

Sucrose application is ineffectual as a restoration aid in a transformed southern African lowland fynbos ecosystem

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Abstract

The addition of carbon (C) to the soil as sucrose has been suggested as a countermeasure to reduce plant available nitrogen (N) and increase the competitive advantage of slower growing native perennial species over faster growing annual species. To make this approach a successful restoration tool, C addition must induce the resident soil bacteria and fungi to immobilize plant available soil nutrients. In this study, both the efficacy of sucrose applications as a restoration aid and their dependence on soil microbial activity were examined in field and greenhouse trials. Carbon as sucrose (200 g m⁻²) was added to normal and sterilized soils containing various combinations of native perennial and annual species. Their effects on soil N levels, as well as on the photosynthetic efficiency, growth and N uptake of the introduced native species, were measured. Diminished foliar chlorophyll contents, effective quantum yields ($\Delta F/F_m'$) of Photosystem II (PSII) and dry mass accumulation in response to sucrose applications were observed in both the annual and perennial introduced species, but were not reflected in corresponding reductions in soil N levels. These sucrose-induced inhibitory effects, as well as diminished plant N uptake, were more pronounced in normal than sterilized soils. This implied a bacterial component immobilizing soil N essential for plant photosynthesis and growth. However, this premise was partly contradicted by the unaltered total bacterial numbers following sucrose application in the normal soils, although coliform numbers did increase with sucrose application in these soils. These findings point to a likely abiotic mechanism of sucrose-induced inhibition of photosynthesis and growth in introduced native plants, which renders sucrose application ineffectual as a restoration aid in transformed lowland fynbos ecosystems.

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1. Introduction

Southern African Mediterranean climate fynbos ecosystems, included among 34 global biodiversity hot spots (Mittermeier et al., 2004), are heavily fragmented, with up to 95% of some, e.g. renosterveld, transformed through agriculture and viticulture (Milton, 2004). Alien grasses of temperate and subtropical origin proliferate in these highly fragmented ecosystems (Steinschen et al., 1996) and are known to impact on ecosystem structure, function and resources (D'Antonio and Vitousek,

1992). Their recent increase in abundance in lowland areas (Steinschen et al., 1996) has been attributed to habitat deterioration caused by plowing, vegetation clearing and burning, soil nutrient enrichment from surrounding agricultural areas and grazing by herbivores, which disperse the grass seeds on their hides and in their dung (Milton, 2004). This has resulted in the displacement of wildflowers that form the basis of a growing, lucrative nature-based tourist industry (Goldblatt and Manning, 2000).

Various methods for restoring transformed lowland fynbos ecosystems (especially renosterveld) invaded by alien grasses have been examined. These include removal of alien grasses by indigenous herbivores (Midoko Iponga et al., 2005;

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Shiponeni and Milton, 2006), mowing, hand clearing, light and intense burning and pre-emergent herbicide application (Musil et al., 2005). An empirical appraisal of the cost effectiveness of different labor-intensive strategies for alien grass removal, linked to a national poverty relief program, concluded that effective long-term control of the invasive grasses required an integrated management approach that would seek to limit factors that promoted their success, such as soil N enrichment (Musil et al., 2005). However, a subsequent study that examined the effects of soil nutrient depletion by carbon-rich mulching on alien grass cover and shrub establishment in a transformed lowland fynbos community reported inconclusive effects of the mulching on soil N levels and the re-establishment of native plants (Holmes, 2008).

Soil nutrient enrichment has been shown to facilitate the competitive advantage of fast growing annuals and alien grass species over slow growing native perennial species (Eschen et al., 2006; Redente et al., 1992), which persists as long as soil nutrient levels remain high. The elevated soil nutrient levels not only impede the growth of the slow growing native species but also their establishment from seed dispersed both naturally and artificially in restoration initiatives (Kindscher and Tieszen, 1998). Different techniques have been proposed for reducing levels of growth-limiting nutrients in transformed ecosystems. These include topsoil removal, the application of Ca-, Al- and Fe-based compounds, which reduce levels of plant available P in soils (Busman et al., 2002), and organic matter additions (Eschen et al., 2006), which comprise a rich source of carbon that stimulates soil microbial activity leading to a depletion of plant available soil N (Eschen et al., 2006; Reeve Morgan and Seastedt, 1999). Various sources of organic matter that are high in carbon and low in nitrogen, such as sucrose, sawdust, straw, grain hulls and chopped wood (Blumenthal et al., 2003), have been applied for decreasing the availability of essential nutrients, especially nitrogen, to plants (Blumenthal et al., 2003; Corbin and D'Antonio, 2004; Eschen et al., 2006). For this to work, the above-mentioned sources of organic matter must increase microbial N immobilization and decrease plant available N (Corbin and D'Antonio, 2004). Under decreased plant available N conditions, the growth of all vegetation would be expected to decrease, but if faster growing species are disproportionately affected by decreased soil N concentrations, slower growing native species may benefit indirectly due to reduced competition from fast growing exotic species (Corbin and D'Antonio, 2004; Eschen et al., 2006).

Previous experiments have shown that the application of various sources of organic matter lead to diminished rates of net N mineralization (Gilliam et al., 2005; Hopkins, 1998) and nitrification (Gilliam et al., 2005), and reduced ammonium (Hopkins, 1998) and nitrate (Blumenthal et al., 2003) concentrations in soils. Such organic matter additions have been applied successfully in restoration initiatives that have sought to stimulate the growth of native and late seral species in alien-invaded ex-arable lands enriched from past fertilization (Blumenthal et al., 2003; Corbin and D'Antonio, 2004).

Conditions for the decomposition of organic matter in Mediterranean climate ecosystems are poor, since microbiological

activity is limited by low temperatures during the wet season, and soil moisture limits decomposers during the summer drought. This is apparent from the low decomposition rates reported in Mediterranean climate sclerophyllous vegetation relative to tropical and temperate forest, savanna and grassland vegetation types (Read and Mitchell, 1983). As a consequence, the application of rapidly decomposable sources of carbon such as industrial sucrose may provide a more efficient means of reducing available soil N than slower decomposable sources of carbon such as sawdust, reeds and chopped wood in fynbos restoration initiatives. However, a potential disadvantage associated with direct sucrose application is the reported inhibition of high exogenous sucrose concentrations on plant photosynthesis and growth (Mosaleeyan et al., 2004), especially under photosynthetic sink limitations of high photosynthetic photon flux density (Van Quy et al., 2001). Consequently, this study examined the efficacy of sucrose applications as a restoration aid in a transformed fynbos ecosystem and its dependence on soil microbial activity.

2. Methods and materials

2.1. Study area and site

The study area was the Elandsberg Private Nature Reserve (EPNR), situated on Bartholomew's Klip farm near Hermon, approximately 25 km north of Wellington in the Cape Floristic Region of South Africa (Midoko Iponga et al., 2005). The reserve was proclaimed in 1973 (Parker, 1982) and declared a natural heritage site in 1988 (Midoko Iponga et al., 2005). The study site comprised an area of degraded natural vegetation (old field) situated in a transition zone (33°44'67" S to 33°44'72" S; 19°03'13" E to 19°03'17" E) between Swartland Shale renosterveld and Swartland Alluvium fynbos vegetation units, as defined by Mucina and Rutherford (2006). It was transformed for the cultivation of oats between 1960 and 1965, and then used for the cultivation of European pasture grasses for livestock grazing between 1965 and 1987 (Midoko Iponga et al., 2005).

Renosterveld is broadly categorized as evergreen fire-prone vegetation lacking the typical fynbos families Proteaceae and Ericaceae, dominated by small leafed asteraceous shrubs, especially *Dicerothamnus rhinocerotis* (L.f) (= *Elytropappus rhinocerotis*), popularly known as renosterbos or rhinoceros bush, with an understory of Poaceae (grasses) and geophytes (Mucina and Rutherford, 2006). Renosterveld is ecotonal to fynbos and succulent karoo, occurring on moderately fertile, clay-rich (shale and granite derived) soils on lower mountain slopes, interior valleys and coastal forelands at annual precipitation levels of between 300 and 600 mm (Cowling et al., 1986; Mucina and Rutherford, 2006). Fynbos develops under this amount of rainfall on oligotrophic soils, and succulent karoo replaces renosterveld on fertile soils under drier conditions. Post-colonial firewood collection, burning and grazing of vegetation are thought to have shaped modern renosterveld by transforming a woody shrubland perennial grassland mosaic into a more uniform shrubland dominated by *D. rhinocerotis*,

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