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**

Lo Bianco Riccardo

Dipartimento S. En. Fi. Mi. Zo., Università degli studi di Palermo, Viale delle scienze 11, 90128 Palermo - rlb@unipa.it

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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
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and environmental conditions (Fitter, 1987; Fitter, 1991; 
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Plant species differ in the capacity of their roots to re-
pond to soil-nutrient enrichment (Robinson, 1994; 
Hodge, 2004). Some species display rapid root prolifera-
tion, 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 condi-
tions (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 wa-
ter 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 di-
chotomous pattern of branching, with larger numbers of 
meristematic root tips per soil volume, should be better 
suited for taking advantage of high nutrient concentra-
tions (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 mainte-
nance 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 re-
sponse to growth-limiting nitrogen supply was a mark-
edly increased link length in Polygala vulgaris, but there 
were also indications of more herringbone-like root sys-
tems in P. vulgaris and Crepis praemorsa under nitrogen 
limitation. On the other hand, low availability of phos-
phate, 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). Herring-
bone branching patterns exhibit a greater proportion of 
high magnitude (magnitude refers to the number of exte-
rior links, where links are root segments between nodes 
and exterior links are those ending with a meristem; Fit-
ter, 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 alloca-
tion toward development of organs which acquire the re-
sources most limiting to their growth. Chapin et al. 
(1987) have found that plants grown at low nutrient lev-
els tend to allocate more of their resources away from 
above-ground portions and into root production, for en-
hanced nutrient uptake and alleviation of its limiting ef-
fects. Root/shoot ratios change as levels of light and nu-
trient 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 
weat, 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 dis-
play 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 al-
locate more of their resources to root growth.

Materials and methods

Plant material

Atriplex patula is an annual herb of uncertain origin, na-
tive to temperate Europe, and found throughout Italy in 
humid sites, cultivated fields, and other recently dis-
turbed sites. This species was chosen because weedy,
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 based on differing proportions of a stock solution at full concentration, at 1/3 of full concentration, and at 1/6 of full concentration.

**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).
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 suboptimal 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 Glinski (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.

References


