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Effects of wildfire ash from native and alien plants on phytoplankton biomass



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- Significant differences among plant species ash metal and nutrient concentration were observed.
- Phytoplankton biomass increased for all plant treatments a week after ash additions.
- Silicate concentrations showed an increasing patterns among all ash treatments.
- No clear patterns were observed between native and alien plant ash on chl-*a* and silicate concentrations.
- Ash effects on water chemistry, chl-*a* and silicate concentrations varied among individual treatments.

ARTICLE INFO

Editor: Damia Barcelo

Keywords: Primary productivity Chlorophyll-a Silicate Diatom Water chemistry



ABSTRACT

Wildfires are natural or anthropogenic phenomena increasing at alarming rates globally due to land-use alterations, droughts, climatic warming, hunting and biological invasions. Whereas wildfire effects on terrestrial ecosystems are marked and relatively well-studied, ash depositions into aquatic ecosystems have often remained overlooked, but have the potential to significantly impact bottom-up processes. This study assessed ash-water-phytoplankton biomass dynamics using six plant species [i.e., three natives (apple leaf Philenoptera violacea, Transvaal milk plum Englerophytum magalismontanum, quinine tree Rauvolfia caffra) and three aliens (lantana Lantana camara, gum Eucalyptus camaldulensis, guava Psidium guajava)] based on a six-week mesocosm experiment with different ash concentrations (1 and 2 g L⁻¹). We assessed concentrations of chemical elements, i.e., N, P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn and B from ash collected, and examined potential differences among the species. High concentrations of P, K, Mn, Fe, Cu, Zn and B were recorded from Transvaal milk plum ash and low concentrations of P, K, Ca, Mg, Cu and Zn were recorded from apple leaf. An increase in phytoplankton biomass (using chlorophyll-a concentration as a proxy) for all treatments i.e., 1 and 2 g L⁻¹ and plant species was observed one week after, followed by decreases in the following weeks, with the exception of 2 g L^{-1} for lantana, gum and control groups. Silicate concentrations (i.e., used as a proxy for diatom abundance) showed increasing patterns among all ash treatments, with the exception of controls. However, no clear patterns were observed between native and alien plant ash for both chl-a and silicate concentrations. We found that ash has notable effects on water chemistry, particularly nitrate, which increased throughout the weeks, whereas, pH and conductivity were high at low ash concentrations. The impacts of ash on water chemistry, chl-a and silicate concentrations vary with individual species and the amount of ash deposited into the system.

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http://dx.doi.org/10.1016/j.scitotenv.2022.155265 Received 1 February 2022; Received in revised form 9 April 2022; Accepted 10 April 2022 Available online 18 April 2022

1. Introduction

For the past million years hominids have been the major igniters of wildfires (accidentally or for management purposes), with other natural processes such as lightning igniting approximately 10% of the wildfires in the savannas (Cassidy et al., 2022). These phenomena are increasing at alarming rates globally, caused by vegetation (i.e., native and alien invasive plants), density, agriculture, hunting and climatic conditions (Pinto et al., 2004; Smith et al., 2011; Dalu et al., 2017). Wildfires are essential for biome structuring (Pinto et al., 2004; Juli et al., 2008); however, they can pose severe threats to biodiversity and habitat quality (Smith et al., 2011; Nunes et al., 2018; Oliveira-Filho et al., 2018; Carvalho et al., 2019; Rhoades et al., 2019). In the process of burning, wildfires release high quantities of organic and inorganic compounds into the natural environment (Ugurlu, 2004; Ferrer et al., 2021; Pelletier et al., 2022). Wildfire ash constitutes the remaining particulate residue, usually deposited on the ground from burnt wildland biomass, and consists of mineral ions and charred organic matter (Bodí et al., 2014). The ash chemical composition mainly relates to the vegetation type and parts burnt (e.g., leaves, barks, roots) (Smith et al., 2011; Hohner et al., 2019). The principal compounds of ash are calcium, phosphates, carbonates, oxides, silicates, oxides, sulphates, and amorphous phases that either exist as primary minerals in the plant materials or transform because of the heating during a fire (Demeyer et al., 2001; Balfour, 2013). Thus, the severity of burning will determine the ash organic carbon concentration, for example, at low combustion completeness; the ash is organic carbon-rich, whereas at high combustion completeness, most organic carbon is volatilised (Bodí et al., 2014).

Whereas much of these compounds is being deposited directly into terrestrial environments, wildfire ash is also dispensed into aquatic ecosystems (Rulli and Rosso, 2007; Bodí et al., 2014; Hahn et al., 2019). The ash deposited on the ground after wildfires can easily be transported to various ecosystem types via post-fire processes, such as water or wind (Silva et al., 2015). Post-fire rainfalls and subsequent runoff act as a primary transport mechanism for ash into aquatic ecosystems (Wetzel, 2001). Thus, the soluble compounds and particulate matter leached from ash enter aquatic environments, affecting water chemistry variables such as nutrients, metals, and ions (Smith et al., 2011; Bodí et al., 2014; Brito et al., 2017; Harper et al., 2019). The insoluble ash particles from wildfires are also responsible for dissolved oxygen depletion in aquatic ecosystems, as they absorb sunlight and consequently increase water temperatures (Flynn et al., 2018). Ash has been highlighted to change water quality, thereby affecting aquatic ecosystems' function and structure (Nunes et al., 2018; Rhoades et al., 2019). The functions and structuring of aquatic ecosystems are supported fundamentally by phytoplankton.

In aquatic ecosystems, phytoplankton has the greatest contribution towards total primary production, forming the basic support for aquatic food webs (Ezekiel et al., 2011). Numerous studies (e.g., Silva et al., 2015; Kramer et al., 2020; Vidal et al., 2021) have reported both beneficial and harmful effects of wildfire ash on the phytoplankton composition and biomass due to its chemical composition. Among ash properties, nitrate and phosphates are widely reported to facilitate aquatic plant growth and pose a severe risk of eutrophication within aquatic environments, thus bolstering primary productivity (Pinto et al., 2004; Smith et al., 2011; Vajda et al., 2020). Aquatic primary productivity, mostly by phytoplankton, in turn, depends on abiotic and biotic factors such as carbon dioxide, pH, temperature, nutrients, solar radiance, and herbivory (Häder et al., 2014; Dalu et al., 2022), and these factors can be substantially changed following the introduction of ash into the aquatic ecosystems.

Wildfires and invasive alien plants have been highlighted to interact, producing marked impacts on terrestrial and riparian environments, and leading to changes in how landscapes are managed (D'Antonio and Vitousek, 1992; Brooks and Matchett, 2006; Brunson and Tanaka, 2011; Weltz et al., 2011). Several invasive alien plants are known to alter the extent, frequency, intensity, type, and/or seasonality of wildfires, resulting in either increased or decreased fire prevalence across the landscape (Tunison et al., 2000; Brooks et al., 2004; Brooks and Matchett, 2006; Bell et al.,

2009). For example, whereas wildfires in native riparian vegetation tend to occur only during extreme drought periods and typically remain in the surface vegetation, wildfires with invasive alien plants can occur over a broader climatic and environmental range, often spreading into riparian woodlands and forest canopies at high intensities (Bell et al., 2009). In turn, their effects may cause species composition shifts, which can have ecosystem-wide effects (Brooks and Matchett, 2006; Faccenda and Daehler, 2021).

Globally, wildfires affect approximately 350 million hectares annually, with Africa accounting for about half of this area burnt (Attri et al., 2020). In South Africa alone, about 1.18% of the national vegetated land surface is burnt annually, and the frequency of fires varies with ecosystem type. For example, wildfires can range from every year in little-grazed, moist grassland ecosystems, 10-20 years in the fynbos, and rarely in desert environments (Forsyth et al., 2010). South Africa records an average of between 35,000 and 40,000 fires per year, but the number could be much higher due to unreported events from human-induced activities (Strydom and Savage, 2016). Compounding this problem, South Africa is continuously experiencing new annual plant invasions at alarming rates, with suggestions that some of these invasive alien plant species may further modify fire regimes (Forsyth et al., 2010). This combination of factors makes South Africa an ideal, practical case study for assessing and comparing how native and invasive alien plants can affect aquatic ecosystem functioning from ash inputs.

The present study thus aimed to assess ash-water-chlorophyll-a dynamics using six plants, of which three were native (apple leaf Philenoptera violacea, Transvaal milk plum Englerophytum magalismontanum, quinine tree Rauvolfia caffra) and three invasive aliens' plants (lantana Lantana camara, red river gum Eucalyptus camaldulensis, guava Psidium guajava), each frequently known to occur near or around aquatic ecosystems. Hence, the ash from these plants is most likely to be deposited into aquatic ecosystems during and post-fire events. The study aimed to assess the effects of native and alien leaf ash of different concentrations on phytoplankton biomass using chlorophyll-a concentrations as a proxy, as well as silicate, which can be used as an indicator for diatom concentrations. We thus assessed (i) ash chemical properties from different plant species, (ii) effects of ash concentrations on water physicochemical parameters, and (iii) chlorophyll-a and silicate dynamics as proxies of phytoplankton and diatom concentrations. We hypothesised that (i) ash will lead to increased localised phytoplankton biomass, with decreased water quality within a few days of ash addition due to increased nutrient, ion, and oxide contents. Further, we expected (ii) ash produced from alien plant species to facilitate phytoplankton and diatom concentration increases more than natives, due to faster plant growth rates which will lead to high nutrient, ion and oxide uptake and accumulation.

2. Materials and methods

2.1. Experimental design

The experiment was conducted at the University of Venda Department of Geography and Environmental Sciences Atrium (-22.977550, 30.443851) using 64×12 L buckets (ø 25 cm and 30 cm depth). The buckets were placed and filled with 10 L filtered ($63 \mu m$ mesh to remove zooplankton) river water collected from the Mvudi River (-22.983544, 30.443331). Five grams of slow-release Wonder plant booster all-purpose 3:2:1 (N:P:K ratio) fertiliser (Wonder Garden Care, Kempton Park) were added into the water to facilitate 'baseline' phytoplankton growth over 30 days before the start of the experiment.

Leaves and twigs (thereafter referred to as leaves) were collected from three native (i.e., *R. caffra*, *E. magalismontanum*, *P. violacea*) and three alien (i.e., *L. camara*, *P. guajava*, *E. camaldulensis*) plant species before being sundried for 40 days in an open yard at Thohoyandou Unit C (September to October 2020). Once the leaves had dried, each plant species was separately placed inside a metal bucket, then ignited with a matchstick and allowed to burn for 50–60 min to produce ash; the fire intensity was not standardised across the species, but adequate in each case to produce a representative ash sample for experimentation. The fire was extinguished by covering each metal bucket with a lid. All the ash was collected separately per species after it had cooled down and placed into labelled ziplock bags to form the six individual ash treatments, and an additional seventh treatment (mixed) was made using equal proportions of the other six individual ash treatments. The seven different ash treatments were sent to a South African National Accreditation System (SANAS) certified laboratory i.e., BEMLAB to assess for the ash nutrient levels [nitrogen (N; %), phosphorus (P; %), potassium (K; %)] and metal contents [i.e., calcium (Ca; %), magnesium (Mg; %), sodium (Na; mg kg⁻¹), manganese (Mn; mg kg⁻¹), iron (Fe; mg kg⁻¹), copper (Cu; mg kg⁻¹), zinc (Zn; mg kg⁻¹), boron (B; mg kg⁻¹)] (see Dalu et al., 2020a, 2020b for detailed methods).

The experiment used a randomised design, with eight species treatments [i.e., 3 native, 3 alien, 1 mixed, 1 control (no ash)] \times 4 replicates imes 2 ash concentrations (i.e., 1 and 2 g L⁻¹) and was run from 05 November 2020 to 10 December 2020. The ash concentrations were based on conservative estimates from Brito et al. (2017, 2021). At the end of the 30 days of phytoplankton growth, before adding ash, physicochemical variables were measured, and 100 mL water for chlorophyll-a determination was collected. Every week during the experiment, a portable handheld multiparameter Cyberscan Series meter (Eutech Instruments, Singapore) was used to measure water conductivity (μ S cm⁻¹), total dissolved solids (mg L⁻¹), pH, temperature (°C), sodium chloride (ppm), oxidation-reduction potential (mV) and resistivity (Ω). After collecting the first water samples (i.e., week 1 was ash-free), ash at 10 g or 20 g mass was randomly introduced into the individual buckets, except controls, where no ash was introduced. We applied 10 g (1 g L^{-1}) and 20 g (2 g L^{-1}) to resemble real world scenarios, particularly in smaller water bodies where such concentrations are likely to be achieved, mostly after the first surface run offs following wildfires. However, we acknowledge that ash concentrations are likely hugely variable in waters empirically, owing to various hydrological processes, and the applied concentrations here are generally high and consequently represent 'worst case' scenarios. The choice of ash mass was to assess the different responses by chl-a and silicate concentrations (as proxies for phytoplankton productivity) to varying ash concentrations. To compensate for water loss, borehole water was used to top up the buckets to initial levels, by replacing the water taken due to sampling or to normal evaporation processes. These water additions were well-balanced among treatments.

2.2. Nutrient and silicate analyses

Approximately 50 mL of water samples was collected from each treatment and replicated weekly for nutrient (ammonium, nitrate, phosphates) and silicate analyses. The nutrients and silicate were analysed at NRF SAEON Elwandle Node Coastal Biogeochemistry Laboratory (Port Elizabeth, now renamed Gqeberha) using an Auto-Analyser model AA3 segmented flow colourimetry (SEAL Analytical). Phosphates were analysed using the calorimetric method, with readings taken at 880 nm, at a test range of 0–50 μ g L⁻¹. Nitrate was analysed, reducing nitrate to nitrite using a copper-cadmium redactor column (Armstrong et al., 1967) and with a test range of 0–50 μ mol L⁻¹. Ammonium concentration was based on the Berthelot reaction, with measurements taken at 660 nm (test range 0–10 μ mol L⁻¹). Finally, silicate concentrations were analysed based on reducing silico-molybdate in an acidic solution to molybdenum blue by ascorbic acid according to Grasshoff et al. (1983), at a test range of 0–41 μ mol L⁻¹.

2.3. Chlorophyll-a concentration determination

Chlorophyll-*a* concentration was determined weekly as a proxy for phytoplankton biomass from all treatment buckets. The 100 mL water sample from each mesocosm was filtered (vacuum <5 cm Hg) through 0.7 μ m pore size (diameter 47 mm) reinforced glass fibre filters (GF/F; GIC Scientific, Roodepoort). After filtration, the GF/F filters were inserted in 15 mL

tubes containing 10 mL of 90% acetone solution and then stored in a freezer for at least 24 h to allow for chl-*a* extraction. After 24 h, samples were centrifuged at 3000 rpm for 10 min before 2 mL was extracted from each sample to measure absorbance at 665 λ and 750 λ using SPECTROstar NANO (BMG LabTech GmbH, Ortenberg). Absorbance was measured through a 10 mm cuvette before and after acidification with 0.01 M hydrochloric acid (HCl). Absorbance readings were recorded before chl-*a* concentration and calculated based on Lorenzen (1967).

2.4. Data analysis

All data were assessed for normality and homogeneity of variance and were found to conform to parametric assumptions using the Shapiro–Wilks W and Levene's tests. A one-way ANOVA was used to analyse differences among treatments for the various nutrient and metal concentrations before the experiment. We tested whether there were significant experimental differences in physicochemical variables and, particularly, chl-*a* concentration and silicate among the study weeks (i.e., 1–6), treatments (i.e., six species) and ash concentrations (i.e., 1 and 2 g L⁻¹) using factorial repeated measures ANOVA in STATISTICA version 8 (StatSoft Inc, 2007). Variables that were retained as significant were further tested, using Tukey's post-hoc analysis to assess differences among treatments and weeks. To evaluate relationships in chlorophyll-*a* and silicate concentrations among study treatments and ash weights, a Pearson correlation was carried out in SPSS v16 (SPSS Inc., 2007).

3. Results

3.1. Leaf metal and nutrient concentrations

In general, P, K, Mn, Zn, Cu and B concentrations were high in the Transvaal milk plum, with lantana and apple leaf having high N and Fe concentrations, respectively. Gum had high Ca, Mg and Na concentrations (Table 1). Low concentrations were generally observed in the gum (N, Fe), quinine tree (Na, Mn, B) and apple leaf (P, K, Ca, Mg, Cu, Zn) groups (Table 1). Using a one-way ANOVA, significant differences (p < 0.001) were observed for all nutrient and metal plant concentrations across treatments, except P, which was not significant (F = 1.00, p = 0.480).

3.2. Water physicochemical variables variation

Using repeated measures ANOVA, significant differences (p < 0.05) were observed among all physicochemical variables across the weeks, treatments and ash weights, with the exception for phosphate (week), temperature (treatment) and temperature (concentration), which were not significantly different (p > 0.05) as single terms (Table 2). No clear weekly patterns were observed for most physicochemical variables, with the exception of nitrate concentrations in both ash concentrations including controls (Figs. 1 and 2). Week 3 generally had high TDS, conductivity and temperature values recorded.

For 2 g L⁻¹ concentrations, the lantana and mixed groups had high phosphate concentrations (Fig. 1). Ammonium, conductivity and TDS concentrations were low for the gum and Transvaal milk plum, whereas the same ash treatments recorded high pH, resistivity and nitrate values (Fig. 1). The pH and conductivity of 1 g L⁻¹ ash treatments showed an increasing trend across weeks. The controls and apple trees had high phosphate concentrations, whereas slightly lower concentrations were observed for the Transvaal milk plum (Fig. 2). Similarly, lantana had high nitrate concentrations at week 6, but with very high error margins, probably due to an outlier. Control, mixed, and apple tree had high ammonium concentrations, whereas guava had high resistivity. The TDS, conductivity and temperature were high at week 3, whereas week 1 had low nitrate, ammonium, pH, TDS and conductivity (Fig. 2). Table 1

Plant ash nutrient and metal concentrations (\pm standard deviation) before the start of the experiment, i.e., addition into the experimental mesocosms. Abbreviations: B – boron, Ca – calcium, Cu – copper, Fe – iron, K – potassium, Mg – magnesium, Mn – manganese, N – nitrogen, Na – sodium, P – phosphorus, Zn – zinc.

Parameter	SI unit	Lantana	Quinine tree	Guava	Gum	Transvaal milk plum	Apple leaf
Ν	%	1.01 ± 0.02	0.72 ± 0.01	0.41 ± 0.01	0.24 ± 0.01	0.28 ± 0.01	0.93 ± 0.04
Р	%	0.84 ± 0.01	1.19 ± 0.02	0.62 ± 0.02	0.82 ± 0.01	0.92 ± 0.01	0.22 ± 0.01
K	%	4.34 ± 0.51	5.68 ± 0.11	4.23 ± 0.02	5.72 ± 0.01	7.25 ± 0.01	1.47 ± 0.04
Ca	%	11.30 ± 0.42	7.71 ± 0.01	15.48 ± 0.04	21.10 ± 0.14	10.15 ± 0.07	6.05 ± 0.04
Mg	%	1.53 ± 0.08	1.21 ± 0.01	2.08 ± 0.1	3.42 ± 0.01	2.30 ± 0.02	1.02 ± 0.02
Na	mg kg ⁻¹	1255 ± 63.6	604 ± 1.4	1305 ± 7.1	$14,630 \pm 56.6$	$13,801 \pm 1.4$	1150 ± 42.4
Mn	mg kg ⁻¹	1415 ± 7.1	527.0 ± 2.8	643.0 ± 4.2	1905 ± 7.8	6627 ± 9.9	599.0 ± 2.8
Fe	mg kg ⁻¹	9053 ± 17.7	9215 ± 21.8	9705 ± 7.1	6384 ± 8.5	$16,587 \pm 4.9$	$22,692 \pm 53.7$
Cu	mg kg ⁻¹	106.5 ± 2.1	68.7 ± 0.4	75.5 ± 0.2	93.5 ± 0.7	181.5 ± 4.9	63.2 ± 0.5
Zn	mg kg ⁻¹	1116 ± 19.8	1770 ± 14.1	391.0 ± 1.4	470.0 ± 1.4	1334 ± 50.9	288.5 ± 2.1
В	mg kg ⁻¹	221.0 ± 1.4	137.0 ± 3.5	323.5 ± 3.5	720.5 ± 3.5	767.0 ± 2.8	318.0 ± 2.8

3.3. Chlorophyll-a and silicate dynamics

Chlorophyll-*a* concentrations generally increased from week 1 to 2, with 1 g L⁻¹ guava and apple leaf increasing to week 3 before decreasing for the following weeks (Fig. 3a, b). However, the 2 g L⁻¹ quinine tree, 2 g L⁻¹ control, 2 g L⁻¹ guava and 1 g L⁻¹ mixed treatments showed different patterns (Fig. 3a, b). Chlorophyll-*a* concentrations generally decreased in 2 g L⁻¹ lantana and guava throughout the weeks.

Silicate concentrations generally increased over time, with very low concentrations recorded in the controls, although other treatments had slightly different patterns (Fig. 3c, d). Among the native species, the quinine tree recorded relatively low silicate concentrations for both 2 g L⁻¹ and 1 g L⁻¹ ash weights, with the apple leaf and Transvaal milkplum showing high silicate concentrations. Guava generally recorded high silicate concentrations followed by lantana, with gum recording low silicate concentrations among the alien species.

Significant differences were observed across weeks (chl-a – F = 9.950, p < 0.001; silicate – F = 22.780, *p* < 0.001), treatments (chl-*a* – F = 15.230, *p* < 0.001; silicate – F = 2.459, p = 0.019) and ash concentrations (chl-a – F = 5.856, p = 0.016; silicate - F = 16.718, p < 0.001). Significant differences were also observed across week \times treatment (F = 1.753, p = 0.008), and week \times ash (F = 2.309, *p* < 0.045) for chl-*a* concentrations, and with silicate concentration significant differences being observed for treatment \times ash (F = 9.473, p < 0.001). Based on post-hoc analysis, significant chl-a concentration differences were for observed for week 1 vs 2 (p =0.007), week 2 vs 3 (p < 0.001), 4 (p < 0.001), 5 (p < 0.001) and 6 (p < 0.001) 0.001), with significant silicate concentration differences being observed for week 1 vs 3 (p < 0.001), 4 (p < 0.001), 5 (p < 0.001) and 6 (p =0.005). However, no significant chl-*a* concentration differences (p > 0.05) were observed for treatments, whereas significant silicate concentration differences were observed to differ for control vs lantana (p = 0.001), guava (p < 0.001), Transvaal milkplum (p < 0.001), mixed (p = 0.001) and apple tree (p < 0.001), and gum vs Transvaal milkplum (p = 0.012).

3.4. Relationship between chlorophyll-a, silicate and physicochemical variables

For the 2 g L⁻¹ weight, positive and significant relationships (p < 0.05) were observed for the control (resistivity), guava (ORP, phosphate) and apple tree (phosphate) treatments with chl-a concentrations, whereas significant negative relationships (p < 0.05) were found for guava (silicate) and mixed (nitrite, nitrate) with chl-a concentration (Table S1). For the 1 g L⁻¹ ash concentration, no significant relationships (p > 0.05) were observed for quinine tree, lantana, guava, Transvaal milk plum and apple tree treatments with chl-*a* concentration (Table S1). The 1 g L^{-1} mixed treatment had negative and significant correlations (p < 0.05) observed for nitrate, nitrite, pH, conductivity, TDS and salinity, with significant positive relationships observed for ORP with chl-a concentration. A negative and significant relationship (p < 0.05) was observed for chl-*a* concentration with silicate, nitrite, nitrate, conductivity and salinity in the gum treatment. For the controls, a significant negative relationship (p < 0.05) was observed for ORP, whereas a significant positive relationship (p < 0.05) was observed for nitrate, conductivity and salinity for chlorophyll-a concentration (Table S1).

For the 2 g L⁻¹ ash treatment, lantana, gum and apple tree treatments had the most significant correlations (p < 0.05) observed with silicate concentrations. No significant differences (p > 0.05) were observed for silicate concentration with most of the physicochemical variables in treatments (Table S2). For silicate under 1 g L⁻¹ ash weights, no significant relationships (p > 0.05) were observed for the control treatment. With lantana, all variables were significant (p > 0.05) (except ammonium, temperature, chl-*a*) as well as for gum (except phosphate, ammonium, ORP, pH, temperature) (Table S2).

4. Discussion

This study assessed the effects of native and alien leaf ash on physicochemical, silicate and chlorophyll-*a* concentrations using ash from three

Table 2

Repeated measures ANOVA based on physicochemical variables for a week, treatment and ash. Bold values indicate significant differences at p < 0.05. Abbreviations: TDS – total dissolved solids, ORP – oxygen reduction potential.

Variable	Week		Treatment		Ash		Week × Treatment		Week \times Ash		Treatment × Ash		Week \times Treatment \times Ash	
	F	Р	F	р	F	р	F	р	F	р	F	р	F	р
Phosphate	0.52	0.757	5.349	< 0.001	4.380	0.037	0.230	1.000	0.630	0.677	8.612	< 0.001	0.258	1.000
Nitrate	47.89	< 0.001	6.322	< 0.001	4.786	0.030	1.384	0.083	0.835	0.526	2.484	0.018	0.914	0.612
Nitrite	29.99	< 0.001	6.354	< 0.001	13.765	< 0.001	1.442	0.059	1.308	0.261	4.643	< 0.001	0.966	0.528
Ammonium	2.35	0.041	9.751	< 0.001	37.452	< 0.001	0.419	0.999	0.572	0.721	14.767	< 0.001	0.368	1.000
pН	117.82	< 0.001	23.574	< 0.001	25.594	< 0.001	3.097	< 0.001	5.333	< 0.001	6.237	< 0.001	1.291	0.137
TDS	3.63	0.003	3.104	0.004	4.227	0.041	2.036	0.001	3.607	0.004	3.095	0.004	2.035	0.001
Conductivity	22.60	< 0.001	15.795	< 0.001	14.250	< 0.001	0.735	0.863	1.874	0.099	7.694	< 0.001	0.472	0.995
ORP	135.33	< 0.001	29.496	< 0.001	30.601	< 0.001	3.648	< 0.001	5.988	< 0.001	6.414	< 0.001	1.844	0.004
Resistivity	44.15	< 0.001	14.025	< 0.001	23.202	< 0.001	1.075	0.364	1.640	0.150	9.604	< 0.001	0.742	0.855
Temperature	6947.71	< 0.001	0.742	0.636	1.850	0.175	0.446	0.997	0.475	0.795	1.167	0.322	1.381	0.085
Salinity	22.78	< 0.001	15.230	< 0.001	16.718	< 0.001	0.681	0.914	1.665	0.144	9.473	< 0.001	0.458	0.997



Fig. 1. Physicochemical variables among the 2 g L⁻¹ ash treatments over the study period. Abbreviations: Qt – quinine tree, C – control, L – lantana, Gv – guava, G – gum, Tt – Transvaal milk plum, M – mixed, At – Apple leaf.



Fig. 2. Physicochemical variables among the 1 g L⁻¹ ash treatments over the study period. Abbreviations: Qt – quinine tree, C – control, L – lantana, Gv – guava, G – gum, Tt – Transvaal milk plum, M – mixed, At – Apple leaf.



Fig. 3. Chlorophyll-*a* (a, b) and silicate (c, d) concentrations among the different treatments and ash concentrations $[(a, c) - 2 g L^{-1}; (b, d) - 1 g L^{-1}]$ over a six-week experimental period. Abbreviations: Qt – quinine tree, C – control, L – lantana, Gv – guava, G – gum, Tt – Transvaal milk plum, M – mixed, At – Apple leaf.

native (Transvaal milk plum, quinine tree, apple leaf) and three alien (lantana, guava, gum) plant species, replicating inputs from wildfires. Wildfires are an increasing problem, especially in the tropics and subtropics, due to changing climates, i.e., extreme temperatures and drought conditions, biological invasions and anthropogenic activities. In assessing the implications of ash inputs for aquatic primary productivity between native and alien plant species, we did not find a clear, significant difference according to invasion history. This suggests that effects among plant species are speciesspecific and cannot be generalised according to invasion history, likely owing to underlying traits that influence the composition of nutrient inputs into waters. Nevertheless, the present study provides insights into the effects of wildfires on aquatic ecosystems in part of the Global South in terms of nutrient inputs and bottom-up processes.

Different metal and nutrient concentrations for ash from each plant species were recorded; however, the ash Ca concentration was not significantly different among ash types, similar to observations by Brito et al. (2017). In comparison with other studies, such as Ulery et al. (1993), Khanna et al. (1994) and Gabet and Bookter (2011), our ash analysis yielded high concentrations of Fe and Zn, but in contrast to Liodakis et al. (2005) who observed Zn concentrations to be higher than those here. In Brazilian savannas (i.e., Cerrado biome), the ash collected had high B, Ca, K, Mg, Mn, P, S, and Zn concentrations, which were higher compared to what we recorded (Brito et al., 2017). This variation in concentrations also corroborates the studies conducted by Ulery et al. (1993), Khanna et al. (1994), Demeyer et al. (2001), Liodakis et al. (2005), Gabet and Bookter (2011) and Brito et al. (2017) who highlighted that ash properties depended on the plant part (i.e., leaves, bark) and vegetation type.

We speculate other contributing factors that might have influenced nutrient and metal concentrations, include burning severity or temperature of combustion, which are known to influence ash properties (Bodí et al., 2014; Santín et al., 2015). However, the intensity was not measured in the current study, and this has been notably an important limitation, because plant species were possibly not subjected to consistent burning conditions given their differences in composition. After burning leaves, we observed different ash colours from each plant, with guava producing light-coloured ash compared to other plants. The apple leaf produced coarse, dark ash filled mostly with pyro-cyclic materials, indicating that the fire intensity at which the plant leaves burnt differed, as highlighted by the proposed ash colour scale (Úbeda et al., 2009). Out of 11 elements studied, six low concentrations (i.e., P, K, Ca, Mg, Cu, Zn) were recorded from apple leaf.

Overall, the ash treatments had significant differences for all of the water physicochemical variables in the mesocosm, except temperature, which only differed significantly through time. Phosphates and nitrates, which are limiting factors for aquatic plant growth (phytoplankton in this case), differed significantly among treatments and ash concentration, which could have been facilitated by the P and N availability, together with the uptake rates by phytoplankton. Generally, pH increased from the 2nd week, with ash treatments recording slightly high pH compared to the controls, and in most scenarios, such increases in concentration are facilitated by the release of base cations i.e., potassium, from ash (Ulery et al., 1993; Son et al., 2015). The TDS generally peaked in week three, due to increases in water temperature in the mesocosms, allowing more solids to dissolve into the water. We generally observed similar patterns between TDS and conductivity for all species, except for the 1 g L^{-1} quinine tree and control, where the conductivity persistently increased throughout the weeks. We speculate that TDS had more influence on the conductivity by adding more ions to the mesocosm while promoting the electrical conductivity of the water.

Chlorophyll-*a* concentrations were found to generally increase a week after the addition of ash, followed by a decrease in the following weeks, however, individual patterns differed among treatments. We measured and recorded chl-*a* peak concentrations seven days after the introduction of ash within the system; however, it is probable that the concentrations temporarily peaked beyond these recordings within six days of the sampling cycle from the addition of ash, corroborating with the short period peak observations by Wang et al. (2021). Furthermore, Meng et al. (2022) indicated that ash dust deposition stimulated an increase in phytoplankton biomass (i.e., chl-*a*) in the Northwestern Pacific during spring within 5–35 days depending on distance from the area where the fire was. An assumption is that a rapid decrease in chl-*a* concentrations after week 2 was due to depletion of ammonium and P in the water among the different ash treatments, following an initial 'boom' in phytoplankton, i.e., due to resource depletion.

Silicate concentrations generally increased throughout the weeks in both 2 g L^{-1} and 1 g L^{-1} ash treatments, with controls recording relatively low concentrations. The recorded silicate concentrations in the mesocosm may have been promoted by the release of Si as ash dissolves over the weeks, however, as we looked at silicate as a proxy for diatom biomass, we speculate that this increase in silicate may indicate that the ash treatment significantly promoted diatom growth and ultimately, their abundances (Earl and Blinn, 2003; Minshall et al., 1995). Indeed, a strong relationship between silicate and diatoms has been reported by Sumper and Kröger (2004) and Hidayat et al. (2019). This consistent increase in silicate concentrations throughout the weeks among ash treatments can be explained by the dissolution and reutilization process, whereby silica shells from diatoms are dissolved, which made silicate sufficiently available in the system while promoting vegetative cell division and formation of new valves (Paasche., 1973; Yun et al., 2018). Another possible explanation for the increase in silicate concentration concentrations could be related to the silicate in ash dissolving as the ash was added in water (Brito et al., 2017).

In the present study, ash treatment has shown numerous potential alterations within the aquatic environment, as evidenced by correlation analyses. We observed increased conductivity in contrast with baseline readings, although guava, gum and Transvaal milkplum yielded slightly lower conductivity at 2 g L⁻¹ compared to 1 g L⁻¹. An inverse relationship between conductivity and resistivity is notable, but the ash effect on these parameters is not significant. The mesocosms showed varying concentrations of physicochemical parameters with increased concentration of ash input i.e., phosphate and nitrate generally increased over time, and while this is also observed in controls, it is more likely that the pre-added ash had an influence in the observed persistent increase. Ammonium showed a weak relationship with increasing ash input.

While this study presents a first approach to examine the effects of ash from these alien and native plants singularly and in total combination, further work should examine the influence of broader plant combinations to better resemble variations in community composition at different invasion stages. In this context, our results could be considered to reflect the composition of ash following burning of invasive alien plants present in monoculture for the most part. Moreover, future work should examine the influence of burn intensity and the effects of different parts of plants, such as leaves and stems, in their influence on aquatic ecosystems. Additional studies could also further examine the influence of wildfire ash on different cation elements over time, whereas the present study was limited to examination in the initial ash samples before their addition to waters, albeit in relatively high concentrations.

5. Conclusions

The study assessed the relationships and effects of wildfire ash on water chemistry, chl-*a* (phytoplankton biomass proxy) and silicate concentrations (diatom proxy), as well as ash properties directly. It is important to highlight that the work was done in a standardised way, for comparing these species as a first, 'pioneering' approach to understand alien-native ash effects. A clear difference between native and alien plant ash influence on chl-*a* and silicate concentrations was not observed among treatments, however individual species exhibited varying effects on chl-*a* concentrations, but broadly similar effects on silicate concentrations. Our results suggest that ash has an influence on water chemistry i.e., elevated pH, altered nutrient levels and chl-*a* together with silicate concentrations, and thus the primary productivity by the aquatic ecosystems is likely to be subjected to either beneficial or detrimental effects in the events of extreme fires and deposition of ash in large quantities, with potentially mixed effects on aquatic taxa. Ash effects on aquatic primary productivity, imposed by restructuring of the primary producers i.e., phytoplankton, are also expected to have significant impacts on higher trophic levels, such as herbivores within the affected aquatic ecosystems, which requires further examination. Future studies should investigate how individual plant nutrient and metal concentration might affect primary production within aquatic ecosystems.

CRediT authorship contribution statement

VTN: Formal analysis, Methodology, Data curation, Writing – original draft, review and editing; RNC: Conceptualization, Methodology, Visualisation, Supervision, Writing – original draft, review and editing; FD: Visualisation, Methodology, Investigation, Supervision, Writing – review and editing; TD: Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Funding acquisition, Supervision, Writing – original draft, review and editing.

Declaration of competing interest

All authors declare no conflict or financial interests exist for the manuscript.

Acknowledgement

We greatly acknowledge the financial support of the University of Venda Niche Grant (SES/18/ERM/10) and NRF Thuthuka Grant (117700). RNC and TD acknowledge funding from the Alexander von Humboldt Foundation and Wissenschaftskolleg zu Berlin/Stellenbosch Institute for Advanced Study, respectively.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.155265.

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