of soil for available nutrients (Fitter, 1987). Glimskar (2000) found that the only clear plastic response to growth-limiting nitrogen supply was a markedly increased link length in *Polygala vulgaris*, but there were also indications of more herringbone-like root systems in *P. vulgaris* and *Crepis praemorsa* under nitrogen limitation. On the other hand, low availability of phosphate, which is highly immobile in soil, favored lateral root growth over primary root growth in *Arabidopsis* (Williamson et al., 2001). Nutrient levels have also been shown to affect root diameter, and the responses are highly variable (Christie and Moorby, 1975). Fine, low-diameter roots tend to be less effective at exploring the soil, due to their limited metabolic transport capacities and resulting lowered ability to extend far from the larger root from which they branched (Fitter, 1993). Herringbone branching patterns exhibit a greater proportion of high magnitude (magnitude refers to the number of exterior links, where links are root segments between nodes and exterior links are those ending with a meristem; Fitter, 1993), and therefore thicker, links than dichotomous root systems (Fitter et al., 1991).

Available nutrient levels also affect whole-plant energy allocation and growth. Plants adjust their biomass allocation toward development of organs which acquire the resources most limiting to their growth. Chapin et al. (1987) have found that plants grown at low nutrient levels tend to allocate more of their resources away from above-ground portions and into root production, for enhanced nutrient uptake and alleviation of its limiting effects. Root/shoot ratios change as levels of light and nutrient limitation change (Davidson, 1969). This allows for the carbon:nutrient balance to be more equitable. Also soil moisture deficit may induce greater allocation to roots as the plant attempts to restore a more favorable balance between resource need and availability. In wheat, for example, long- and short-term water limitation increases root/shoot ratios mainly by reducing above-ground growth (Wang et al., 2007).

In this study, the following hypotheses were tested:

- 1) root systems receiving high nutrient levels should display more dichotomous branching patterns, while root systems receiving low nutrient levels will display more herringbone-like branching patterns,
- 2) root diameters should be larger under low nutrient concentrations, and
- 3) plants grown under low nutrient conditions should allocate more of their resources to root growth.

Materials and methods

Plant material

Atriplex patula is an annual herb of uncertain origin, native to temperate Europe, and found throughout Italy in humid sites, cultivated fields, and other recently disturbed sites. This species was chosen because weedy,

Tab. 1 - Means \pm standard errors for growth parameters measured on 12-day-old seedlings of *Atriplex patula* supplied with nutrient solution at full concentration, at 1/3 of full concentration, and at 1/6 of full concentration.

Tab. 1 - Medie \pm errore standard dei parametri di crescita misurati su semenzali di 12 giorni di *Atriplex patula* trattati con soluzione nutritiva a concentrazione piena e a 1/3 e 1/6 della concentrazione piena.

	<u>Treatments</u>		
	Full Concentration	1/3 Full Concentration	1/6 Full Concentration
Shoot Dry Weight (kg)*	0.153 \pm 0.009 ^a	0.143 \pm 0.012 ^a	0.080 \pm 0.006 ^b
Root Dry Weight (kg)*	0.030 \pm 0.003 ^a	0.034 \pm 0.007 ^a	0.024 \pm 0.002 ^a
Total Dry Weight (kg)*	0.183 \pm 0.013 ^a	0.177 \pm 0.019 ^a	0.104 \pm 0.008 ^b
Root Length (m)	10.22 \pm 0.920 ^a	12.93 \pm 2.033 ^a	9.76 \pm 0.773 ^a
Root Diameter (mm)	0.211 \pm 0.010 ^a	0.201 \pm 0.007 ^a	0.201 \pm 0.006 ^a
Root/Shoot Ratio*	0.192 \pm 0.018 ^b	0.221 \pm 0.020 ^b	0.310 \pm 0.030 ^a

Means with different letters along rows differ significantly ($P \leq 0.05$, ANOVA followed by Tukey test; *Kruskal-Wallis non-parametric test followed by Mann-Whitney rank sum test).

fast-growing species must adapt to a variety of conditions and therefore have a large degree of architectural plasticity (Fitter, 1994).

Experimental assessment

Three treatments were imposed to manipulate the concentration of nutrients given to the plants. The treatments were based on differing proportions of a stock Hoagland's solution (macro- and micro-nutrients) diluted to 75% (Epstein, 1972), and the proportions for the treatments were full, 1/3, and 1/6 strength (in terms of concentration) of the stock solution. Seeds were germinated in trays filled with sand, and watered with deionized water. After germination, seedlings were transplanted individually in 84 round 15-cm diameter pots filled with sterilized sand. Plants were divided into three groups of 28 plants each, randomly arranged in a growth chamber, and fertilization with the different solutions was applied, as the tiny seeds had already exhausted their reserves. Plants received fifteen hours of light at around 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in order to prevent premature flowering. Daytime temperature was maintained at 32° C and nighttime temperature was 28° C.

Seedlings were harvested after 12 days. Specimens did not appear to show any signs of root binding. Roots were carefully extracted and washed free of sand, and shoots were immediately placed in envelopes for drying. Inspection of the discarded sand and water yielded very little stray root matter; therefore the root systems were retained in good condition. A subsample of five root systems for each treatment was spread on transparencies and scanned into a computer before drying in an oven at 60° C.

Root lengths, diameters, and topological measurements (*sensu* Fitter, 1993; altitude, the number of links in the longest unique path through the root system from its base, and magnitude) were determined with the root analysis software WinRHIZO Pro (Regent Instruments,

Inc., Canada). A topological index was also calculated for each root system as the log (altitude):log(magnitude) ratio, as it is indicated to be independent on plant size (Glimskar, 2000). Dry weights were measured for shoots and for a subsample of the roots, consisting of 20 root systems per treatment.

Data analysis

An Analysis of Variance followed by Tukey's multiple comparison test was used to analyze and separate differences among treatments. The Kruskal-Wallis non-parametric test was used to determine differences among treatments for shoot dry weight, root dry weight, total dry weight and root/shoot ratio, as data for these parameters were not distributed normally. When Kruskal-Wallis test suggested significant differences among treatments, Mann-Whitney rank sum test was used to compare each pair of groups.

Topology was analyzed by comparing slopes of lines from linear regressions of log magnitude on log altitude for the three treatments. A steep slope should indicate a herringbone pattern of branching, whereas a less steep slope should indicate a more dichotomous branching pattern. Slopes were compared by Analysis of Variance using slopes (means), standard errors of the slope, and number of replicates from the regression model.

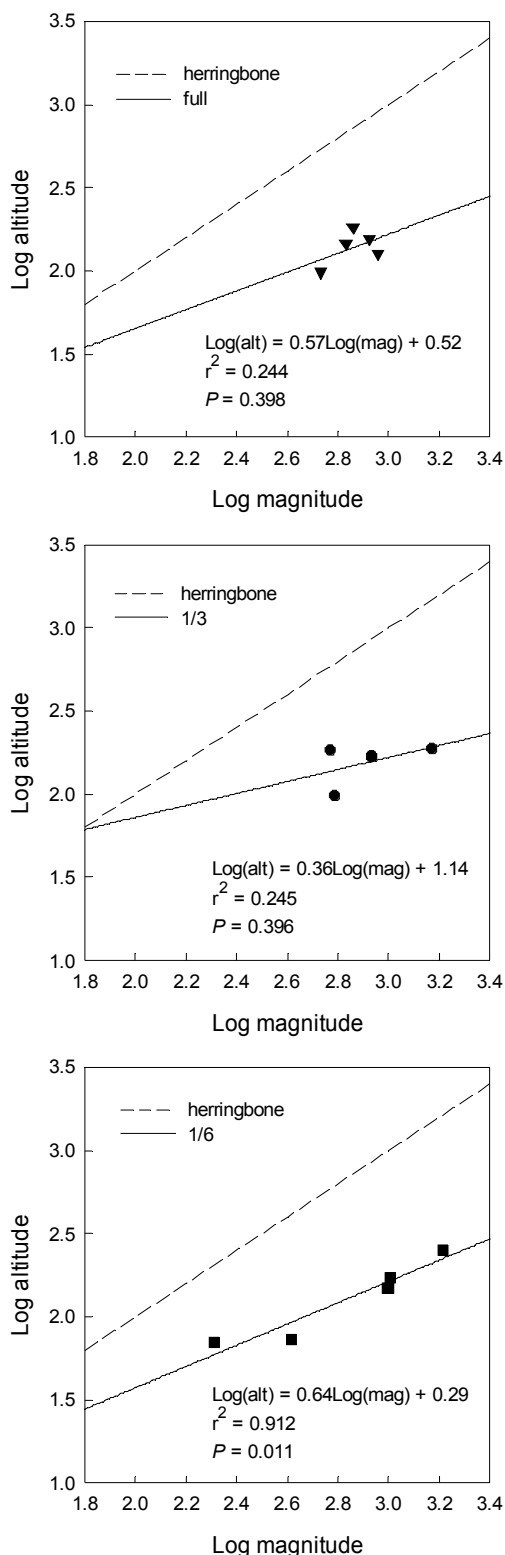
Results

Root topology

When slopes of the log magnitude vs. log altitude were compared no significant difference was detected among the three treatments ($P = 0.878$). However, the slope of the log magnitude vs. log altitude for the low nutrient treatment was significantly different from zero (Fig. 2). It is difficult to conclusively state that this implies a more herringbone branching pattern. Also topological indexes resulted similar for the three treatments ($P = 0.961$).

Fig. 2 - Relationships between logarithm of altitude and logarithm of magnitude for the root systems of 12-day-old seedlings of *Atriplex patula* supplied with nutrient solution at full concentration (▼), at 1/3 of full concentration (●), and at 1/6 of full concentration (■) as compared to the ideal herringbone pattern (-----)

Fig. 2 - Relazioni tra il logaritmo dell' altitudo e il logaritmo della magnitudo per gli apparati radicali di semenzali di 12 giorni di *Atriplex patula* trattati con soluzione nutritiva a concentrazione piena (▼) e a 1/3 (●) e 1/6 (■) della concentrazione piena rispetto al modello ideale a lisca di pesce (-----)



Allocation patterns

There were no significant differences found between the treatments receiving full and 1/3 strength nutrient solution, for any of the parameters measured (Tab. 1). For shoot dry weight, total dry weight, and root/shoot ratio there were significant differences between the two treatments of higher nutrient strength and the plants receiving nutrient solution at 1/6 strength. Total dry weight of the plants in the low nutrient treatment was around 60% of the intermediate and high nutrient treatments. Shoot dry weights for the plants receiving the low nutrient solution were on average about half the dry weight values for the high and intermediate nutrient concentrations.

Root dry weight, root length, and root diameter did not differ among treatments (Tab. 1). As a result, the root/shoot ratios for the low nutrient treatment plants were significantly higher than for the two higher nutrient treatments.

Discussion and conclusions

The lack of significant differences between plants grown in the full and 1/3 strength nutrient solution treatments indicates that the strength of the intermediate treatment was at a sufficiently high enough level not to limit growth. As *Atriplex patula* is often found growing on poor sites, it is adapted to tolerate low nutrient levels. The differences between these two treatments and the 1/6 strength in parameters associated with growth allocation patterns suggest that there is a nutrient availability threshold occurring between the concentrations found in the 1/3 and 1/6 strength solutions. Above this threshold, light and photosynthetic capacity are most likely the limiting factors to growth, whereas below this threshold available nutrient levels are limiting.

The specimens maintained similar root systems (weights, diameters, and branching patterns) over different nutrient levels, indicating a resource allocation strategy. The plants grown under low nutrient conditions allocated more of their total resources to root formation and therefore nutrient acquisition, to minimize their nutrient limitation. Other researchers, such as Kudoyarova et al. (1989), found similar results in plants grown under sub-optimal nutrient conditions. On the other hand, plants receiving higher nutrient levels put more of their resources into shoot growth. This agrees with the economic theory that it is beneficial for plants to adjust allocation so that all resources become equally limiting (Bloom et al., 1985). Plants receiving the full and 1/3 strength nutrient solution were able to obtain nutrients at non-limiting levels, so they allocated more towards the development of above-ground parts, to allow for higher photosynthetic capacities and make use of the available nutrient resources. This allocation plasticity suggests that *Atriplex patula* should be a good competitor, and this is borne out in its designation as a “weedy species”.

The results of this study do not seem to support predictions for plasticity of topology. In some species, topology has been demonstrated to be relatively insensitive to changes in nutrient levels (Fitter et al., 1988). According to Fitter (1991), evidence has shown that parameters such as root diameter or length are often more plastic

than topology. However, due to the relatively small number of species and systems so far studied, this is still an area open to speculation. While this study does not negate these findings, it can not be said to support them. This may be due to the fact that topology may not vary as a result of different nutrient concentrations, as suggested; or differences may develop at a later stage than studied; or, as suggested by Glimskar (2000), variation in plant size together with low replication may obscure the differences. More often significant changes in branching and proliferation of portions of root systems have been observed in response to nutrient-rich patches and have been interpreted as adaptations to the soil environment (Hodge, 2004). In our case, no (or a weak) topological response to different nutrient concentrations applied uniformly to entire root systems of different plants may indicate a strong genetic component over any plastic response to nutrient levels.

In this study, specimens did not follow the prediction of larger root diameters for lower nutrient concentrations, and their total root lengths were not significantly different among treatments. This species does not appear to demonstrate much plasticity in root geometric aspects. However, due to the relatively short growing period for our specimens, the photosynthetic capacities of the plants may not have been developed for a long enough period to allow for sufficient processing and utilization of the available resources to allocate to their roots. However, allowing plants to grow to a later date would have posed practical difficulties in terms of scanning their root systems.

Lynch and Beem (1993) found that topological indexes can vary substantially over time, and therefore an area for future research would be the effects of differing nutrient levels on plants at varying developmental stages, to further explore whether plants of varying ages exhibit different response strategies

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