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# Foliar flavonol concentration in *Sclerocarya birrea* saplings responds to nutrient fertilisation according to growth-differentiation balance hypothesis

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ABSTRACT

The growth-differentiation balance hypothesis (GDBH) postulates a nonlinear, 'hump-shaped' response of plant secondary metabolites (PSMs), such as flavonoids, in relation to nitrogen (N) availability. The response is most easily detected when there are at least five levels of N availability, but very few studies that directly or indirectly tested the GDBH have used three or more levels. Fifty *Sclerocarya birrea* (marula) saplings (mean basal diameter = 35.5 mm, SEM = 0.52; mean height = 80.9 cm, SEM = 1.02), were randomly assigned to five fertiliser application rates in an orchard. Fertilizer [N:P:K (3:1:5) (26)] containing slow release nitrate was applied to each sapling as a top dressing every two months during the growing season at rates equivalent to 0, 20, 40, 80 and 120 g N $m^{-2}$. Average flavonoid content of 30–35 recently matured leaves per sapling was indirectly measured every two months during the growing season using the Dualex® Series 4 instrument. The nonlinear, 'hump-shaped' response predicted by GDBH was observed, indicating that allocation of carbon to PSMs was more limited at both high and low nutrient availability than at intermediate nutrient availability. Successful detection of the quadratic response was probably facilitated by only measuring flavonols, which are the main PSMs in *S. birrea*, and by conducting the experiment on soils of very low fertility.

## 1. Introduction

Approximately 5% of plant secondary metabolites (PSMs) are flavonoids, most of which are flavonols, flavan-3-ols (also known as proanthocyanidins or condensed tannins) and anthocyanins (Routaboul et al., 2012). Flavonoids are ecologically important compounds in plants for several reasons, e.g., as protection against herbivores, pathogens or UV radiation (Stolter et al., 2010; Persson et al., 2012; Julkunen-Tiitto et al., 2015). As with other PSMs, flavonoid concentrations within plant species vary qualitatively and quantitatively in both time and space (Persson et al., 2012; Moore et al., 2014). Among other factors, the availability of resources (e.g., light, water, or specific nutrients) affects the source–sink balance governing the allocation of molecules to vital functions of plants, such as growth, reproduction, storage and protection against stress factors (Moreira et al., 2014).

Most plant species have common primary metabolites, but rarely do any plant species share with any other plant species the same or similar profiles of PSMs (Salminen and Karonen, 2011). Thus, testing hypotheses that address variation in PSMs within species is less likely to yield conflicting results than tests among species. One of the foremost hypotheses proposed for explaining intra-specific variation in PSMs, especially nitrogen-free (N-free) compounds such as flavonoids, is the growth-differentiation balance hypothesis (GDBH). The GDBH was first described by Loomis (1932) and later developed by Herms and Mattson (1992) to explain how the physiological trade-off between growth and differentiation processes interacts with nutrient availability to influence phenotypic expression of PSMs (Stamp, 2003). The GDBH subsumes other resource-based hypotheses of intra-specific variation in PSMs, such as the carbon-nutrient balance hypothesis (CNBH) and growth rate hypothesis (GRH), and has therefore been regarded as the most advanced hypothesis of its type (Stamp, 2003). Some modified versions of the GDBH have been proposed to incorporate specific features such as effects of mutualisms or $CO_2$ concentration (Kleczewski et al., 2010; Novick et al., 2012), but the fundamentals remain the same. The GDBH assumes that any factor that reduces N availability limits growth more than photosynthesis. The hypothesis predicts that when N availability is low, then both growth rate and net assimilation rate (NAR) are low, but when N availability is high, then both growth rate and NAR are high. Under both of these conditions, limited carbon (C) is available for allocation to N-free PSMs. However, when N availability is intermediate, then growth rate is limited, but NAR is high, resulting in C being available for allocation to N-free PSMs. The resulting 'hump-shaped' response of N-free PSMs is most easily detected when there are at least five levels of N availability (Stamp, 2004).

The aim of this study was to evaluate the GDBH, as applied to *Sclerocarya birrea* (A. Rich) Hochst subsp. *caffra* (Sond.) Kokwara

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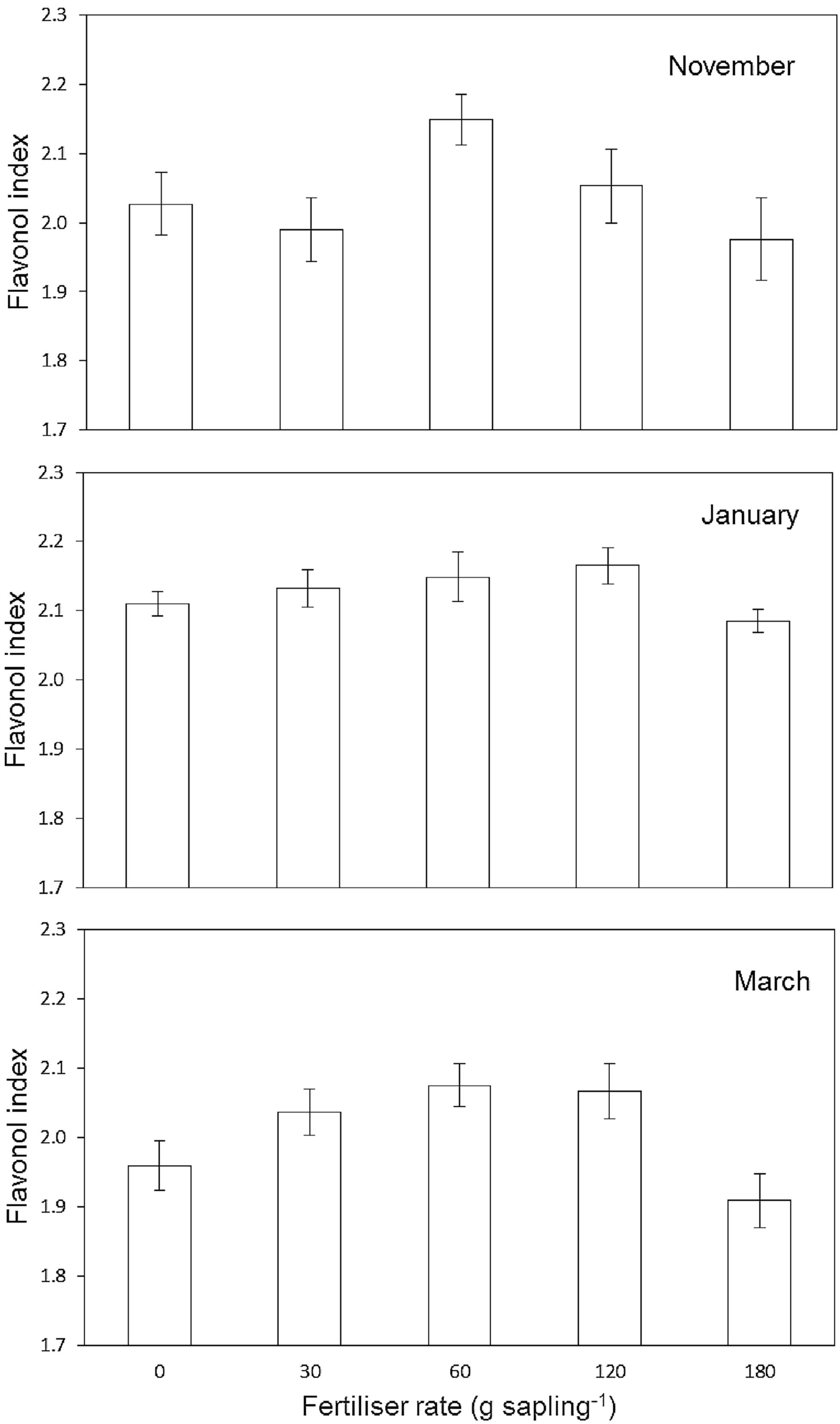


**Fig. 1.** Mean flavonol index of recently matured leaves of *Sclerocarya birrea* saplings given a composite fertilizer, N:P:K (3:1:5) (26) (Wonder™), containing slow release nitrate top-dressed at rates per plant that are equivalent to 0, 20, 40, 80 and 120 g N $m^{-2}$ in early September 2013, early November 2013, and late January 2014. Flavonol index was measured in mid-November, mid-January and late March using Dualex® Series 4 instruments. Error bars are standard errors of the means.

(commonly known as marula). The marula tree is widely considered to be both iconic and keystone in the semi-arid savannas of southern Africa (Helm and Witkowski, 2012). Its leaves, fruit, bark and roots are heavily used by both herbivores and people, leading to its widespread cultivation (Nyoka et al., 2015; Li et al., 2015). Marula leaves are known to contain various flavonoids, especially quercetin, kaempferol and myricetin compounds (all flavonols), which contribute to the medicinal properties of marula leaves (Braca et al., 2003). The focus of this investigation was on detection of the hypothesized 'hump-shaped' response of flavonols in *S. birrea*.