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Combustion properties of *Bromus tectorum* L.: influence of ecotype and growth under four CO_2 concentrations

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Abstract. We grew from seed the exotic invasive annual grass *Bromus tectorum* L., collected from three elevation ecotypes in northern Nevada, USA. Plants were exposed to four CO_2 atmosphere concentrations: 270, 320, 370, and 420 $\mu mol\ mol^{-1}$. After harvest on day 87, above-ground tissue was milled, conditioned to 30% relative humidity, and combustion properties were measured using a cone calorimeter. Plants exposed to 270 $\mu mol\ mol^{-1}$ CO_2 had significantly less total heat released than plants exposed to higher CO_2 concentrations. Total heat released was least for the low-elevation ecotype, statistically similar for the mid-elevation ecotype, and significantly increased for the high-elevation ecotype. Plant attributes that significantly correlated with heat release included tissue concentrations of lignin, glucan, xylan, potassium, calcium, and manganese. The data suggest that a decline in tissue concentrations of lignin, xylan, and mineral constituents, as CO_2 concentration increases from 270 $\mu mol\ mol^{-1}$ to higher levels, affects the combustion process. We suspect that as tissue concentrations of lignin and inorganics decline, char formation decreases, thereby allowing more complete combustion. Changes in combustion parameters of *B. tectorum* induced by different CO_2 concentrations and elevation ecotype may be a strong consideration to understanding fire behaviors of the past, present, and future.

Additional keywords: char; flammability; global change; lignin; wildfire.

Introduction

Invasion of western North America by exotic annual grasses, particularly *Bromus tectorum* L., has altered historic fire regimes (D'Antonio and Vitousek 1992). Physiological traits of *B. tectorum* that assist its competitive profile and ability to alter fire regimes are manifold. *Bromus tectorum* is a prolific seed producer with rapid growth kinetics; if edaphic conditions are optimal, densities and spatial coverage are sufficient to fuel and carry wildfires (Young and Evans 1973; Mack 1981). Wide phenotypic plasticity of *B. tectorum* fosters invasion into a host of environments including those thought to be relatively fire-safe owing to aridity (Pellant 1990; Young and Tipton 1990; Rice *et al.* 1992). Leaves of *B. tectorum* have a high surface area to volume ratio – it is a fine fuel – a topology very conducive to heightened flammability and chance of ignition (Brown 1970*a*, 1970*b*).

A linkage between fire behavior and anthropogenic increases in atmospheric CO_2 has been suggested (Mayeux *et al.* 1994). Elevated CO_2 could potentially influence fire behavior in enumerable ways, from higher surface atmospheric temperatures, and landscape-scale changes in patterns of precipitation and relative humidity, to alteration of fuel moisture content. By and large, however, the principal factor speculated to alter fire behavior is increased fuel loads and areal extent of fuel coverage due to heightened growth, a consequence of elevated CO_2 – particularly important for invasive annual grasses (Sage 1996; Ziska *et al.* 2005). This speculation is reasonable given the strong relationship between fire behavior and fuel loads (Dimitrakopoulos 2002).

Combustion of plant material is an extraordinarily complex process (Lobert and Warnatz 1993). The measure of a plant's ability to support combustion, or flammability, is affected by many factors. Fuel moisture content is a major factor affecting flammability, but its biochemical composition (concentrations of volatile organic compounds, cellulose, hemicellulose, and lignin), its concentration of mineral constituents such as silica, and its density and topology as measured by surface areas to volume or weight (specific leaf

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area), and leaf thickness all affect the combustion process (Brown 1970*a*, 1970*b*; Philpot 1970; Rundel 1981; Dimitrakopoulos 2001; Dimitrakopoulos and Panov 2001). These same biochemical and topological factors that influence vegetation flammability can also be affected by the concentration of CO_2 in which the plants are grown. Exposing vegetation to elevated CO_2 can alter the biochemical makeup of tissue, including increasing total non-structural carbohydrates, starches, and phenolic and lignin concentrations (Allen *et al.* 1988; Farrar and Williams 1991; Roumet *et al.* 1999; Coley *et al.* 2002; Tuchman *et al.* 2003). Leaf morphological properties such as the ratio of leaf surface area to weight can also be affected by elevated CO_2 (Roumet *et al.* 1999). Moreover, as atmospheric CO_2 concentration increases, most research has determined that the mineral concentration in leaf tissue declines (Lincoln *et al.* 1986; Prior *et al.* 1998; Fangmeier *et al.* 2002; Pal *et al.* 2004).

Relatively little research on the interaction between plant ecotype and fire behavior has been undertaken. Ecotypes growing in environments with differing fire characteristics, such as length of time between fire and intensity of fire, alter growth forms and reproductive strategies to maximize survival (Vasek and Clovis 1976). Limited research is available that has examined the interaction of atmospheric CO_2 concentration with ecotype. Norton *et al.* (1995) determined that only one of five ecotypes of *Arabidopsis thaliana* grew significantly larger in response to elevated CO_2. Plant biochemistry of two Mediterranean grass species was not affected by a CO_2 by ecotype interaction (Castells *et al.* 2002). Among 14 ecotypes of *Bromus erectus*, biochemical parameters including lignin, phenolic concentration, and specific leaf areas were similar (Roumet *et al.* 1999).

Based on the relationships between flammability, plant biochemical and morphological characteristics, and the potential for those characteristics to be altered depending on atmospheric CO_2 concentration and interaction with ecotype, the following hypotheses were proposed for testing:

- Ho1: Combustion properties of *B. tectorum* are unaffected by growth at different atmospheric CO_2 concentrations;
- Ho2: Combustion properties of *B. tectorum* do not vary among ecotypes.

Materials and methods

Hypothesis testing began by collecting seeds from three elevation ecotypes of *Bromus tectorum* L. (cheatgrass) from northern Nevada, USA. The low elevation site (low) was at 1220 m at Poker Brown Flat just west of Rye Patch Reservoir (40.28°N, 118.19°W). This site receives ~160 mm of annual precipitation and is a salt desert community dominated by *Atriplex confertifolia* Torr. & Frém. S. Watson (shadscale). This site is representative of the most recent invasion by *B. tectorum*, which occurred in the early 1980s. In 1999, *B. tectorum*-fueled wildfire consumed this site. Seeds were collected in 2000. The middle elevation site (mid) was at 1737 m near Emigrant Pass, NV (40.38°N, 116.18°W) and receives on average 300 mm of yearly precipitation. This site has historically been dominated by *Artemisia tridentata* ssp. *vaseyana* Nutt. (mountain big sagebrush) and perennial bunchgrasses and is typical of areas where cheatgrass invasion has fostered immense landscape wildfires so detrimental to sagebrush ecosystems. This site burned in 1999 and seeds of *B. tectorum* were collected in 2000. The high elevation site (high) was at 2171 m at Fox Mountain, NV (41.00°N, 119.33°W). This high elevation community receives on average ~400 mm annual precipitation and is dominated by *A. tridentata* ssp. *vaseyana*, *Pseudoroegneria spicata* Pursh A. Love (bluebunch wheatgrass) and *Cercocarpus ledifolium* Nutt. (curl-leaf mountain mahogany). These high elevation communities are somewhat resistant to *B. tectorum* invasion. Seeds were collected in 2000.

Seed lots were shipped to Dr Lewis Ziska's CO_2 controlled environment facility at USDA Agricultural Research Service (ARS), Beltsville, MD. More detail on experimental protocols can be found in Ziska *et al.* (2005). Seeds were pretreated at 5°C until germination (testa was visible), then planted. Two to three seeds were sown in pots filled with a 1 : 1 mixture of sand and vermiculite and thinned to one seedling 4–6 days after emergence. A pot volume of 22.1 L was used. Plants from a given ecotype were grouped together, but groups spaced so as to minimize mutual shading. Both individual plants and groups were rotated biweekly inside the chambers until 72 days after sowing to minimize border effects. For each CO_2 treatment, pots were watered to the drip point daily with a complete nutrient solution containing 14.5 mmol m^{-3} nitrogen.

Controlled environment chambers were used (EGC, Chagrin Falls, OH, USA) with a given chamber set at one of four CO_2 concentration set-points (270, 320, 370 and 420 μmol mol^{-1}) for 24 h per day. The concentrations used approximate atmospheric [CO_2] at the beginning of the 19th century, that during the 1960s, current ambient, and that projected by the year 2020. Actual average 24 h [CO_2] values ($\pm$ s.d.) were 283 ± 16, 323 ± 12, 372 ± 9 and 425 ± 14 μmol mol^{-1}. For all chambers, temperature was altered in a diurnal fashion from an overnight low of 15°C to a maximum afternoon value of 25°C, with an average daily (24 h) value of 18.3°C. Similarly, photosynthetically active radiation (PAR) was also altered concurrently with temperature, with the highest PAR value (900–1000 μmol m^2 s^{-1}) occurring during the afternoon (1200–1500 hours). Daily PAR was 14 h, supplied by a mixture of high pressure sodium and metal halide lamps. The [CO_2] of the air within each chamber was controlled by adding either CO_2 or CO_2-free air to maintain the set concentration. Temperature, PAR, and humidity did not differ between chambers. Typical examples of a diurnal temperature/PAR curve for these experimental chambers can be found in Ziska *et al.* (2001). Plants were grown until 87 days after sowing, by which time floral spikes had matured for the lowest elevation ecotype (bolting did not occur for the other two ecotypes). A [CO_2] increase of 150 μmol mol^{-1} decreased floral times for this ecotype by approximately 10 days.

Following harvest, above-ground tissue was dried at 60°C and weight recorded. Samples were shipped to the Reno, NV, USDA ARS plant and soils laboratory for further processing. Tissue was milled separately using a 1-mm sieve opening. A portion of the milled tissue was dried for 48 h in a desiccator and analyzed for the following. Quantification of tissue C used the Walkley-Black procedure (Walkley 1947), which consists of digestion with acidified $K_2Cr_2O_7$ with supplemental heating to 180°C and back titration of unreacted dichromate with $FeSO_4$. Tissue N was determined using the micro-Kjeldahl method of catalyzed oxidation in sulfuric acid and H_2O_2 (Isaac and Johnson 1976). Ammonium released was quantified using the total N module on the Lachat autoanalyzer (salicylate method; Hach, Loveland, CO, USA). Ashing at 550°C followed by solubilization in 1 M HCl was used to measure tissue P, K, Ca, Mg, and Na (Campbell and Plank 1998). Ortho-P was quantified using a total P module (vanomolybdate chemistry) for the Lachat autoanalyzer system. Calcium, Mg, Fe, and Mn were quantified using atomic absorption spectrophotometry. Sodium and K were quantified using atomic emission spectroscopy.

A portion of the milled tissue was shipped to Dr Robert H. White at the USDA Forest Service, Forest Products Laboratory (FPL), Madison, WI, for measurement of combustion properties and additional biochemical analyses. The combustion or flammability properties of the samples were determined in an oxygen consumption calorimeter. This apparatus is commonly known as the cone calorimeter and is described in the ASTM standard E 1354 (Babrauskas 1984, 2002; ASTM International 2004). The cone calorimeter determines the heat release rate by measuring the O_2 consumption during combustion (Huggett 1980; Janssens 2002). The cone calorimeter is widely used to obtain heat release rate data on building materials. Some testing of vegetation samples has been conducted (White *et al.* 2002; Weise *et al.* 2005). Typically, the cone calorimeter is used to test planar samples of materials; thus, it was decided that the milling of the samples to uniform size would produce a more planar test specimen and the most comparable results for a limited number of test samples. Physical characteristics affect the ignition and thermal degradation of a test sample in the cone calorimeter. The testing of un-milled samples as done in other studies (Weise *et al.* 2005) would have introduced the potential changes in the physical characteristics of the cheatgrass as a factor in the results. However, testing of un-milled samples introduces its own problems of undefined exposed surface area and potential increased variability in the test data. The testing of milled samples allowed the initial sample mass to be controlled and ensured that the entire sample holder was covered with the test material. Initial testing of milled cheatgrass indicated that variations in initial sample mass increased the variability of the test results. Samples were conditioned at 27°C, 30% relative humidity, to obtain an average moisture content of 5%. The cone calorimeter tests were conducted in accordance with ASTM E 1354 (ASTM International 2004). The conical electric heater subjects the specimen to a constant heat flux. The standard 100 by 100 mm horizontal sample holder was used. The 10 g samples were placed in an aluminum foil base. The average sample thickness was ~5.5 mm. An electric spark ignitor located 13 mm above the center of the horizontal test specimen provided the external ignition of the combustible gases. The ignitor was removed once sustained flaming was observed. The operating conditions for all samples were as follows: horizontal orientation, radiant heat flux = 30.0 kW m^{-2}, exhaust flow = 0.012 m^3 s^{-1}, orifice plate = 41 mm, and scan rate = 1 scan s^{-1}.

After the completion of the cone calorimeter tests, the remaining uncombusted material was sent to the FPL Analytical Chemistry and Microscopy Laboratory (ACML) for lignin and carbohydrate compositional analysis. There was not sufficient material remaining to send samples to the ACML from all the replicates of the different conditions. In the lignin and carbohydrate compositional analysis, the milled samples were vacuum-dried and hydrolyzed with H_2SO_4 (Davis 1998). The acid-insoluble residue (Klason lignin) was quantitated gravimetrically (Effland 1977). Klason lignin values are corrected for ash content determined by combustion of the lignin. In most grasses, this acid-insoluble ash consists primarily of silica. Sugar contents of the hydrolysates were determined by anion exchange high performance liquid chromatography using pulsed amperometric detection (Davis 1998). Sugars were quantitated using an internal standard method.

Data analysis

Data structure is as follows: 4 CO_2 treatments × 3 elevation ecotypes × 5 replications = 60 total samples. All measured parameters were analyzed using a two-way analysis of variance with [CO_2] and ecotype as the classification variables. Treatment and ecotype comparisons were made using Fisher's protected least significant difference. Unless otherwise stated, significant differences for any measured parameter were determined at the $P < 0.05$ level. Correlations between combustion parameters and plant tissue parameters used Spearman's rank test (Statview 1998).

Results

The main results of the cone calorimeter tests are the times for sustained ignition and the curves for the heat release rate and mass loss *v.* time (Fig. 1). The heat release and the mass loss data were combined to compute the effective heat of combustion. Generally, the results for the heat release rate curves were reported as either averages or peak values. The averages are for the duration of the test or for a period of 60, 180, or 300 s after the observation of sustained ignition of the test sample. The heat of combustion results used in the analysis are for an effective heat of combustion as there was a residual charred sample remaining at the completion of the test. In a cone calorimeter test, 20–30% of a wood sample would not be consumed and the effective heat of combustion would be 12–13 kJ g^{-1} (Janssens 2002). In contrast, nearly all of a wood sample would be consumed in an oxygen bomb calorimeter, and the net heat of combustion of wood would be 16–18 kJ g^{-1} (Janssens 2002). In these tests of cheatgrass, up to 19% of the sample was not consumed.

Carbon dioxide concentration and elevation ecotype significantly affected some combustion parameters of *B. tectorum* (Table 1). Average mass loss rate and average effective heat of combustion, however, were not influenced by ecotype or CO_2 concentration. The combustion parameters total heat released, heat released for the 180 s duration after ignition, and heat released for the 300 s duration were all affected by

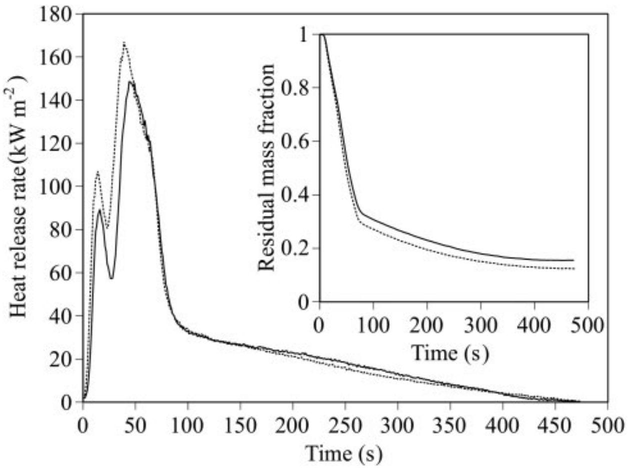

Fig. 1. Typical patterns of heat release rates and residual mass fraction *v.* time for the combustion of *Bromus tectorum* tissue. Dotted lines refer to one replicate of the high-elevation ecotype grown at 420 μmol mol^{-1} CO_2; solid lines refer to one replicate of the low-elevation ecotype grown at 270 μmol mol^{-1} CO_2.

a main effect due to CO_2 concentrations and elevation ecotypes (Fig. 2). For these combustion attributes, heat released was significantly less for tissue grown at 270 μmol mol^{-1} CO_2 compared with tissue grown at higher CO_2 concentrations. In addition, the high elevation ecotype had significantly greater heat released than the other ecotypes.

A significant CO_2 treatment by ecotype interaction affected the combustion parameters time to sustained ignition, heat released in the initial 60 s after ignition of the test sample, and peak heat release rate (Fig. 2). For the mid ecotype only, time to sustained ignition was significantly greater for plants exposed to 370 μmol mol^{-1} CO_2 than the other CO_2 treatments. Heat released in the initial 60 s duration was significantly less for low ecotype plants exposed to 420 μmol mol^{-1} CO_2, and significantly less for mid ecotype plants exposed to 270 μmol mol^{-1} CO_2. For the low-elevation ecotype, peak heat release rate declined when plants were grown at higher CO_2 concentrations. Elevation ecotype affected the previous three combustion parameters similarly; the high ecotype was significantly greatest.

Many tissue attributes correlated significantly with combustion parameters (Table 2). Tissue concentration of C, N, and C : N ratio, however, did not significantly correlate with any combustion parameter. Patterns of correlation were evident. Heat release rate for 60, 180, and 300 s durations highly correlated with tissue concentrations of lignin, xylan, Mn, and K. Total heat released significantly correlated with tissue concentrations of lignin, xylan, Mn, and K. Time to sustained ignition correlated with tissue concentrations of glucan, Ca, and the P : Ca ratio. Peak heat release rate only correlated with tissue glucan concentration.

Carbon dioxide treatment and elevation ecotype significantly affected tissue concentration of the same attributes that correlated with combustion parameters (Fig. 3). Tissue concentration of these substances was greatest for plants grown at 270 μmol mol^{-1} CO_2. Moreover, the largest decline in these tissue nutrient concentrations occurred from 270 to 320 μmol mol^{-1} CO_2. Overall, tissue concentration declined from the low-elevation to high-elevation ecotypes; however, only tissue concentrations of Ca and lignin declined significantly.

Table 1. ANOVA probability values for combustion parameters generated by the cone calorimeter

Variable	CO_2	Ecotype	CO_2 × ecotype
Time to sustained ignition (s)	0.6295	0.0005	0.0158
Peak heat release rate (kW m^{-2})	0.7503	<0.0001	0.0138
Average mass loss rate (g s^{-1} m^{-2})	0.6871	0.3150	0.7208
Average effective heat of combustion (MJ kg^{-1})	0.5511	0.7657	0.6964
Average heat release rate at $t = 60$ (kW m^{-2})	0.0050	<0.0001	0.0066
Average heat release rate at $t = 180$ (kW m^{-2})	0.0016	0.0010	0.1004
Average heat release rate at $t = 300$ (kW m^{-2})	0.0112	0.0044	0.1564

Discussion

Combustion properties of *B. tectorum* tissue were significantly affected by the CO_2 concentration that the plants were grown in and by elevation ecotype, thus refuting our working hypotheses. As tissue was milled to a uniform size, combustion differences attributable to CO_2 treatments and ecotype elevation are due to fundamental biochemical differences in tissue of *B. tectorum* caused by the CO_2 treatments and seed source, not its physical shape.

A statistically significant CO_2 treatment by ecotype interaction affected the combustion parameters time to sustained ignition, heat released in the initial 60 s after ignition, and peak heat release rate. These results for the cone calorimeter reflect the initial surface reaction of the test sample to the fire exposure and the initial flaming combustion of the sample. Time to sustained ignition correlated with tissue concentrations of glucan, Ca, and the P : Ca ratio. Peak heat release rate only correlated with tissue glucan concentration. Heat release rate in the initial 60 s after ignition was highly correlated with tissue concentrations of lignin, xylan, Mn, and K. Elevated tissue concentrations of silica, other inorganics, and lignin can reduce flammability and heat release rates through the formation of char, or the incomplete oxidation of C (Philpot 1970; Shafizadeh 1981; Lobert and Warnatz 1993; Hogenbirk and Sarazin-Delay 1995). The influence of these elevated tissue concentrations on char formation would likely affect the heat release over the initial 60 s period more than the peak heat release rate that occurred shortly after ignition of the sample. The times for sustained ignition ranged from 7 to 13 s. The times for the peak heat release rates ranged from 29 to 65 s.

Total heat released and average heat released for the 180 and 300 s durations were significantly less for plants grown at the pre-industrial CO_2 level of 270 μmol mol^{-1} compared to higher CO_2 concentrations. These data suggest that combustion of *B. tectorum*, for example in 1850, may have evolved less heat than combustion presently or in the future. Results for total heat released and average heat released for the 180 and 300 s durations in the cone calorimeter tests reflected the overall combustion during the entire test and included char oxidation after flaming had ceased. Average heat released for the 180 and 300 s durations and the total heat released were significantly correlated with tissue concentrations of lignin, xylan, Mn, and K. The final residual mass fraction of the test specimen was recorded as an indicator of the amount of char formation. The residual mass fraction was further reduced by

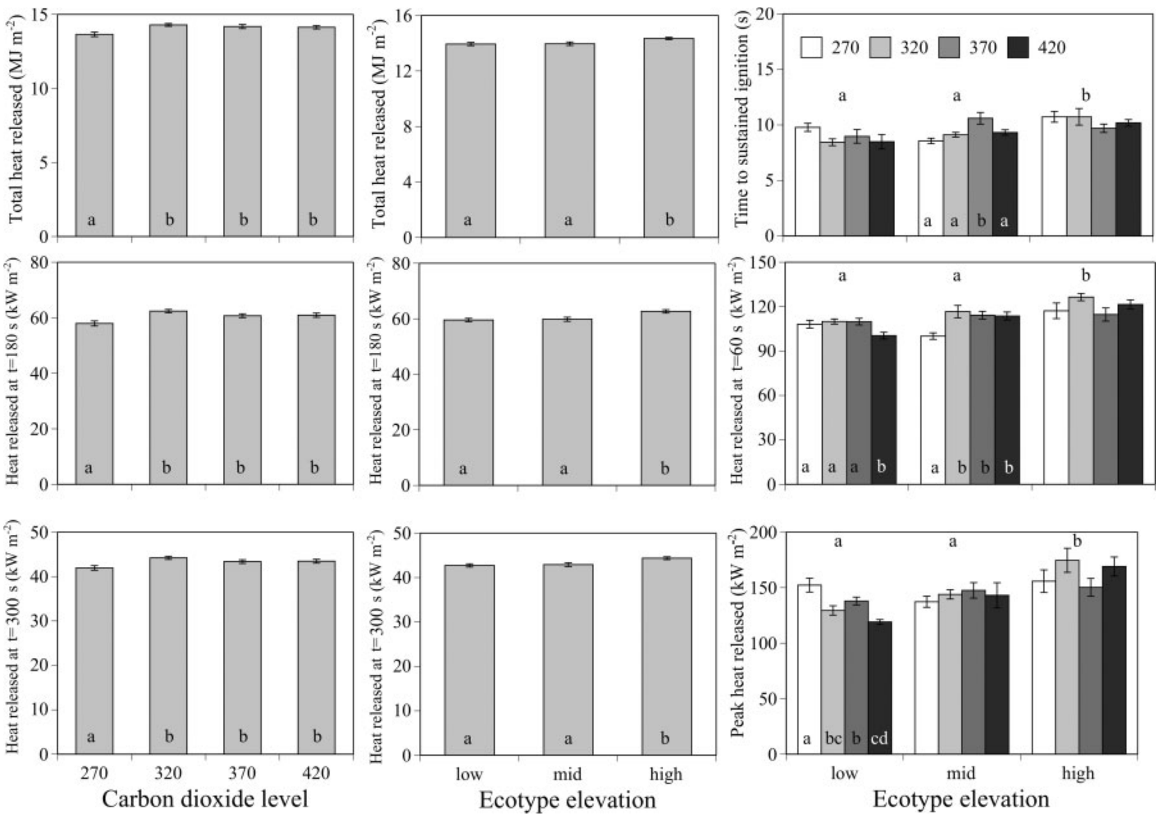

Fig. 2. Combustion parameters derived from the cone calorimeter showing significant main effects or interactions with CO_2 treatment and elevation ecotype. Bars denote standard errors. For each panel showing a main effect, significance is denoted by different letters. For panels showing a significant interaction, the top letters denote significant differences among ecotype and the bottom letters denote significant differences among CO_2 treatments.

Table 2. Spearman's correlation coefficients (*r*) and probability values (*P*) by combustion parameters for selected plant tissue attributes
Bold-face type denotes significant *P* values

Attribute	N		C		C : N		Lignin		Glucan		Xylan		Ca	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Total heat released (MJ m^{-2})	0.007	0.961	0.259	0.053	0.051	0.703	**−0.556**	**0.022**	−0.200	0.413	**−0.556**	**0.022**	−0.165	0.212
Time to sustained ignition (s)	−0.111	0.405	−0.058	0.667	−0.033	0.807	−0.064	0.797	**−0.500**	**0.046**	−0.093	0.710	**−0.358**	**0.007**
Heat release at $t = 60$ s (kW m^{-2})	0.183	0.170	0.142	0.291	−0.190	0.158	**−0.651**	**0.009**	**−0.554**	**0.027**	**−0.728**	**0.004**	**−0.414**	**0.001**
Heat release at $t = 180$ s (kW m^{-2})	0.160	0.230	0.210	0.119	−0.119	0.379	**−0.704**	**0.005**	−0.333	0.182	**−0.777**	**0.002**	−0.230	0.085
Heat release at $t = 300$ s (kW m^{-2})	0.119	0.374	0.194	0.149	−0.095	0.480	**−0.654**	**0.009**	−0.314	0.210	**−0.703**	**0.005**	−0.231	0.084
Peak heat release (kW m^{-2})	0.102	0.446	−0.081	0.549	−0.216	0.170	−0.369	0.139	**−0.664**	**0.008**	−0.316	0.206	**−0.281**	**0.036**

Attribute	P		Zn		Fe		Mn		K		Mg		P/Ca	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Total heat released (MJ m^{-2})	−0.260	0.050	−0.176	0.184	−0.252	0.058	**−0.421**	**0.002**	**−0.571**	**<0.001**	**−0.293**	**0.027**	**0.278**	**0.037**
Time to sustained ignition (s)	−0.099	0.457	**0.311**	**0.020**	−0.205	0.124	−0.175	0.192	−0.173	0.196	−0.014	0.917	**0.277**	**0.004**
Heat release at $t = 60$ s (kW m^{-2})	−0.115	0.391	0.090	0.501	**−0.366**	**0.006**	**−0.502**	**<0.001**	**−0.434**	**0.001**	0.279	0.037	**0.381**	**0.004**
Heat release at $t = 180$ s (kW m^{-2})	−0.172	0.199	−0.106	0.429	**−0.374**	**0.005**	**−0.537**	**<0.001**	**−0.564**	**<0.001**	**−0.382**	**0.004**	0.188	0.159
Heat release at $t = 300$ s (kW m^{-2})	−0.161	0.227	−0.098	0.465	−0.304	0.123	**−0.512**	**<0.001**	**−0.557**	**<0.001**	**−0.352**	**0.008**	0.184	0.167
Peak heat release (kW m^{-2})	0.019	0.887	**0.341**	**0.011**	−0.184	0.168	−0.186	0.164	−0.092	0.493	0.121	0.363	**0.327**	**0.014**

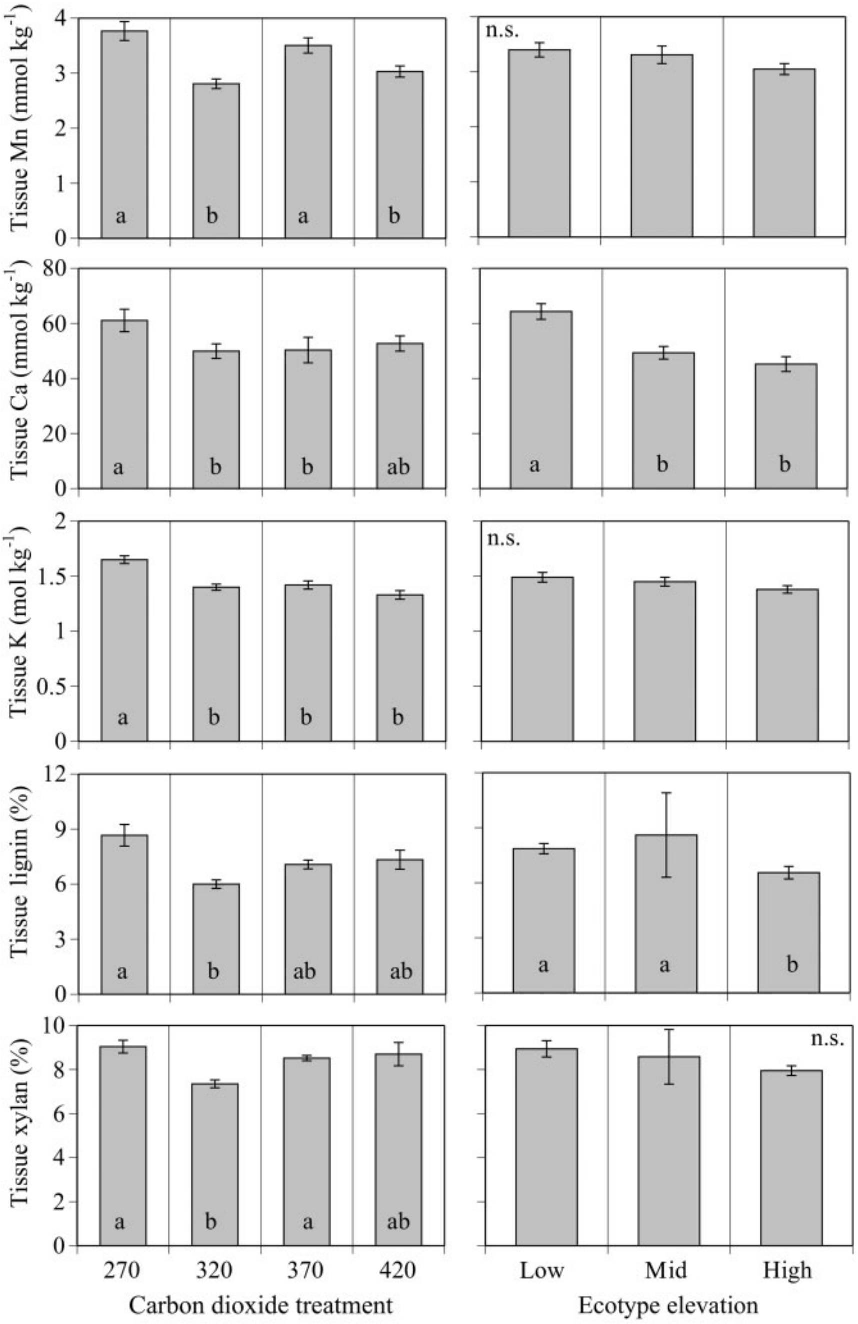

Fig. 3. Selected *B. tectorum* tissue components as affected by CO_2 treatment and ecotype elevation. For each panel, significant differences are denoted by different letters. Bars denote standard errors and n.s. denotes non-significant results.

the oxidation of the char after sustained flaming had ceased. A number of obvious outliners in the residual mass fraction data were observed. Separate thermal gravimetric analysis (TGA) in an inert atmosphere would have provided a more reliable measure of char formation but the amount of material for testing was limited. The residual mass fraction remaining after the test was also significantly correlated to the lignin content. Whereas the residual mass fraction significantly correlated with the average heat release rates data, the correlations of the residual mass fractions with the CO_2 concentration and ecotype were not significant.

Compared with the more common oxygen bomb calorimeter, the influence of lignin content on heat release is different for a test like the cone calorimeter, in which there is a residual char material at the end of the test. The total heat released depends on the amount of the sample that is consumed. Lignin on pyrolysis yields more residual char than is obtained from cellulose (Browne 1958). Thus, the impact is to reduce the total heat that is released. In contrast, White (1987) reported a significant correlation between the higher heating value of different wood samples in the oxygen bomb calorimeter and the Klason lignin content for extractive-free wood. These higher heating values in the oxygen bomb calorimeter likely reflected the higher heating value of lignin relative to cellulose and hemicellulose (Tillman 1978; Baker 1983).

We attribute lower total heat release and heat release rates for the various durations for plants grown at 270 μmol mol^{-1} CO_2, compared to higher CO_2 treatments, to elevated char formation due to higher tissue concentrations of lignin, K, Mn, and Fe. Although we did not measure silica or ash content of tissue, the literature suggests that high concentrations of K, Mn, and Fe in plant tissue also increase char formation (Carty and White 1994; Gilman *et al.* 1997). Moreover, research has shown that ash concentration of vegetation does decline with increased CO_2 (Schenk *et al.* 1997). That there is a general trend in decreased concentration of nutrients in plant tissue with elevated CO_2 – greater nutrient use efficiency (Poorter 1993) – suggests that plants growing presently may have less char formation than those same plants grown in pre-industrial CO_2 levels of 270 μmol mol^{-1}. The previous argument can also be applied to explain the effects of ecotype on heat released. Lower tissue concentration of Mn, Ca, Fe, lignin, and xylan for the high-elevation ecotype contributes to less char formation and greater heat release than the low- and mid-elevation ecotypes.

In the intermountain west of the USA, where *B. tectorum* is so dominant, by late spring to early summer the fuel is extremely flammable, ready to burst into a wildfire given the chance of ignition. The cone calorimeter measurement time to sustained ignition for the high-elevation ecotype, therefore, has potential bearing. That time to sustained ignition decreased significantly from *B. tectorum* grown at pre-industrial CO_2 levels of 270 μmol mol^{-1} to higher levels of CO_2 suggests perhaps the chance of ignition of *B. tectorum* is greater now than would have occurred 150 years ago. With similar reasoning, it would appear that the low- and mid-elevation ecotypes would have greater chance of ignition than the high-elevation ecotype. That time to sustained ignition correlates negatively with tissue glucan and Ca concentration and that tissue concentrations declined with increasing CO_2 and with increasing elevation suggests these attributes are controlling factors.

In summary, the concentration of CO_2 under which *B. tectorum* was grown and the elevation ecotypes of *B. tectorum* significantly affected its combustion characteristics. Our data suggest that higher mineral content in plants grown at the pre-industrial level of 270 μmol mol^{-1} CO_2 results in greater char formation such that the combustion process is less efficient, evolving less heat during burning. On the surface, these data suggest that wildfires presently consuming *B. tectorum* would produce more heat per unit mass than fires during pre-industrial time. Without a modeling effort, however, it is perilous to extrapolate our results to real field environments.

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