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Root hair anatomy and morphology in *Posidonia oceanica* (L.) Delile and substratum typology: First observations of a spiral form

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ABSTRACT

The morpho-anatomical root hair features of *P. oceanica* ramets collected in meadows settled on different substrata (sand, *matte* and rock) were analysed. On each substratum, nine plagiothropic rhizomes each one composed by 3–6 interconnected short shoots were collected between April and May 2016 at 10 m of depth. On sand and on rock, the adventitious roots showed two distinct tubular and spiral-shaped hairs, clustered in yellowish-gray gelatinous pads. Tubular root hair tips were dactiliform and generally attached to grains of rock fragments. Moreover, a sub-circular swelling zone occurred. On *matte*, root hairs did not form gelatinous pads, were very short and had a simple distal portion. The root hair anatomy and morphology described here provides new information on the *P. oceanica* root system that can express a remarkable root hair polymorphism.

1. Introduction

The seagrass *Posidonia oceanica* (L.) Delile forms the most common, productive and widespread meadows of the Mediterranean Sea (Gobert et al., 2006), likely representing the marine ecosystem with the highest levels of biodiversity (Hemminga and Duarte, 2000). It is able to grow on different types of substrata, including sand that is easily penetrable by the roots; rock, in which the very sturdy roots are able to enter through crevices (Mazzella et al., 1993) and *matte*, a typical self-built terraced formation consisting of intertwined rhizomes, roots and sediment (Boudouresque and Meinesz, 1982). Several studies have highlighted the importance of substratum features for the distribution and colonization process of *P. oceanica* (De Falco et al., 2008; Marbà and Duarte, 1997) as well as its morphology and growth dynamics (Di Maida et al., 2013), root development and architecture in particular (Alagna et al., 2013; Alagna et al., 2015; Balestri et al., 2015). Different strategies of root adaptation to different substrata have been documented at different levels. For example, it was observed that biomass allocation was more or less unbalanced between root and leaf bundle structures, according to substratum type (Di Carlo et al., 2007). Moreover, variations in root structure, orientation and diameter can be affected by substratum typology, at least during the first stages of clone development, as reported in a detailed study on root topology (Balestri et al., 2015). Recently, adhesive root hairs in *P. oceanica* seedlings have been discovered and described (Badalamenti et al., 2015), while knowledge on these structures in adult shoots are still quite limited. In this study, the morpho-anatomical root hair features of *P. oceanica* shoots collected in meadows settled on different substrata were analysed in order to gain a better understanding of the adaptive mechanisms of root systems, which enable this species to colonize marine environments.

2. Materials and methods

The study was carried out in North Western Sicily (Italy), within the Marine Protected Area of Capo Gallo – Isola delle Femmine, where an extensive *P. oceanica* meadow grows on three types of substratum. For substratum differentiation, we chose shoots growing on sand, plants settled on visibly exposed rock, and plants growing on *matte*. On each substratum, nine plagiothropic rhizomes, each composed of 3–6 interconnected short shoots, were collected between April and May 2016 at 10 m of depth for morpho-anatomical analysis. For rock, in particular, shoots anchored in calcarenitic substratum were sampled using a hammer and chisel.

The pieces of rock with anchored shoots were sliced at the laboratory for better analysis of root development (Fig. 1A). Then integer roots were isolated by chemical dissolution of rock using 1% hydrochloric acid.

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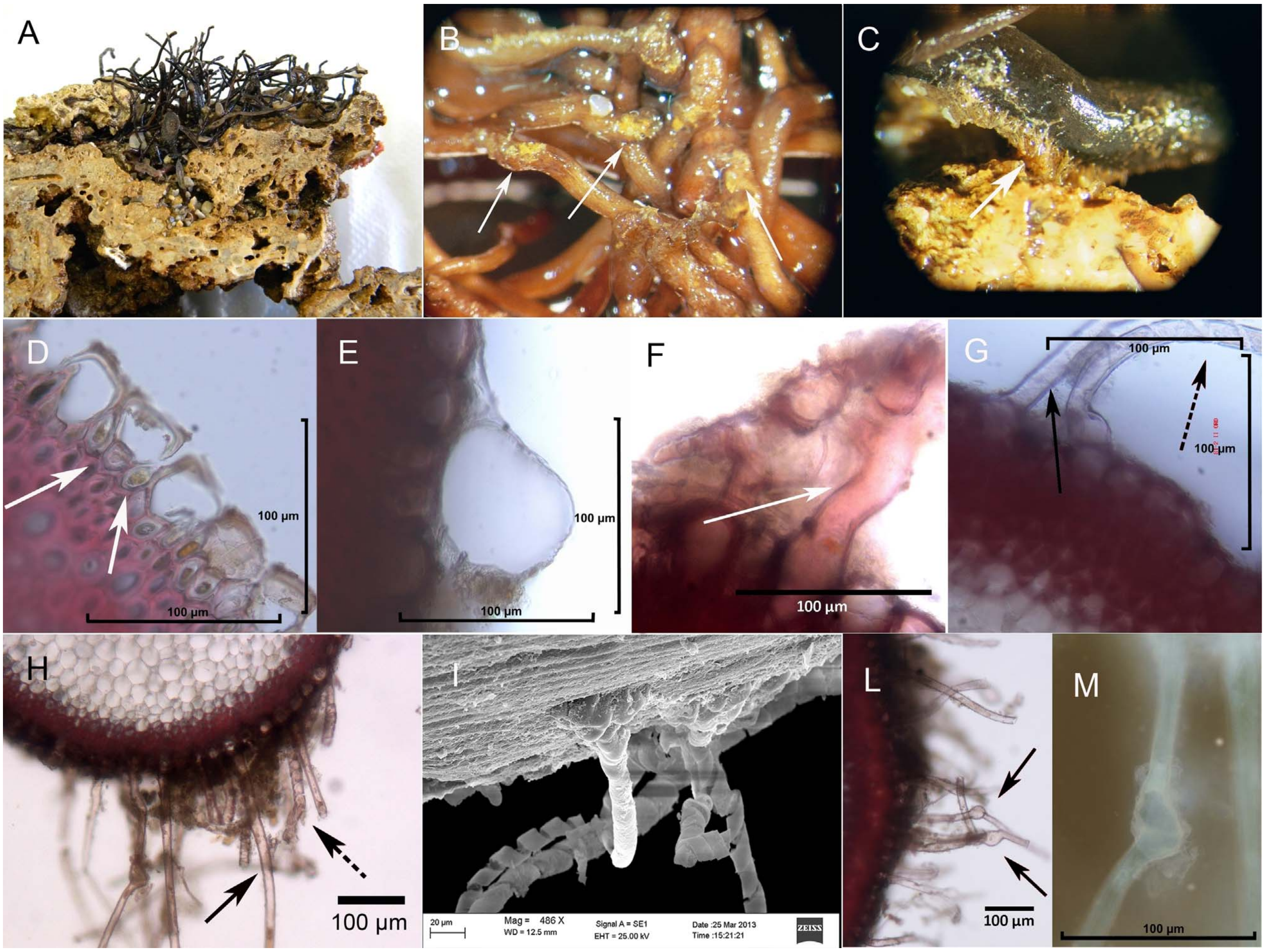

Fig. 1. Light, scanning electron and stereo micrographs of root hair forms and structures of *P. oceanica* and their development. Section of calcarenitic rock with attached root system (A), yellowish-gray gelatinous pads in roots of third order detached from the substrate (B) and in roots of first order attached to the substrate with root hairs very densely clustered (C); cross-section of the roots of the first order on calcarenite: clavate cells (arrows) supporting trichoblast activity (D); base of trichoblast (E); body of root hair in the rhizodermis (F); light (G, H) and scanning electron (I) micrographs of tubular (continuous arrow) and spiral (dotted arrow) root hairs (SEM image was taken from the archive acquired in the workplace of Torta et al., 2015); light (L) (arrows) and polarized light (M) micrographs of root hair with circular swelling zones in cross-section of the roots of the third order on calcarenite. Scale bars: = 100 µm; I = 20 µm.

For each group of interconnected shoots, morpho-anatomical observations were carried out on one adventitious root, first and second lateral root order respectively for overall total of 81 roots. Ten fresh sections were obtained by cutting each adventitious root, first and second lateral root order, at 1 cm, 3 mm and 2 mm respectively, from their branching point and prepared with a manual microtome (A.M.G. Diagnostic) to investigate root histo-anatomy. Subsequently, they were subjected to the following histo-chemical tests: hydrochloric fluoro glucyn for detection of lignified cells and tissues and Sudan III for suberized and cutinized tissues (Catalano, 1925; Colombo, 2003). This allowed better distinguishing of root hairs during their development and differentiation. Morpho-anatomical observations were carried out on several root hairs (hundreds). Fifteen of them (5 per substratum) were selected among the best isolated and distinguishable for the morphometric measurements.

The samples were examined using a transmitted light microscope (LM) (Leica DMLS) and a stereomicroscope (SM) (Leica MZ12). Roots samples and sections were then fixed in 5% formalin–5% acetic acid–90% ethanol (FAA) (Sass, 1958). Moreover, exsiccatae of the samples relevant to the populations analysed are deposited at the Department of Earth and Marine Sciences, University of Palermo.

3. Results

3.1. Root hair traits and development

Root hairs can be very densely clustered in yellowish-gray gelatinous pads scattered along the radical axis (Fig. 1B and C) at the points of contact with the substratum. They originate from a basal ampoule inserted in the rhizodermis as a direct evolution of the trichoblast, flanked by two clavate cells (Fig. 1D). From the trichoblast swelling (Fig. 1E), root hair emerges (Fig. 1F) with body length ranging from 150 to 600 µm and width 14.43 µm ± 1.65 (SE.; N = 15) on average. Two distinct root hair forms have been recognized: tubular and spiral (Fig. 1G–I). The body of tubular hairs can show a sub-circular swelling zone associated with a change in direction (Fig. 1L and M). Their tips were on average 66.95 µm ± 50.68 (s.e.; N = 11) in length and 33.24 µm ± 3.52 (s.e.) in width, displaying considerable morphological variability classified into the following types: simple (Fig. 2A), *stomifid* (stome like) (Fig. 2B), and *dactiliform* (Fig. 2C–E). In spiral root hairs, no sub-circular swelling zones were detected and it was not possible to observe their tips because they appear broken.

3.2. Root hair types in the different substrata

On sand, the adventitious roots appeared smooth with rare root hair