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Comparative morphology of epicortical roots in Old and New World Loranthaceae with reference to root types, origin, patterns of longitudinal extension and potential for clonal growth

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Abstract

The large mistletoe family, Loranthaceae, contains 75 genera, three of which are terrestrial root parasites. The remaining 72 genera are aerial parasites. Four basic haustorial system types are found in aerial genera: epicortical roots (ERs), wood roses, clasping unions and bark strands. The focus of this report is on genera in which ERs are present. Presence of ERs is based on our worldwide collection of haustoria and from literature sources. Our collections include 78% of all aerial genera and 72% of genera with ERs. Collections were analyzed using comparative morphological methods. Of the 72 aerial genera 40 (56%) have ERs and 75% of these are Old World. ERs are the most common haustorial type for Loranthaceae on every major landmass except Africa. Three ER types are described, basal, cauline and adventitious. Basal and adventitious ERs occur in both the Old and New World, whereas cauline ERs are exclusively New World. Adventitious ERs form in a few species in response to injury or epiparasitism. Significant differences occur between basal and cauline ERs in the extent and pattern of elongation, frequency of lateral root formation, and production of haustoria and shoots. Three patterns of axis extension of ERs are recognized, the monochasial sympodium, dichasial sympodium and monopodium. Marked differences in patterns of axis elongation occur between the Old and New World genera analyzed. In Old World taxa 94% of lateral roots contributed to a monochasial sympodium, whereas in New World taxa 84% of root extension was monopodial. Two strategies of resource procurement occur in genera with ERs; the "phalanx" strategy is found in species with basal ERs only, the "guerilla" strategy in New World species with cauline ERs. Species with ERs have the potential for clonal growth through fragmentation of stems, ERs, or both, but the extent of clonal growth in nature is unknown. The large number and wide distribution of genera with ERs add support to the hypothesis that the presence of ERs is an ancestral trait for aerial Loranthaceae.

Keywords: Clonal growth; Epicortical root; Loranthaceae; Mistletoe; Parasitic angiosperm; Root architecture

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Introduction

The Loranthaceae is the largest flowering-plant family with aerial branch parasites termed mistletoes. The family originated in the Southern Hemisphere and apparently dispersed early between the fragments of

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Gondwana (Raven and Axelrod, 1974). Of the approximately 75 genera in the Loranthaceae three are terrestrial root parasites, a habit considered ancestral for the family (Hamilton and Barlow, 1963; Kuijt, 1969; Nickrent and Duff, 1996; Wilson and Calvin, 2006). The remaining genera are woody, branch parasites of woodlands and forests. All members of the family form direct contacts with their hosts by means of haustoria. Four basic haustorial types are recognized in aerial members of the family (Calvin and Wilson, 1998): (1) epicortical roots (ERs) that grow along the host branch surface and at intervals form haustorial attachments to the host; (2) clasping unions where the **parasite haustorium enlarges** partially encircling the host branch; (3) wood roses where the **host tissue proliferates** forming a placenta to which the haustorium of the parasite is attached; and, (4) bark strands that spread within the host bark and at intervals tap host xylem (illustration for *Viscum* (Viscaceae): Zuber, 2004). Plants with wood roses, clasping unions and bark strands are often described as having "solitary unions" with their hosts (Barlow, 1997; Fineran, 2001). In contrast, plants with ERs have multiple, visible haustorial connections to their hosts.

Several terms, including epicautical roots and/or runners (Bell, 1991; Hamilton and Barlow, 1963), aerial roots (Thoday, 1961) and adventitious roots (Singh, 1954) have been used to describe ERs. Kuijt (1965) considers ERs as secondary roots because they arise after the root pole of the embryo has formed the initial haustorium, termed the primary haustorium. Structurally, ERs have some stem-like features such as a large central pith and at least some centrifugally maturing primary xylem (Beaman, 2002). However, most ER characteristics, including non-articulation, leaflessness, endogenous origin, xylem that is largely exarch and a small but recognizable root cap, are shared with roots.

Kuijt (1982) recognized three main types of ER: (1) basal roots that emerge only from the base of the plant; (2) stem roots that emerge from shoots; and, (3) roots formed along shoots that function as tendrils (*Tripodanthus flagellaris* only). Later he merged type three within type two, because the stem roots of *T. flagellaris* do not always function only as tendrils (Kuijt, 1989). The more common type is the basal ER that emerges only from the base of the primary shoot (Calvin and Wilson, 1998). In some genera with basal roots there also are roots that form along shoots at nodes and/or internodes. These cauline roots, termed stem ERs by Kuijt (1982), have been reported for one or more species of six New World genera (Kuijt 1964, 1982, 1989). We use the terminology proposed by Groff and Kaplan (1988) for shoot/root relationships in the family.

ERs have been described and illustrated in Kuijt's (1964, 1969, 1982, 1989) systematic work on New World genera. Hamilton and Barlow (1963) provide details on mature ER morphology for most Australian Loranthaceae, and Calvin and Wilson (1998) provide similar data for African genera. Thoday (1961) describes ERs in several Loranthaceae that are primarily from the Old World. Devkota (2003) undertook a comparative study, of ERs in four *Scurrula* species from Nepal. Menzies (1954) and Condon and Kuijt (1994) report on ER morphology and structure in *Ileostylus micranthus*, a monotypic New Zealand genus. None of this research has used a comparative approach to study haustorial morphology in the family as a whole. Our extensive New and Old World collections now make a comparative study possible.

The primary goal of our research on haustorial systems in Loranthaceae is to understand the transition from a terrestrial root-parasitic habit to an aerial habit within the forest canopy. To achieve this goal we utilize morphological, structural, quantitative and molecular methods. The first step in our approach is to gain an understanding of the haustorial morphologies of extant taxa. This report focuses on Loranthaceae with ERs, the haustorial type recently confirmed as ancestral in aerial members of the family (Wilson and Calvin, 2006). Here we provide basic distributional and morphological information, quantify patterns of axis extension and correlate ER morphology with the potential for clonal growth. In a subsequent report, we will explore the approximately 30 genera with solitary unions.

Materials and methods

Table 1 lists the genera of Loranthaceae included in this study and their distribution (Old or New World). Appendix A provides a comprehensive list of the haustorial collections studied, voucher information and relevant literature for genera where we lacked haustorial collections. Where possible we have collected seedlings and older infections that illustrated the range of haustorium developmental stages characteristic of the species at that site. We collected entire infections (when possible), voucher specimens of mistletoe and host, and plant material preserved in alcohol and/or silica gel. We also recorded features such as host, position of infection on host branch and direction(s) of mistletoe growth. Nearly, all of the haustoria illustrated, described or referenced in this study are from our collections (see Appendix A). Haustoria and corresponding voucher collections were numbered to indicate the country, year and sequential number within the country. Thus, NZ98-04 was the fourth collection from New Zealand in 1998. Voucher specimens were deposited at RSA, Claremont, CA.