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# Red/purple leaf margin coloration: Potential ecological and physiological functions



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#### 1. Introduction

#### Almost every color imaginable has been observed in foliage of some plant taxa due to variations in concentrations and combinations of vacuolar pigments (e.g., anthocyanins and betalains), photosynthetic pigments (chlorophylls and carotenoids), cuticular waxes, and iridescent structures (e.g., iridisomes) (Lee, 2007). Yet, despite this conspicuous rainbow of variability, we still remain very much in the dark regarding the adaptive significance, if any, of many of these color patterns (see reviews by Archetti et al., 2009; Glover and Whitney, 2010). One such example is a pervasive, but rarely examined, thin band (sometimes <1 mm in width) of orange/red/purple-colored cells that outline the borders of individual leaves of many plant species (e.g., Figs. 1-3). In some species, reddening/purpling of the leaf margin is inducible by environmental stress, such as phosphorus deficiency (Raghothama, 1999; Lloyd et al., 2001) or freezing stress (Ball et al., 2002). In other species, red/purple leaf margins are a constitutive

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#### ABSTRACT

Leaf margins of many plant species belonging to the floras of several continents feature a conspicuous band of red/purple color around their periphery. Despite the widespread distribution of this leaf trait, very few studies have proposed or tested hypotheses to explain its significance (if any). Common explanations for leaf coloration, such as photoprotection, plant camouflage, attraction of seed dispersers, or undermining herbivorous insect camouflage do not seem, at first glance, to be applicable to this color pattern. Could pigments localized at the leaf margin still function in these traditional ecological or physiological roles? Or should new hypotheses be devised that are more specific to coloration at the leaf margin? The purpose of this paper is to review and explore potential ecological and physiological functions of pigmented leaf margins, in hopes of inspiring further inquiry into this topic.

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trait, displayed during leaf development or persisting throughout the lifespan of the leaf (e.g., Bayly and Kellow, 2006; Hughes et al., 2010). Since red leaf margins are a constitutive trait rather than a stress response in many taxa, they have been used as a character for species identification by taxonomists (Bayly and Kellow, 2006; Versieux and Wanderley, 2007; Redden, 2008), as well as a marker to study genetic linkages in crop species (Hadagal et al., 1981; Jarret et al., 1993; Nick et al., 1993; Sabharwal and Doležel, 1993; Flint-Garcia et al., 2005).

While observations regarding the occurrence of red/purple leaf margins are numerous, studies on their ecological and/or physiological significance are almost completely lacking in the literature. Similarly, no studies to our knowledge have examined whether any phylogenetic, biogeographic, or ecological patterns exist which correspond with the presence or absence of red leaf margins as a constitutive trait. In this review, we speculate on the potential ecological and physiological roles that red pigments might play within the context of the leaf margin specifically (Table 1). In most described cases of leaf margin coloration, the pigment responsible for reddening/purpling was shown or presumed to be anthocyanin, and no reports have been made, to our knowledge, of leaf margin reddening by carotenoids or betalains.



Fig. 1. Herbivory on the leaf margin of *Kalanchoe luciae* (A); hoarfrost on a New Zealand *Veronica* sp. (B); symptoms of phosphorus deficiency in *Zea mays* leaf (C), and plants (D). Photo credits: S. Lev-Yadun (A), N. Hughes (B), and IPNI (C and D).



Fig. 2. Macroscopic to microscopic views of red (anthocyanic) leaf margins of two New Zealand Veronica species. Top row (A–C): Veronica speciesa A. Cunn; bottom row (D–F): Veronica pinguifolia Hook.f. A, C, D, and F adapted from Hughes et al., 2010 by permission of Oxford University Press; photos in B and E taken by N. Hughes.

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