From Forest Nursery Notes, Winter 2010

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Ecol Res (2009) 24: 1057–1065
DOI 10.1007/s11284-009-0583-8

ORIGINAL ARTICLE

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Growth responses of *Salix gracilistyla* cuttings to a range of substrate moisture and oxygen availability

Received: 23 October 2007 / Accepted: 17 December 2008 / Published online: 11 February 2009

Abstract The objective of this study is to determine the effects of substrate moisture and oxygen availability on growth traits of *Salix gracilistyla* Miquel, which colonizes gravel bars along rivers, the shoot growth schedule, biomass production, and resource allocation were examined under greenhouse conditions. We used four treatments representing a range of substrate moisture and oxygen availability: drought (D), flooding with standing water (FS), flooding with running water (FR), and control without drought or flooding (C). Cuttings in D stopped flushing and had low biomass production, reduced total leaf mass, and small leaves. Under anaerobic conditions, cuttings in FS stopped flushing and had low biomass production, small root biomass, low biomass allocation to roots, shallow roots, high biomass allocation to hypertrophied lenticels, and a few small, thick leaves. Under aerobic conditions, cuttings in FR showed continuous branch elongation and flushing, large biomass production, and large leaf biomass, similar to cuttings in C, in addition to low allocation to hypertrophied lenticels and many large leaves. The growth of cuttings was not inhibited by flooding of the roots throughout the experiment unless the conditions were anaerobic. Thus, cuttings respond to water stress under low moisture conditions by reducing the transpiration area and respond to flooding under low oxygen conditions by high allocation to hypertrophied lenticels and reduced transpiration area. Plasticity in the shoot growth schedule, biomass production, and resource allocation according to moisture conditions and the ability to develop hypertrophied lenticels upon flooding allow *S. gracilistyla* to colonize sites in which both desiccation and flooding occur.

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Keywords Desiccation · Flooding · Growth · Resource allocation · *Salix gracilistyla*

Introduction

Gravel bars along rivers are unstable sites subject to disturbances such as floods; moreover, the substrate moisture content is dramatically affected by flooding or desiccation, depending on fluctuations in the river water level. Salicaceous species tend to dominate at such sites, implying their physiological adaptation to these types of riparian environments. Karrenberg et al. (2002) classified the physiological and morphological adaptations and growth traits of salicaceous species adapted to riparian environments as being tolerant to anaerobic conditions (e.g., Dionigi et al. 1985; Donovan et al. 1988) and characterized by the production of adventitious roots (Krasny et al. 1988; Houle and Babeux 1993), rapid root growth following a decline in the water table (van Splunder et al. 1996; Kranjcec et al. 1998; Mahoney and Rood 1998), flexible stems and roots (Jonasson and Callaghan 1992; Vischer and Oplatka 1998), and brittle twig bases (Dewitt and Reid 1992; Beismann et al. 2000). Furthermore, the salicaceous species that colonize lower elevations have greater physiological tolerance to flooding, whereas those that colonize higher elevations have greater tolerance to desiccation and possess associated growth traits for alleviating desiccation (Dionigi et al. 1985; van Splunder et al. 1996; Amlin and Rood 2001). These characteristics suggest that salicaceous species can establish themselves on riverside sites because they can tolerate both flooding and desiccation.

In general, soil flooding restricts soil–atmosphere gas exchange, leading to soil oxygen depletion (Pezeshki 2001). Soil oxygen is consumed by plant roots and their associated microorganisms, soil reductants (Ponnamperuma 1972), and soil chemical reactions (Ponnamperuma 1984). Many studies of the responses of salicaceous species to flooding have focused on the response to oxygen shortages following flooding (e.g., Dionigi et al.