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Do Soil Chemical Changes Contribute to the Dominance of Blady Grass (*Imperata cylindrica*) in Surface Fire-Affected Forests?

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Abstract: *Imperata cylindrica* is a perennial grass that often proliferates in fire-affected forests. Recent fire events have been consistently associated with a lowering of soil nitrogen (N) to phosphorus (P) ratios. Thus, *I. cylindrica* might have a tendency toward P-limited growth and/or tolerance for low soil N availability that confers a competitive advantage post-fire. We contrasted soil and *I. cylindrica* chemistry between recently burned and unburned areas in eastern Australia. *Imperata cylindrica* foliar N:P ratios were 21% lower in burned areas than in unburned areas, reflecting an increase in the uptake of P, but not N, post-fire, consistent with P-limitation. We then grew *I. cylindrica* seedlings in soils with differing fire-exposure histories and subjected them to various resource amendments (including N and P addition). Survival of *I. cylindrica* seedlings was not affected by the fire-exposure history of soil, but was reduced by 66% through N-addition. Soil fire history did not significantly affect *I. cylindrica* growth, but addition of P greatly enhanced *I. cylindrica* growth, particularly on unburned soils. Our results indicate that the association between *I. cylindrica* and forest fire regime could be facilitated, in part, by the short-term positive effect of fire on soil phosphorus and the long-term positive effect of fire-exclusion on soil nitrogen, particularly on well-weathered soils.

Keywords: burning; stoichiometry; nutrient limitation; phosphorus; nitrogen; alang-alang; cogongrass; fire weed



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1. Introduction

Periodic fire events are a normal and necessary feature of many terrestrial ecosystems [1,2]. When consistent with the natural fire regimes to which such ecosystems have adapted, fire events generally have positive implications for biodiversity, ecosystem function, and ecosystem stability [3–6]. This is because fires can remove accumulated plant necromass, enrich soils with essential nutrients [7,8], stimulate and/or facilitate plant reproduction and germination [2,9–11], and generate spatial heterogeneity in environmental variables (i.e., light, openness, soil temperatures) and community successional stages [12]. In some cases, however, fires have the potential to facilitate the invasion and proliferation of invasive plant species [13]. This is largely due to the combination of anthropogenic climate change [14], which is changing fire regimes in ways that can affect the fitness of native plant species [15], and the increasingly intercontinental mobility of invasive plant propagules that comes as a consequence of humanity's economic globalisation [16,17].

One such invasive species is *Imperata cylindrica* (L.) Beauv. (commonly referred to as alang-alang, cogongrass, and blady grass, among numerous other local names, depending on region), a perennial, rhizomatous C₄ grass in the Poaceae family (tribe Andropogoneae) [18]. The positive association between *I. cylindrica* and fire has long been recognized [17]: the species has a strong propensity to proliferate in areas that have been

recently and/or frequently burned across a range of ecosystems along with a tendency to increase ecosystem flammability [17,19–25]. *Imperata cylindrica* is generally regarded as native to tropical and subtropical regions of the eastern hemisphere [18], but precise estimates of the ‘natural’ range of *I. cylindrica* are complicated by its aggressively invasive nature. The species is now established on every vegetated continent [18], and research published in 1998 estimated that the global extent of *I. cylindrica* ‘infestation’ was over 500 million hectares [16]. Much of this extent is in tropical and subtropical Asia [26], where repeated burning, along with logging and other land-use changes, has facilitated the invasion and subsequent monodominance of *I. cylindrica* across vast areas of previously highly biodiverse forested landscapes [18,27,28]. Thus, both within and outside of its native range, changes in fire regime, and particularly increases in fire frequency, can enable the proliferation of *I. cylindrica*, with significant negative consequences for forest biodiversity [26,29] and agricultural production [30]. As such, there is a need to understand the mechanisms through which *I. cylindrica* gains a competitive advantage in recently and/or frequently burned forest ecosystems and is likewise potentially disadvantaged by the long-term absence of burning [21].

The positive association between *I. cylindrica* and recent and/or frequent fire is likely due in no small part to changes in forest structure and light availability that can accompany some fire events [19,26]. However, prior studies have shown that rates of clonal invasion by *I. cylindrica* are not related to understory light inputs [31], and *I. cylindrica* has been shown to perform better than most C₄ grasses under reduced light availability in numerous studies [18]. Moreover, many plant species (and particularly herbaceous species) other than *I. cylindrica* respond positively and rapidly to increased light levels in the understory. Thus, in our view, fire-induced changes in understory light availability cannot fully explain the increased prevalence and dominance of *I. cylindrica* in understories of fire-affected forests. Likewise, the abilities of *I. cylindrica* to spread through rhizomatous growth and to resprout following the combustion of its above-ground tussock biomass are also likely to contribute to the *I. cylindrica*–fire relationship, as the species will generally be able to rapidly regenerate from intact roots in the nutrient-enriched post-fire environment [18]. However, rhizomatous growth and resprouting do not provide a means through which *I. cylindrica* can become established in a burned area if it is not already established nearby. Indeed, the dispersal (through wind) of *I. cylindrica* seeds into recently burned areas and the subsequent competitive success of seedlings is likely a critical step in *I. cylindrica* invasion, after which rhizomatous growth and resprouting can serve to bolster *I. cylindrica* dominance over time [18,21,32], particularly since the fast resprouting ability of *I. cylindrica* can enable the rapid production of more *I. cylindrica* seeds [23]. Given that neither changes in light availability following fire nor the resprouting ability of *I. cylindrica* can completely explain the tendency for *I. cylindrica* to proliferate in recently and/or frequently burned areas of forest, we argue that additional, complementary mechanisms must contribute to the competitive success of *I. cylindrica* in such areas.

In particular, given the importance of soil fertility as a determinant of general post-disturbance plant community invasibility [33,34], the potential for fire-induced changes in soil nutrient chemistry to give *I. cylindrica* an advantage over native species in the post-fire environment warrants investigation. One of the most consistent effects of fire on soil chemistry is a lowering of the concentration of nitrogen (N) relative to the concentration of phosphorus (P), i.e., a lowering of the N:P ratio, in both the total and labile pools of soil N and P [35–37]. This effect is likely due, at least in part, to the fact that a significant portion of soil and plant litter N can be converted to gaseous forms (i.e., volatilized) and consequently lost from the ecosystem to the atmosphere during fires [38,39]. Phosphorus does not undergo the same conversion, having no common gaseous form, so total and/or plant-available P concentrations in surface soils tend to be higher following fire due to ash deposition and thermal mineralization of organic P [7,35,40,41]. On the other hand, in the long-term absence of fire or other disturbance, the total concentration of P in soil declines over time, as does the concentration of plant-available PO₄³⁻, while concentrations

of N tend to increase through biological fixation, following the normal trajectory of soil development [42–44].

Given the strong tendency for different fire regimes to alter soil N and P concentrations in characteristic ways and for recent and/or frequent fire events to facilitate *I. cylindrica* invasion, it is plausible that these effects are related. Certainly, they have been observed to coincide in the few studies where both variables were measured (e.g., [45]). In particular, because *I. cylindrica* proliferates in recently and/or frequently burned areas, it seems reasonable that the growth of this species tends to be limited by P rather than N, such that it is most successful when growing in soils that have high levels of P and comparatively low levels of N. Researchers have certainly flagged the potential role of post-fire soil nutrient enrichment as a catalyst for *I. cylindrica* establishment [46], and others have noted a tendency for *I. cylindrica* to proliferate on low fertility soils [47]. However, the reported responses of *I. cylindrica* to nutrient inputs are varied, with N and P both eliciting positive and negative growth responses in different studies. Thus, the ways in which fire regime-altered soil nutrient availability could influence processes of *I. cylindrica* invasion remain uncertain.

Thus, we combined some unpublished results associated with two prior studies that were carried out in south-east Queensland, Australia [48,49] to investigate (a) whether the nutritional status of *I. cylindrica* is affected by fire and (b) whether the growth and survival of *I. cylindrica* seedlings are affected by the fire-exposure history of their soil media or by the addition of N, P, micronutrients, or ash. Based on our initial idea that a fire-induced lowering of soil N:P confers some competitive advantage on *I. cylindrica*, we expected to observe the following: (1) *I. cylindrica* should have a low requirement for N and a high requirement for P relative to other co-occurring plant species; (2) the tissues of *I. cylindrica* growing in recently and/or frequently burned areas should be enriched with P relative to unburned areas, reflecting enhanced P uptake from the P-enriched soil; (3) *I. cylindrica* seedlings growing in soil that has been recently and frequently exposed to fire should have higher rates of survival and growth than seedlings growing in soils that have not been exposed to fire, due to higher levels of P and lower levels of N in the former soil; and (4) *I. cylindrica* seedlings should respond more favorably to P fertilization than to N fertilization, reflecting a tendency toward P-limited growth that, in natural systems, is stimulated by post-fire increases in soil P availability.

2. Materials and Methods

2.1. Effects of Fire History on Foliar Stoichiometry of *Imperata cylindrica*

The first component of our investigation was carried out in the field [48], and consisted of a comparison of the foliar stoichiometry of mature *I. cylindrica* plants growing in adjacent areas that had either been burned recently (and typically repeatedly over the preceding decades; hereafter referred to as ‘recently, frequently burned’ areas or ‘RFB areas’) or where there had been no recent fire (i.e., no known fire for at least ten years prior to sampling; hereafter referred to as NRF areas). In 2013, three dry eucalypt forest sites in south-eastern Queensland, Australia, were selected for our study based on their fire histories (Table 1). One of these sites was located within Toohey Forest (27°32′24″ S, 153°3′0″ E), which grows on shallow, sandy Leptosols (FAO soil taxonomy), while the other two sites were located within the White Rock-Spring Mountain Conservation Estate (WRSMCE), and a hereafter referred to as WRSMCE A (27°43′12″ S, 152°51′36″ E) and WRSMCE B (27°41′60″ S, 152°50′60″ E), respectively. Soils in the WRSMCE have developed on Cainozoic and Mesozoic sediments and have been characterized as Lixisols.

Table 1. Location, vegetation community, climatic, and fire regime details for study sites.

Site	Vegetation	MAP ^{††} (mm)	MAT (°C)	Fire Regime Contrast(s)
Toohey Forest (27°32'24" S, 153°3'0" E)	Open eucalypt forest. Key species include <i>Eucalyptus acmenoides</i> , <i>Corymbia citriodora</i> , <i>Acacia leiocalyx</i> , and <i>Lophostemon confertus</i> .	1030	20.5	NRF: No burning since at least 1998 (date of most recent fire unknown); RFB: Low intensity prescribed surface fire in August 2013, July 2005, and August 1998.
WRSMCE [†] A (27°43'12" S, 152°51'36" E)	Shrubby-to-tall eucalypt forest. Key species include <i>C. citriodora</i> , <i>E. crebra</i> , and <i>L. confertus</i> .	995	23.4	NRF: Low intensity prescribed surface fire in June 1999; RFB: Low intensity prescribed surface fire in September 2009, April 2008, May 2003, and 1995.
WRSMCE B(27°41'60" S, 152°50'60" E)	Shrubby-to-tall eucalypt forest. Key species include <i>E. crebra</i> , <i>E. siderophloia</i> , and <i>C. henryi</i> .	995	23.4	NRF: No burning since at least 1998 (date of most recent fire unknown); RFB: Moderate to high intensity wildfire in October 2012, and previous medium intensity wildfires in August 2004 and ca. December 2000.
Peachester (26°52'12" S, 152°50'60" E)	Wet sclerophyll forest. Key species include <i>E. pilularis</i> , <i>E. microcorys</i> , <i>C. intermedia</i> , and <i>L. confertus</i> .	1684	23.3	NB: No burning since 1969; 4yB: low-to-medium intensity (<2500 kW m ⁻²) prescribed surface fire, every four years (on average) since 1972; 2yB: low-to-medium intensity (<2500 kW m ⁻²) prescribed surface fire, every two years (on average) since 1972.

[†] WRSMCE = White Rock Spring Mountain Conservation Estate. ^{††} MAP and MAT = mean annual precipitation and mean annual temperature up until the year of sampling.

At each of the three sites, the RFB and NRF areas were separated clearly by walking or vehicle tracks. We established two transects of 75–100 m running parallel to these tracks, with one transect in the RFB area and one transect in the NRF area. Transects were distanced more than 5 m from the tracks. Along each transect we collected samples of surface soil (0–5 cm) at five points, with points on a given transect spaced 15–20 m apart. Each soil sample consisted of 3–5 sub-samples that were collected from an area of approximately 5 m² and bulked together to form a composite sample. Soil samples from the RFB and NRF areas were paired based on location along the parallel transects (i.e., RFB samples were paired with their closest NRF sample). This resulted in five pairs of RFB and NRF soil samples per site, and 15 pairs of RFB and NRF samples in total. We used an equivalent pairing approach during our collection of *I. cylindrica* foliar samples along the same transects. Each of these samples consisted of 5–10 mature green leaves collected from a single plant. Although it was difficult to be certain that plants were of similar age, we tried to sample plants of similar size and only sampled plants in apparently robust condition. Due to the low abundance of *I. cylindrica* in the NRF areas, we were only able to collect three paired samples of *I. cylindrica* leaves at both of the WRSMCE sites. At Toohey Forest we collected five paired samples, giving a total of eleven pairs of RFB and NRF samples across all sites. Additionally, as part of a broader study, at each site we had collected leaf samples from three to five prominent native plant species in both the RFB and NRF areas. Samples were collected in the same manner as for *I. cylindrica*, except not all species were represented at each site. This gave an opportunity to contrast the foliar chemistry of these naturally occurring species against that of *I. cylindrica* within each site.

Methods of soil and foliar chemical analysis have been described in detail previously [36,50]. Soil samples were air-dried (two weeks) and leaf samples oven dried (105 °C for 2 h to halt enzyme activities and then 65 °C for one week) prior to analyses. Soil pH and EC were measured in water (1:5). Soil total C and N were measured via dry combustion of finely ground samples using a Leco TruMac TCN Determinator, and soil total P (and total organic and inorganic P) were measured via the combustion method (550 °C) coupled

with the molybdenum-blue spectrophotometric method [51,52]. ‘Labile’ forms of N, P, and organic C were extracted from soils using the hot-water-extraction method and subsequently quantified with a Shimadzu TOCN analyzer in the case of N and organic C [53,54], and with molybdenum-blue spectrophotometry (following autoclaving to convert labile organic P forms to phosphate) in the case of P for Toohey Forest and WRSMCE soils, and with inductively coupled plasma optical emission spectroscopy (ICP–OES) in the case of P for the soils that were used for our *I. cylindrica* growth trial (described below) [49,55]. The total C and N contents of *I. cylindrica* leaves were determined in the same way as soil total C and N. The total P content of *I. cylindrica* leaves was determined by molybdenum-blue spectrophotometry after finely ground leaf samples were digested in nitric and perchloric acids [56].

2.2. Effects of Soil Fire History and Fertilization on Survival and Growth of *Imperata cylindrica*

The second component of our investigation involved a laboratory-based *I. cylindrica* growth trial, for which we leveraged a long-term prescribed burning experiment located in Peachester State Forest (hereafter ‘Peachester’; Table 1), Australia (26°52′12″ S, 152°50′60″ E). Peachester is a wet eucalypt forest dominated by *Eucalyptus pilularis* growing on Alfisols (yellow Kandosols in the Australian Soil Taxonomy). The prescribed burning experiment at Peachester consists of three replicated ($n = 4$), randomized fire regimes: burned every two years (on average) since 1972 (hereafter referred to as ‘2yB’), burned every four years (on average) since 1972 (‘4yB’), and no burning since 1969 (‘NB’; Table 1). Soil properties, and particularly soil N:P ratios, differ widely among these three treatments [37,49]. The methods used to quantify the soil properties at Peachester are similar to those used for the Toohey Forest and WRSMCE sites as described above, and have been described in detail elsewhere [49].

In March 2017 we commenced a multi-factorial, laboratory-based *I. cylindrica* growth trial using surface soils (0–10 cm) that had been collected from the Peachester treatments in July 2011. At this time, the most recent burns had been in 2007 for the 2yB treatment plots and in 2005 for 4yB (and 2yB) treatment plots. Shortly after sampling, these soils were sieved at 4 mm, air dried, and stored indoors in sealed plastic bags. We did not mix soils from the four replicate plots within a fire regime treatment; thus, the inherent spatial variation in the field at Peachester was preserved in our growth trial. The first factor in the growth trial was fire regime, with levels of NB, 4yB, and 2yB. The second factor was ‘resource amendment’, of which there were six levels: N addition (hereafter ‘+N’), P addition (‘+P’), N, P, and micronutrient addition (‘NPmicro’), ash addition (‘ash’), water restriction to simulate drought conditions (‘drought’), and no amendment (i.e., the control). Each treatment combination was replicated four times, corresponding to the four replicate plots in the field for each level of the fire regime treatments at Peachester. Thus, there were $3 \times 6 \times 4 = 72$ individual observations in the experiment. Details of each level of the resource amendment factor are summarized in Table 2.

Seventy-two black plastic pots (149 mm wide, 110 mm high) with no drainage holes (to prevent loss of added soluble nutrients) were filled with 1100 g (oven-dry basis) of air-dry Peachester soil. We added deionized water to 75% of the soil water holding capacity, and several hours later seeds of *I. cylindrica* were sown directly onto the moist soil surface. Soil water holding capacity was kept at 75% for six weeks while the seeds germinated. After six weeks, the germinated seedlings were thinned to the two largest individuals in each pot. The following week we reduced the soil moisture content to 50% of soil water holding capacity and this moisture level was maintained for the remainder of the experiment, with plants being watered twice weekly. Plants were grown under laboratory conditions with ambient air temperature of 22 °C and light intensity of 108–122 W m⁻² provided by Sylvania GroLux fluorescent bulbs (twelve hours of light per day).

Table 2. Details of levels of the resource amendment factor in the *Imperata cylindrica* growth trial.

Resource Amendment Levels †	Treatment Details	N
Control	Plants grown for 219 days; soil moisture at 50% WHC; no soil amendments.	12
+Nitrogen	Plants grown for 219 days; soil moisture at 50% WHC; 100 mg N kg soil ⁻¹ added (as NH ₄ NO ₃) to pots on days 0 and 96 (220 mg N added in total).	12
+Phosphorus	Plants grown for 219 days; soil moisture at 50% WHC; 100 mg P kg soil ⁻¹ added (as NaH ₂ PO ₄) to pots on days 0 and 96 of growth period (220 mg P added in total).	12
NPmicro †	Plants grown for 219 days; soil moisture at 50% WHC; 100 mg N, 100 mg P, 25 mg K, 12.5 mg Ca, 12.5 mg Mg, 5.45 mg Fe, 3.95 mg Mn, 2.0 mg Zn, 0.5 mg Cu, 0.45 mg Mo, 0.1 mg B, 37.3 mg Na, 81.9 mg Cl, and 5.7 mg S per kg soil ⁻¹ added to pots on days 0 and 96.	12
Ash	Plants grown for 219 days; soil moisture at 50% WHC; 1.5 g of laboratory-produced <i>Imperata cylindrica</i> ash applied to soil surface of pots on day 0.	12
Drought	Plants grown for 219 days; soil moisture at 50% WHC from days 0–96 and 35% WHC from days 96–219 of the growth period; no soil amendments.	12

† NPmicro = addition of nitrogen (N), phosphorus (P), and micronutrients; K = potassium; Ca = calcium; Mg = magnesium; Fe = iron; Mn = manganese; Zn = zinc; Cu = copper; Mo = molybdenum; B = boron; Na = sodium; Cl = chlorine; S = sulfur.

Two weeks after seedlings were thinned, fertilizer solutions were added to the pots. This served as the first day (day '0') of the experimental period. Nitrogen (as NH₄NO₃) and P (as NaH₂PO₄) were supplied at rates of 100 mg per kg of soil (oven-dry basis). Other elements were supplied at the following rates: 25 mg potassium per kg soil, 12.5 mg calcium per kg soil, 12.5 mg magnesium per kg soil, 5.45 mg iron per kg soil, 3.95 mg manganese per kg soil, 2.0 mg zinc per kg soil, 0.5 mg copper per kg soil, 0.45 mg molybdenum per kg soil, 0.1 mg boron per kg soil, 37.3 mg sodium per kg soil, 81.9 mg chlorine per kg soil, and 5.7 mg sulfur per kg soil. An additional round of fertilizer solutions was applied on day 96 of the experimental period (12 weeks after the first round of fertilizer). The drought treatment was also implemented on day 96, at which time the moisture content of relevant pots was reduced to 35% of soil water holding capacity. Pots subject to the drought treatment were not provided with any other amendments at any time during the experiment. For the ash addition treatment, we prepared ash using samples of dried *I. cylindrica* leaves that had been collected from Peachester at around the same time the soils were obtained. Ash was produced by combusting the *I. cylindrica* leaves at 550 °C in a muffle furnace for 15 min and then grinding the combusted material by hand with a mortar and pestle. We applied 1.5 g of this ash material (equivalent to 97 g ash per m² or 1.15 kg of dry biomass per m², a quantity that simulated a 'moderate' *I. cylindrica* fuel load [24,57,58]) to the soil surfaces of relevant pots, which had received no other amendments, on day 0 of the pot trial. We measured the elemental content of ash in duplicate using ICP–OES; the P, calcium, magnesium, potassium, and sulfur concentrations of ash were 0.97%, 0.20%, 2.21%, 11.7%, and 0.92%, respectively. We assume that combustion of the *I. cylindrica* leaves resulted in the volatilization of most, if not all, N in the samples, such that the N:P content of ash was <<1. We note that the use of *I. cylindrica* leaves to produce ash limits our ability to draw conclusions about the potential role of ash deposition as a factor contributing to the invasion of *I. cylindrica* into areas where it was not already present. This is because the effects of ash might be influenced by or specific to the material from which the ash was produced. If this is the case, the effects of ash addition are better interpreted as evidence of the potential for *I. cylindrica* ash to 'reinforce' the dominance of *I. cylindrica* following fire in a positive feedback process. However, it is also a safe assumption that ash will always have a lower N:P than the original plant material, due to the greater volatilization of plant N than plant P [38]. Plants were grown for 219 days, with the growth trial ending on the 1 of December 2017. Surviving *I. cylindrica* seedlings, including all roots, were gently removed from the soil, rinsed with deionized water, and then oven-dried at 65 °C for five days and weighed to determine total biomass gain during the growth period.

2.3. Statistical Analyses

All statistical analyses were carried out using R. All of the stoichiometric ratio data were natural log-transformed prior to statistical analyses. *Imperata cylindrica* foliar N, P, C:N, C:P, and N:P ratios were compared between the RFB and NRF areas at Toohey Forest and WRSMCE A and B using Student's paired *t*-tests. These comparisons were made across all observations ($n = 11$). We then examined the correlation between (a) foliar N (natural log-transformed) and foliar N:P and (b) foliar P (natural log-transformed) and foliar N:P to determine which element underpins more variation in foliar *I. cylindrica* N:P values. Stoichiometric ratios are reported on a mass basis.

The effects of soil fire history and resource amendment on the survival and growth of *I. cylindrica* seedlings were assessed using a binomial-distributed generalized linear model (survival) and a Gaussian-distributed linear model (growth) with the R package 'cars'. Survival was coded as a binary variable, with a value of 0 corresponding to death of both seedlings in a pot and a value of 1 corresponding to survival of one or both seedlings in a pot by the end of the growth trial. Growth data were equivalent to the total dry biomass of the living *I. cylindrica* seedlings (divided by the number of live seedlings to give biomass per individual plant). Pots without surviving seedlings were designated a biomass value of zero. This can be interpreted as a complete absence of living biomass at the end of the experimental period. Growth data were natural log-transformed ($\log x+1$) prior to statistical analyses. The significance of fire regime and resource amendment terms in the models of survival and growth were evaluated based on chi-squared values in an analysis of deviance table in the case of survival and *F*-values in an analysis of variance table in the case of growth. In all of our analyses, *p*-values < 0.05 were considered statistically significant. Our model of growth indicated that there was a significant interaction between fire regime and resource amendment (Section 3.2). Thus, we carried out simple main effect tests using the 'pairs' function in the 'emmeans' package. This allowed us to assess (a) the effect of resource amendment with each level of fire regime factor held constant and (b) the effect of fire regime for just the 'control' samples from our resource amendment experiment, all while preserving the full experimental design's degrees of freedom and statistical power. Post hoc means contrasts were made with the Least Significant Difference method.

3. Results

3.1. Soil Properties and Foliar Chemistry under the Different Fire Regimes

The effects of the different fire regimes on soils at Toohey Forest, WRSMCE, and Peachester State Forest at the respective times of sampling are summarized in Table 3 and have been described in detail elsewhere [36,49,50]. In brief, the RFB and NRF contrasts at Toohey Forest and WRSMCE yielded few effects that were quantitatively or qualitatively consistent across the three sites. The key exceptions were that (a) soil labile P concentrations tended to be higher in RFB areas and (b) soil labile N:P ratios tended to be lower in RFB areas (Table 3; [36]). The long-term, high-frequency fire regimes at Peachester State Forest brought about much stronger effects (Table 3; [49]). In particular, soil pH and labile P concentrations were substantially higher in 2yB soils than in NB soils, while EC, total C, total N, labile organic C, and labile N were substantially lower [49]. Moreover, soil total and labile N:P ratios were 44% and 87% lower, respectively, in 2yB soils relative to NB soils [49]. Soils from the 4yB treatment were generally similar to NB soils [49].

Table 3. Key surface soil properties (means \pm 95% confidence intervals) at each of the study sites, contrasted between the different fire regimes [†] ($n = 5$ for each fire regime at Toohey Forest, WRSME A, and WRSME B; $n = 4$ for each fire regime at Peachester State Forest).

Soil Property ^{†††}	Toohey Forest		WRSME A		WRSME B		Peachester State Forest		
	NRF	RFB	NRF	RFB	NRF	RFB	NB	4yB	2yB
Bulk density (g cm ⁻³)	1.04 (0.83–1.26)	1.03 (0.89–1.18)	1.15 (1.05–1.24)	1.00 (0.74–1.26)	1.21 (1.03–1.39)	1.21 (1.05–1.37)	0.81 (0.63–1.00)	0.83 (0.64–1.02)	0.91 (0.66–1.17)
pH	4.88 (4.58–5.17)	4.65 (4.48–4.83)	5.85 (5.75–5.95)	5.65 (5.36–5.94)	5.25 (5.17–5.32)	5.58 (5.29–5.86)	3.77 (3.69–3.85)	3.89 (3.66–4.11)	4.21 (3.75–4.66)
EC (μ S cm ⁻¹)	38.0 (23.6–52.3)	33.9 (25.2–42.5)	19.0 (15.8–22.1)	16.7 (15.3–18.1)	20.9 (18.1–23.8)	29.2 (20.7–37.7)	52.1 (41.4–62.8)	52.4 (42.0–62.8)	38.5 (33.2–43.8)
Total C (%)	2.31 (1.60–3.01)	2.64 (2.16–3.12)	1.70 (1.24–2.17)	1.63 (1.44–1.82)	1.50 (1.22–1.78)	1.72 (1.40–2.04)	4.28 (2.93–5.63)	6.53 (4.86–8.20)	3.07 (−0.3–6.45)
Total N (%)	0.080 (0.05–0.11)	0.075 (0.06–0.09)	0.066 (0.05–0.08)	0.057 (0.04–0.07)	0.058 (0.04–0.08)	0.072 (0.06–0.09)	0.176 (0.12–0.23)	0.259 (0.17–0.34)	0.101 (0.01–0.19)
Total P (mg kg ⁻¹)	73.7 (59–88)	86.4 (70–103)	168.2 (150–186)	110.8 (104–118)	120.5 (111–130)	148.0 (130–166)	81.1 (60–102)	123.0 (60–186)	81.6 (14–149)
Total P _i (mg kg ⁻¹)	6.8 (6–8)	9.2 (6–13)	41.0 (33–49)	27.0 (22–32)	25.6 (21–30)	36.8 (28–46)	22.2 (14–30)	33.6 (21–46)	20.4 (2–38)
Total P _o (mg kg ⁻¹)	66.9 (53–81)	77.1 (57–97)	127.2 (106–148)	83.8 (81–87)	94.9 (85–105)	111.2 (91–131)	58.9 (42–75)	89.4 (37–142)	61.2 (11–112)
Labile OC (mg kg ⁻¹)	690 (550–831)	578 (459–698)	433 (333–533)	354 (287–420)	339 (284–393)	406 (302–511)	1134 (724–1543)	1323 (878–1768)	758 (441–1075)
Labile N (mg kg ⁻¹)	54.5 (43.7–65.3)	44.0 (35.0–53.0)	54.0 (42.9–65.1)	37.1 (28.5–45.6)	30.2 (28.4–32.1)	48.4 (39.1–57.7)	97.6 (60.1–135)	84.3 (44.2–125)	62.7 (36.1–89.3)
Labile P (mg kg ⁻¹)	1.05 (0.87–1.24)	1.61 (0.65–2.57)	1.05 (0.59–1.51)	1.22 (0.91–1.53)	1.05 (0.76–1.35)	1.71 (1.31–2.12)	0.31 (−0.3–0.86)	0.20 (0.02–0.38)	0.88 (0.69–1.08)
Total N:P ratio ^{††††}	10.6 (7.7–14.7)	8.7 (6.1–12.3)	3.9 (2.9–5.2)	5.1 (3.8–6.7)	4.7 (3.5–6.2)	4.8 (3.4–6.8)	15.2–30.5	17.8–25.9	12.18 (8.6–17.3)
Labile N:P ratio	51.6 (43.3–61.5)	29.3 (15.8–54.5)	53.7 (41.0–70.3)	30.4 (24.9–37.2)	29.3 (21.7–39.5)	28.4 (19.7–40.8)	517 (57–4697)	457 (195–1067)	69.4 (51–95)

[†] NRF = area with no recent fire; RFB = area that has been recently and/or frequently burned; NB = no burning since 1969; 4yB = burned every four years since 1972; 2yB = burned every two years since 1972. ^{††} WRSME = White Rock Spring Mountain Conservation Estate. ^{†††} EC = electrical conductivity; C = carbon; N = nitrogen; P = phosphorus; P_i = inorganic phosphorus; P_o = organic phosphorus; labile OC, N, and P = forms of organic C, total nitrogen, and total phosphorus extractable with hot (70 °C) water. ^{††††} Means and 95% confidence mean range of stoichiometric ratio variables are back-transformed values after averages and mean ranges were calculated across RFB and NRF areas using natural log-transformed data.

Across the three sites, the concentrations of C, N, and P in *I. cylindrica* leaves averaged $48.5 \pm 0.1\%$ (errors are standard errors; range: 47.45–49.44%), $0.72 \pm 0.04\%$ (range: 0.44–1.10%), and $0.059 \pm 0.004\%$ (range: 0.027–0.105%). Foliar C:N, C:P, and N:P ratios averaged 69.5 ± 4.2 (range: 44.8–111), 875 ± 79 (range: 458–1789), and 12.6 ± 0.7 (range: 7.62–20.3). Foliar chemistry of *I. cylindrica* varied among the three sites (Table 4); however, at each site, *I. cylindrica* leaves contained markedly lower levels of N than co-occurring native species, and had correspondingly higher C:N ratios (Table 4). By comparison, the P content and C:P ratios of *I. cylindrica* leaves were not strongly or consistently different from those of co-occurring native species at each site, but foliar N:P ratios of *I. cylindrica* were consistently lower than those of other species (Table 4). The difference in foliar N:P between *I. cylindrica* and the species with the next lowest mean foliar N:P was 26.0% at Toohey Forest, 27.1% at WRSME A, and 29.7% at WRSME B.

Concentrations of C, N, and P in the leaves of mature *I. cylindrica* plants growing at WRSME and Toohey Forest were not significantly different between RFB and NRF areas according to Student's paired *t*-tests (Figure 1). Foliar P concentrations tended to be higher in RFB areas ($0.066 \pm 0.005\%$) than in NRF areas ($0.052 \pm 0.007\%$), but this difference was not statistically significant ($p = 0.083$). Correspondingly, foliar C:N and C:P ratios did not differ significantly between the RFB and NRF areas (Figure 1c,d). However, foliar N:P ratios were 21% lower ($p = 0.003$) in RFB areas (mean back-transformed foliar N:P = 11.19) than in NRF areas (mean back-transformed foliar N:P = 14.16; Figure 1e). Values of log-transformed foliar N:P were strongly negatively correlated with foliar P content (Pearson's $r = -0.69$; $p < 0.001$), but were not correlated with foliar N (Figure 2).

Table 4. Foliar nitrogen (N) and phosphorus (P) concentrations and carbon (C):N:P stoichiometric ratios (means [†], with 95% confidence mean range shown in brackets) of *Imperata cylindrica* and several naturally occurring understory plant species at each of the three study sites.

	Species	Foliar N (%)	Foliar P (%)	Foliar C:N	Foliar C:P	Foliar N:P
Toohey Forest	<i>Imperata cylindrica</i>	0.71 (0.60–0.83)	0.048 (0.036–0.060)	69.7 (59–82)	1068 (822–1387)	15.3 (13–18)
	<i>Acacia disparrima</i>	2.15 (1.93–2.37)	0.084 (0.063–0.104)	25.0 (22–28)	670 (518–867)	26.8 (22–32)
	<i>Acacia leiocalyx</i>	2.03 (1.78–2.27)	0.053 (0.037–0.070)	25.7 (22–30)	1048 (758–1447)	40.7 (33–51)
	<i>Alphitonia excelsa</i>	1.64 (1.45–1.83)	0.074 (0.063–0.085)	32.1 (28–36)	720 (615–842)	22.4 (21–24)
	<i>Lomandra confertifolia</i>	1.01 (0.80–1.21)	0.049 (0.038–0.060)	50.2 (41–62)	1036 (824–1301)	20.7 (19–22)
	<i>Lophostemon confertus</i>	1.29 (1.08–1.50)	0.063 (0.045–0.081)	41.1 (34–49)	858 (639–1153)	20.9 (17–25)
WRSMCE A	<i>Imperata cylindrica</i>	0.56 (0.43–0.68)	0.053 (0.043–0.062)	88.7 (71–111)	933 (758–1148)	10.5 (8–13)
	<i>Acacia concurrens</i>	2.06 (1.68–2.44)	0.061 (0.050–0.072)	26.9 (22–33)	909 (737–1119)	33.8 (30–39)
	<i>Alphitonia excelsa</i>	1.53 (1.27–1.79)	0.106 (0.090–0.122)	33.5 (28–40)	481 (416–557)	14.4 (11–19)
	<i>Jacksonia scoparia</i>	1.65 (1.45–1.85)	0.056 (0.040–0.071)	31.6 (28–36)	966 (694–1344)	30.6 (24–39)
WRSMCE B	<i>Imperata cylindrica</i>	0.91 (0.75–1.04)	0.083 (0.067–0.100)	54.3 (47–63)	590 (489–710)	10.9 (10–12)
	<i>Acacia concurrens</i>	1.81 (1.60–2.03)	0.063 (0.050–0.076)	29.9 (27–34)	871 (724–1048)	29.2 (27–32)
	<i>Alphitonia excelsa</i>	1.71 (1.50–1.92)	0.115 (0.079–0.152)	29.9 (26–34)	464 (354–607)	15.5 (12–20)
	<i>Lophostemon confertus</i>	1.21 (1.11–1.31)	0.068 (0.050–0.087)	42.4 (39–46)	767 (582–1010)	18.1 (15–22)

[†] Means and 95% confidence mean range of stoichiometric ratio variables are back-transformed values after averages and mean ranges were calculated across RFB and NRF areas using natural log-transformed data.

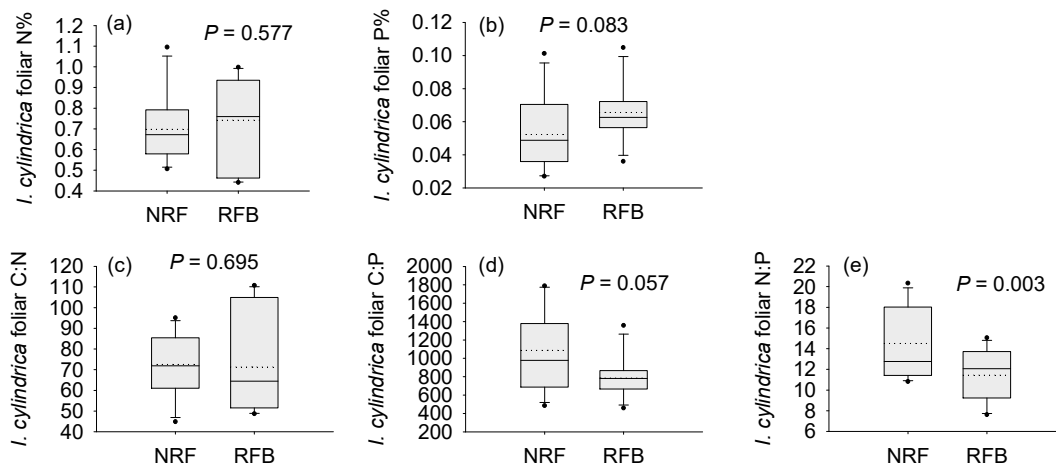


Figure 1. Box-and-whisker plots showing (a) nitrogen (N) content, (b) phosphorus (P) content, (c) carbon (N):N ratios, (d) C:P ratios, and (e) N:P ratios of leaves of mature *Imperata cylindrica* growing in areas of eucalypt forests that have either had no recent fires (NRF) or that have been exposed to recent and/or frequent burning (RFB). The NRF and RFB areas were compared using Student’s paired *t*-tests ($n = 11$ for all variables; *p*-values are shown in each panel). In each box, the median is shown by the solid line and the mean is shown by the dotted line.

3.2. Growth and Survival of *Imperata cylindrica* Seedlings in Response to Soil Fire History and Resource Amendment

In our growth trial, *I. cylindrica* seeds germinated successfully in every pot. However, at the end of the 219-day growth period, pots containing NB soils had an *I. cylindrica* survival rate of 75%, compared to 83% for pots containing 4yB soils and 92% for pots containing 2yB soils (Figure 3a). This difference in survival rate was not statistically significant ($p = 0.287$). On the other hand, the effect of resource amendment treatment on survival was statistically significant ($p < 0.001$), and was characterised by a 66% reduction in survival rate with N addition and a 25% reduction in survival rate with addition of N, P, and micronutrients together (Figure 3b). Neither addition of P nor reduction in water availability had consequences for *I. cylindrica* survival relative to the unamended controls.

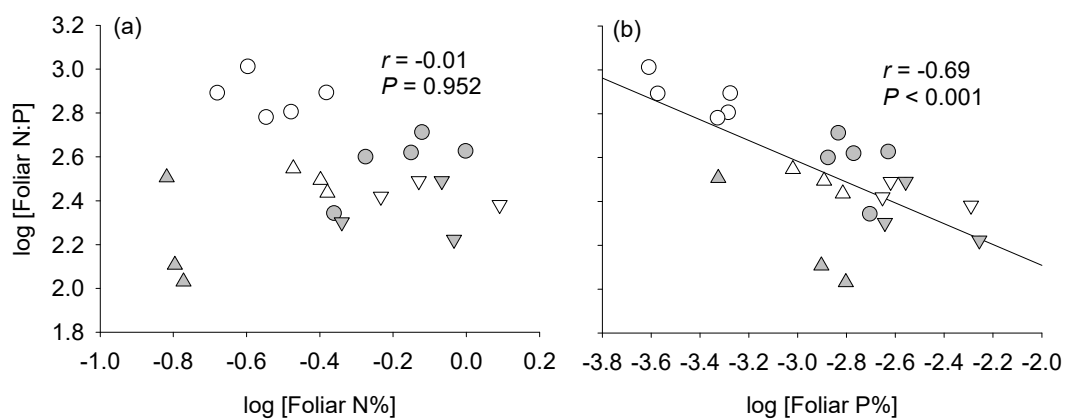


Figure 2. Correlations between (a) *Imperata cylindrica* foliar N content and foliar N:P ratios and (b) *Imperata cylindrica* foliar P content and foliar N:P ratios across the three study sites (Toohey Forest [circles], WRSMCE A [upward triangles], and WRSMCE B [downward triangles]) and across NRF [white-filled symbols] and RFB [grey-filled symbols] areas; Pearson's correlation coefficient (r) and p -values are shown in each panel ($n = 22$).

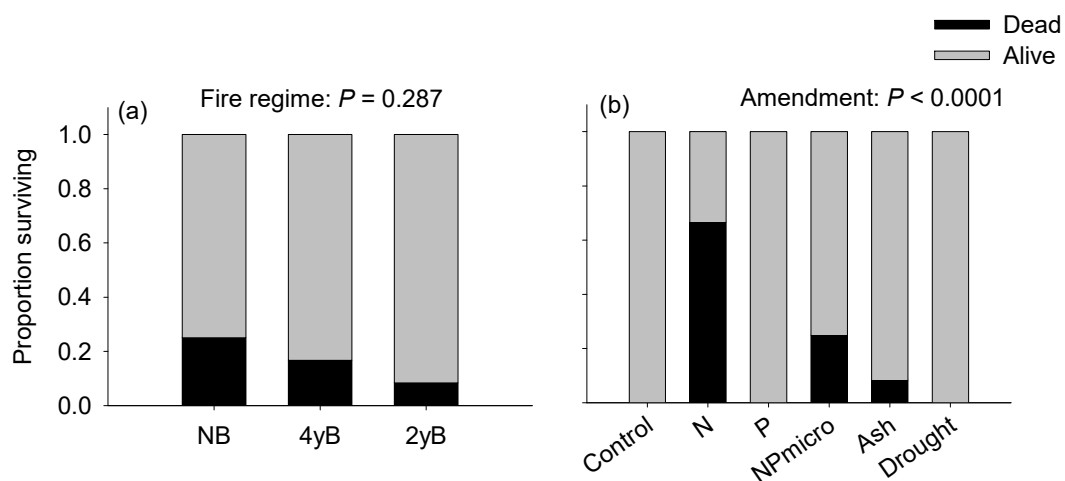


Figure 3. Proportions of pots with surviving or dead *Imperata cylindrica* seedlings at the end of the 219-day growth trial, contrasted among (a) soil fire regime treatments (NB = unburned; 4yB = quadrennially burned treatment; 2yB = biennially burned treatment; $n = 24$ for each level of fire regime) and (b) resource amendment treatments (control = no resource amendment; N = nitrogen addition; P = phosphorus addition; NPmicro = addition of N, P, and micronutrients together; ash = simulated ash deposition treatment; drought = treatment with lower levels of soil moisture; $n = 12$ for each level of resource amendment); p -values indicate the significance of fire regime (panel 'a') and resource amendment (panel 'b') as factors in binomial-distributed generalised linear models of survival (total number of observations = 72).

In our factorial ANOVA of *I. cylindrica* growth, there was a significant interaction between fire regime and resource amendment ($p = 0.002$). Our follow up tests indicated that, for control soils (i.e., those soils with no amendments), fire regime had no significant effect on *I. cylindrica* growth over 219 days. The growth of *I. cylindrica* (i.e., the biomass produced over 219 days) was influenced by resource amendment, but the nature and strength of this effect varied based on the soil's history of fire exposure (Figure 4). For unburned soils (Figure 4a), the addition of P enhanced *I. cylindrica* growth relative to all other treatments, and the addition of ash enhanced *I. cylindrica* growth relative to the N-addition treatment. For the quadrennially burned soils (Figure 4b), effects of resource amendments were similar to unburned soils, except that the treatment with N, P, and micronutrients added together resulted in similar growth to the treatment that involved only P-addition. For the biennially burned soils (Figure 4c), N-fertilized *I. cylindrica* seedlings had significantly lower growth rates than the seedlings in all the other treatments. Seedlings that had been fertilized with P alone or in combination with N and micronutrients were significantly larger than

control and drought treatment seedlings. Seedlings in biennially burned soils that had been amended with ash were larger than those in the drought and nitrogen treatments, but did not differ from the seedlings in control pots (Figure 4c).

Fire regime x resource amendment:
 $F_{10,54} = 3.40$; $P = 0.002$

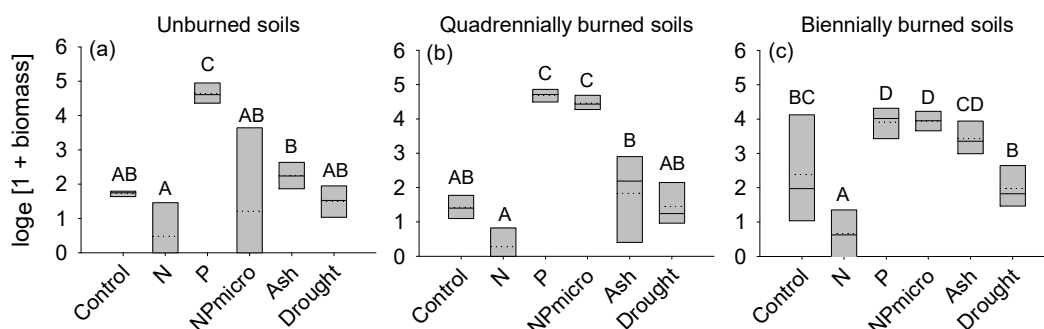


Figure 4. Box-plots showing log-transformed *Imperata cylindrica* biomass ($\log_e[1 + x$ mg of dry biomass per plant]) gain over the 219-day growth trial compared among each level of resource amendment in (a) soils that have not been exposed to fire since 1969, (b) soils that have been exposed to surface fire every four years, on average, since 1972, and (c) soils that have been exposed to surface fire every two years, on average, since 1972 ($n = 4$ for each fire regime x resource amendment combination; total number of observations = 72); control = no resource amendment; N = nitrogen addition; P = phosphorus addition; NPmicro = addition of N, P, and micronutrients together; ash = simulated ash deposition treatment; drought = treatment with lower levels of soil moisture); the F -statistic and p -value indicate the significance of the fire regime \times resource amendment interaction term in a Gaussian-distributed linear model of *I. cylindrica* biomass. Means of each level of resource amendment were compared within fire regimes using ‘simple main effect tests’ ($d.f.$ error = 54 in all cases) based on the Least Significant Difference method in the ‘emmeans’ R package.

4. Discussion

Our results are generally consistent with fire-altered soil chemistry, and particularly fire-induced lowering of soil N:P, playing a meaningful role in the post-fire proliferation of *I. cylindrica* in eucalypt forest understories. It seems highly likely that this mechanism would often operate in concert with other environmental changes that can occur as a result of fire, such as increased understory openness and light intensity, but it also seems that the lowering of soil N:P ratios could greatly benefit *I. cylindrica* in the absence of any other environmental changes.

4.1. Patterns of Variation in Foliar N:P Ratios in the Field

Foliar N:P ratios are often used as an indirect means of assessing plant N and P nutritional status [59–61]. As shown by our results in Table 4, the mean foliar N:P of *I. cylindrica* at our sites was low (mass-based N:P mean = 12.6) compared to most other understory species, with this difference apparently attributable to low concentrations of N in *I. cylindrica* leaves, rather than high concentrations of P. *Imperata cylindrica* is known to have an extraordinarily high N uptake efficiency [46], and prior studies indicate that *I. cylindrica* N content is often low relative to C (reported C:N as high as 90), even for specimens growing in the tropics where soils tend to be relatively rich in N and depleted of available P [26]. Thus, even though low foliar N:P is often associated with N-limitation [59–61], we suggest that *I. cylindrica* plants were not N-limited at our Toohey Forest and WRSME sites. Instead, we suggest that *I. cylindrica* biomass is inherently N-poor compared to other species, reflecting an inherently low N requirement for biomass production and metabolism, and resulting in a tendency toward P-limitation that confers a post-fire advantage on this species due to the temporary enhancement of soil P availability associated with burning. Our finding that *I. cylindrica* foliar N:P ratios were lower in our RFB areas than they were in our NRF areas supports this view (Figure 1), because it

indicates that *I. cylindrica* took up more P, but not more N, per unit of above-ground biomass in the post-fire environment. Such a response seems unlikely if those *I. cylindrica* plants were genuinely N-limited. Although we cannot discount the possibility that aboveground *I. cylindrica* biomass was younger in RFB areas than in NRF areas, potentially confounding the influence of soil nutrients [62], this result is consistent with our expectations and probably reflects an ‘easing’ of P-limitation due to fire-enhanced soil P availability [63]. This conclusion is reinforced by our finding that variation in *I. cylindrica* foliar N:P was due primarily, if not completely, to variation in foliar P concentration (Figure 2). Further studies involving factorial clipping and N and P fertilization treatments may validate our conclusions and give further insight into the nutritional and growth responses of mature *I. cylindrica* to fire-altered soil chemistry.

4.2. Performance of *Imperata cylindrica* Seedlings in Response to Site Fire History and Amendments

Invasion of *I. cylindrica* into burned areas of forest likely necessitates the vigorous growth and successful competition of wind-dispersed *I. cylindrica* seeds [18]. Sensitivity of newly germinated *I. cylindrica* seedlings to variation in soil N and P availability can, therefore, give insight into the potential role of fire-altered soil chemistry in facilitating *I. cylindrica* establishment. On average, *I. cylindrica* growth rates were low in our experiment, with individual plants gaining only 36.6 ± 6 mg of biomass over the experimental period, suggesting that light availability might have been sub-optimal for this species in our laboratory set-up [64]. By definition, surface fires are unlikely to markedly increase understory light intensity in forest ecosystems by consuming the forest canopy. Thus, we believe the low growth rates of *I. cylindrica* in our experiment do not detract from the validity of our results, but do, perhaps, make their applicability exclusive to forest ecosystems under surface fire regimes.

We had initially anticipated that *I. cylindrica* seedlings growing in 2yB soils would have higher rates of survival and growth than seedlings growing in the 4yB and particularly the NB soil, but this was not the case (as shown by Figures 3 and 4 and the results of our ANOVA using only the control pots). Given that the growth of *I. cylindrica* seedlings was clearly limited by P availability (Figure 4), the similar rates of growth among the three fire regimes are most readily attributed to the similar levels of total and labile P in these soils. Although fire events consistently increase soil PO_4^{3-} concentrations [35], these effects tend to be strongest in the short-term and decline over time [8,35]. Thus, the similar soil P levels among the fire regime treatments are probably due to the long period between the collection of soil samples for our growth trial and the most recent fires in the 2yB (4 years) and 4yB (6 years) treatments. Further studies will be needed to show whether the short-term effects of fire on soil P availability have meaningful positive effects on *I. cylindrica* growth and survival. However, given that soil N concentrations and N:P ratios were lower in 2yB soils than in NB and 4yB soils, we are able to conclude that *I. cylindrica* seedlings are not negatively impacted by the severe depletion of soil N associated with protracted increases in surface fire frequency, and that repeated burning did not induce N-limitation in *I. cylindrica* seedlings at Peachester.

The limitation of the growth rate of *I. cylindrica* seedlings by P supply was reflected by their very strong response to addition of dissolved NaH_2PO_4 (Figure 4). This effect was evident across all fire regimes, but was arguably stronger for the NB and 4yB soils, possibly due to their substantially higher total and labile N:P ratios which might have induced a stronger state of ‘transactional’ P-limitation [65]. These effects were consistent with our expectations, and lead us to conclude that short-term increases in soil P availability brought about by fire have the potential to give newly germinated *I. cylindrica* seedlings a short-term competitive advantage in the post-fire environment. In addition, prior research found that the inflorescence length and leaf area of mature *I. cylindrica* plants were strongly positively associated with soil P content on a regional scale in Mississippi, consistent with P-limited (or co-limited) growth between the surface soil ‘available’ P range of 6 to 190 kg ha^{-1} (0–6 cm depth [66]). Peachester soil available P stocks (0–10 cm) were lower than those

of the Mississippi soils studied by Bryson, et al. (2010) [66] (Peachester Bray-extractable (i.e., 'available') P concentrations ranged from 3.91–4.86 mg kg⁻¹ across the fire regime treatments [49], equivalent to 3.17–4.43 kg Bray-extractable P per hectare, and labile P concentrations ranged from 0.2–0.88 mg kg⁻¹, equivalent to 0.17–0.80 kg of labile P per hectare; Table 3). Thus, the likelihood of *I. cylindrica* growth being P-limited at Peachester is high for both seedlings and mature plants. The positive effects of fire-enhanced P-availability could, therefore, extend to mature plants that resprout following fire or are located downslope of burned areas and thus receive P inputs through post-fire run-off. Moreover, forest soils with total and available P concentrations and total N:P ratios similar to or below those of Peachester are common throughout eastern Australia [67,68]. Thus, the mechanism we propose, in which fires benefit P-limited *I. cylindrica* by temporarily increasing soil P availability, could apply to a wide range of Australian forest ecosystems.

The deposition of alkaline ash rich in P and other nutrients is an important means by which fires can enhance soil P availability in the short-term [7]. However, we found that the average growth rates of *I. cylindrica* seedlings subjected to our simulated ash-deposition treatment were not significantly different from the respective controls, regardless of the soil's fire regime history, according to Least Significant Difference tests (Figure 4). We added 1.5 g of ash with a P content of ca. 0.97% to 1100 g soil, equivalent to 13.2 µg ash-P per gram of soil, a much lower value than the 100 mg P per gram of soil added in our +P treatment. This quantity of ash was chosen to represent a 'moderate' fuel load [49] and might have been insufficient to induce a significant growth response. It is also unclear whether all of this added P was available for uptake by *I. cylindrica* or whether it was sorbed to soil particles. Importantly, fires can increase surface soil P availability in the short-term by mechanisms other than ash deposition, such as thermal and biological mineralization of organic P [69]. These effects, in combination with ash deposition and associated soil pH increase, may illicit a larger growth response than ash deposition alone. Future studies should simulate fire-induced P mineralisation along with ash-deposition to build a greater understanding of whether and how *I. cylindrica* seedlings respond to fire-altered soil P availability.

A particularly intriguing aspect of our results was the apparently inhibitory effect of soil N on the survival and growth of *I. cylindrica* (Figures 3 and 4). This effect was demonstrated directly by the contrasts between the +N treatment and the control and +P treatments, but also by the contrast between the +P and NP_{micro} treatment for plants growing in unburned soils, in which the addition of P alone stimulated growth to a greater extent than the addition of P and N (and various micronutrients) together (Figure 4). Rates of survival of *I. cylindrica* were also somewhat lower for NB soils than 2yB soils (Figure 3a), although this difference was not significant, likely due to the marginal effects of the resource amendment treatment (Figure 3b). It seems unlikely that this effect was due to soil acidification caused by N addition, given that a prior study found *I. cylindrica* can grow more vigorously under acid than neutral soils [70]. The authors of the same study actually suggested that acidification through addition of nitrogenous fertilisers could enhance *I. cylindrica* growth, which contrasts with our results for *I. cylindrica* seedlings. Prior studies have shown that *I. cylindrica* has an exceptionally high N use and uptake efficiency that might contribute to its success as an invasive species [47,71]. Our results from Toohey Forest and WRSMCE show that *I. cylindrica* has substantially higher C:N ratios than co-occurring species (Table 4), supporting this view. *Imperata cylindrica* can take up surprisingly large quantities of N relative to root biomass [46], and soil N levels can even be depleted by excessive N uptake by *I. cylindrica* [72]. However, the data from our growth experiment suggest that this high N use and uptake efficiency might have a significant cost when N availability is high relative to P availability and *I. cylindrica* is, therefore, limited by P rather than N. Thus, the gradual increase in forest soil N:P ratios that typically occurs in the long-term absence of fire could serve to suppress *I. cylindrica*, particularly where soil P levels are inherently low. The finding of Yassir et al. (2010) that

the prevalence of *I. cylindrica* in a grassland declined with both time since fire and soil N concentration [28] is consistent with such a conclusion.

Interestingly, one of the main techniques for suppression of *I. cylindrica* is the cultivation of leguminous cover crops, based on the rationale that legumes will shade out and, therefore, eliminate the light-demanding *I. cylindrica* [17,26,47]. The choice of legumes appears to be due to the ability of legumes to compete with *I. cylindrica* on soils where N availability is low [26]. To our knowledge, few studies have given serious consideration to whether the N added to the soil by N-fixation could have detrimental impacts on *I. cylindrica* that complement the shading effects, or continue to suppress *I. cylindrica* even after leguminous crops have been harvested [26]. At our study sites, as in many Australian forest ecosystems, many of the plant species that dominate during the post-fire successional stage are N-fixing *Acacia* species [73]. Thus, it seems plausible that the success of *I. cylindrica* invasions into recently and/or frequently burned sclerophyll forests could hinge on the outcomes of competition between *I. cylindrica* and N-fixing plants such as *Acacia*. A similar idea was introduced by Woods 1989 [19], who argued that the recovery of disturbed tropical forests could be contingent on the abilities of secondary tropical tree species to compete with *I. cylindrica*. Results from previous studies of other species that compete with *I. cylindrica*, along with the general narrative of resource-ratio competition theory [74], indicate that these competitive outcomes could be shaped by soil P availability or soil N:P ratios [47,71]. We advocate for further research to test experimentally whether and how *I. cylindrica* competes with *Acacia* and other key post-fire successional species, with a focus on the influence of soil nutrient availability and/or nutrient stoichiometry in such competitive interactions.

Although the effects of N and P fertilization on *I. cylindrica* performance observed in our study were largely consistent with our expectations, they were not necessarily consistent with effects observed in other study systems. For example, Blair et al. (1978) found that P addition reduced the contribution of *I. cylindrica* to the overall biomass of a pasture vegetation community after one year in Sulawesi [75]. Similarly, Brewer and Cralle (2003) found that P fertilization reduced the rates of clonal invasion of *I. cylindrica* into a longleaf pine savanna in south-eastern Mississippi [31]. We suspect that the qualitatively different responses of *I. cylindrica* to P in our study is due to substantially higher P levels in the control soils of the above-mentioned studies. In the Sulawesi pasture studied by Blair et al. (1978), 150 kg ha⁻¹ of triple superphosphate was added in the two years prior to the experiment. In the longleaf pine savanna studied by Brewer and Cralle (2003), the soil total P concentration was reportedly 0.25%, compared to 0.008–0.0123% at Peachester. This indicates that the mechanisms we hypothesize are context-specific, and likely apply only to highly weathered soils in which P availability is low, particularly relative to N availability. Moreover, it is important to note that the potential process of fire-altered soil phosphorus and nitrogen levels facilitating *I. cylindrica* invasion necessarily occurs in tandem with other major environmental changes associated with recent fire (e.g., increased light levels and reduced density of potentially competing species). This is evidenced by the fact that the regional-scale spatial distribution of *I. cylindrica* is not restricted to a specific soil type or fertility level [47]. Burn severity, along with burn frequency, may thus be a critical determinant of *I. cylindrica* invasion success in fire-affected forests. Overall, our results give important insights into the relationships between fire, soil nutrients, and *I. cylindrica* in Australian subtropical eucalypt forests on soils with low P availability. Our study provides an important starting point for further research on this topic that will have direct implications for the management of Australian eucalypt forests under the shifting fire regimes associated with climate change.

5. Conclusions

Results of our investigation generally support our hypothesis that fire regime-induced changes in soil P and N availability, and particularly in soil N:P ratios, could have meaningful implications for the competitive success of *I. cylindrica* in Australian eucalypt forest

ecosystems. We found that increases in soil P levels likely benefit *I. cylindrica*, while increases in soil N levels appear to be detrimental, such that the lowering of soil N:P associated with recent and/or frequent fire is likely to confer an advantage on this species. Positive effects of enhanced soil P availability are likely short-term, and underpinned by combined effects of ash-deposition and organic P mineralization. The negative effects of increasing soil N levels suggest that the extent of proliferation of N-fixing species in post-fire environments could determine the invasive success of *I. cylindrica*, and potentially vice versa. Further experimentation is warranted to validate our conclusions and test more rigorously our hypotheses, particularly those regarding competitive interactions with other species. Overall, our results indicate that the well-established relationship between fire regime and *I. cylindrica* in forest ecosystems could be facilitated, at least in part, by the short-term enrichment of soil P availability following fire and the long-term enrichment of soil N under protracted fire exclusion. These mechanisms necessarily interact with other environmental effects of fire regime and are likely to be most important in ecosystems on highly weathered soils with low P availability.

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