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Article

Interactions between Fine Wood Decomposition and Flammability

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Abstract: Fire is nearly ubiquitous in the terrestrial biosphere, with profound effects on earth surface carbon storage, climate, and forest functions. Fuel quality is an important parameter determining forest fire behavior, which differs among both tree species and organs. Fuel quality is not static: when dead plant material decomposes, its structural, chemical, and water dynamic properties change, with implications for fuel flammability. However, the interactions between decomposition and flammability are poorly understood. This study aimed to determine decomposition's effects on fuel quality and how this directly and indirectly affects wood flammability. We did controlled experiments on water dynamics and fire using twigs of four temperate tree species. We found considerable direct and indirect effects of decomposition on twig flammability, particularly on ignitability and burning time, which are important variables for fire spread. More decomposed twigs ignite and burn faster at given water content. Moreover, decomposed twigs dry out faster than fresh twigs, which make them flammable sooner when drying out after rain. Decomposed fine woody litters may promote horizontal fire spread as ground fuels and act as a fuel ladder when staying attached to trees. Our results add an important, previously poorly studied dynamic to our understanding of forest fire spread.

Keywords: carbon cycle; cellulose: lignin ratio; forest functioning; fine woody fuels; fire; plant functional traits; tree; water dynamics; wood decay

1. Introduction

Fire has been a worldwide common phenomenon since the establishment of terrestrial plants and has profound effects on landscape, community composition, carbon and nutrient cycles, and climate [1–4]. Severe wildfires return large amounts of stored carbon into the atmosphere [5], representing the major substitute C release pathway, in addition to decomposition [6]. With increasing temperatures and duration of fire seasons due to climate change, the frequency and severity of wildfires is increasing [7–9].

At local scale, fire has complex effects on soil carbon concentration: by combusting soil organic carbon and increasing deposition of carbon as char, the effects can be positive or negative, depending on the intensity of the fire, the composition of the organic carbon, and the time scale of interest [10,11]. Following fire, the community composition of both flora [12] and fauna [13–15] is substantially affected either directly via the death of individuals or indirectly via altered resource availability. Compared to our knowledge about these and other consequences of fire in ecosystems, we have a much poorer understanding about the factors that determine the susceptibility of different ecosystems, including forests, to fire. In addition to abiotic factors such as temperature and moisture regimes, biotic drivers, such as amount and quality of living and dead plant material are very important [2].

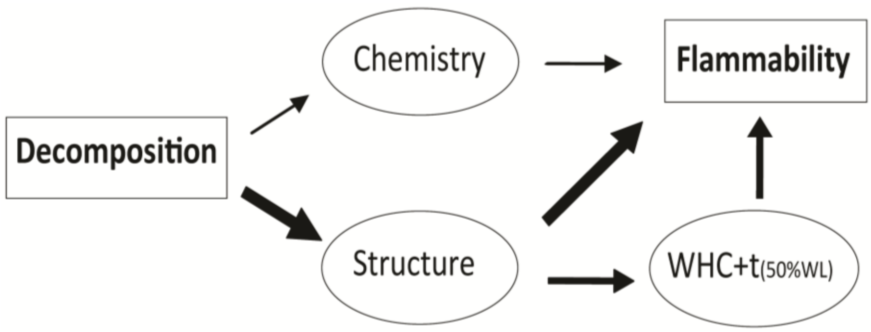
Both wild and prescribed fires are fuelled by plant material, and plant species vary greatly in their ignitability and other flammability characteristics [16]. Different properties of living plants or their litter, including moisture content, chemistry, and structure, have large effects on flammability [17–19]. In addition, different plant organs differ in flammability [20] and in their importance at different stages of fires. Early stage wildfires in woody ecosystems are more likely to start and spread with leaves and twigs since they are more easily ignited than coarser stems due to their higher surface to volume ratio [21–23]. In addition, the dead twigs may either be dropped to the ground in some species or retained on the main stem; on the ground the twigs may promote ground fire, while on the main stem they may act as a fuel ladder [24,25].

Traits including moisture content and leaf shape and size have been linked to interspecific variation in leaf flammability [16,26–29]. Here, we focus on twigs, which are important drivers of forest fires but have been studied much less for trait-fire relationships. The moisture content of twigs is partly dependent on their water holding capacity. In addition, twig water loss rate influences its moisture content in dry periods [21]. Another essential fire-related trait of twigs is their internal structure, including the bulk density of the fuel, which affects flammability through its influence on fuel-air interactions. A lower fuel density promotes the fuel-air contact and therefore increases flammability [20,26]. Chemical properties such as secondary metabolites, lignin, and cellulose concentration may also promote or suppress flammability [21,23,29].

Traits of living twigs differ among tree species, and in addition after senescence these properties change with decomposition. Decomposition is (generally) a gradual process that affects wood structure and chemical properties, due to the activities of invertebrates, fungi, and bacteria [6,30–32]. As decomposition proceeds, the density of wood decreases, while the volume of the twig is maintained by its lignin "skeleton" and in some cases by the persistence of recalcitrant bark [6,33,34]. At a certain point in the decomposition process, the twig loses structural integrity and crumbles. Before the loss of structural integrity, twig density can be used as a proxy for decomposition stages [33]. Wood chemical properties may also change during decomposition [32]. Those changes may have considerable influences on wood flammability directly, via the changing structure and chemistry of the wood, or indirectly, through the effects of changing wood structure on moisture dynamics (Figure 1).

This leads to the following research questions: (1) What are the effects of decomposition on twig structure and chemical properties within tree species? (2) How does decomposition directly and indirectly (via water properties) affect twig flammability of given tree species? How do the relationships in (1) and (2) vary among tree species? To disentangle the effects of fuel properties from effects of fuel amount and (litter) fuel bed structure, this study focuses on flammability of individual twigs. We hypothesize that the direct effects of structural changes have the biggest influence on flammability (Figure 1). In addition, indirect effects through changes in water dynamics will also affect flammability, but to a lesser extent than direct effects of structural changes. The smallest effect is expected for changes in chemistry. We tested these hypotheses through a series of controlled water dynamics experiments and controlled experimental burns with twigs of four temperate tree species.

Figure 1. Interactions between twig decomposition and flammability; Decomposition may directly affect twig flammability by altering chemical and structural properties, as well as indirectly via changing twig water dynamics: water holding capacity (WHC) and time until 50% water loss ($t_{(50\%WL)}$) of saturated twigs; In hypothesized magnitude from low to high (as indicated by width of arrows), change in chemistry, indirect effects of structure via water dynamics, and direct effects of structure will affect flammability.



2. Materials and Methods

2.1. Experimental Design and Sampling

Twig litter from four species was sampled from the ground at two different locations during January–March 2013. *Betula pendula* Roth and *Larix kaempferi* (Lamb) Carrière twigs were collected at the Schovenhorst estate near Putten (Veluwe, center of the Netherlands) (52°25' N, 5°62' E). *Populus* × *canadensis* Moench and *Quercus robur* L. twigs were collected in woodland near Amsterdam (Amsterdamse Bos, Western Netherlands) (52°32' N, 4°85' E). All species are deciduous, but they have a broad taxonomic spread consisting of one gymnosperm, *Larix kaempferi*, and three angiosperm species.

Three experiments were conducted: first, a drying experiment was performed to examine the decomposition effect on twig water dynamics: water holding capacity and time until 50% water loss within all four species; second, after the drying experiment, a selection of air-dried twigs of all four species was burned to examine the effects of decomposition stage on air-dry twig flammability; third, *Quercus robur* twigs of a variety of decomposition stages were progressively dried. Flammability experiments were performed at a series of time points through the drying process. The aim of the third experiment was to determine the interactive effects of decomposition stage (with lignin and cellulose concentration as covariates) and water dynamics on twig flammability.

For all experiments, decomposition stages were measured by twig density [33]. Twigs for the first and second experiment were collected during the first sampling (January 2013). *Q. robur* twigs for the third experiment were collected during the second sampling (February 2013). A large number of twigs were first collected to assure a large range of densities in the field. Later in the lab, different numbers of twigs with proper diameter and density range were chosen for each experiment.

2.2. Water Holding Capacity and Time until 50% Water Loss

For the drying experiment, we selected 30–35 twigs for each of the four species based on a diameter 5.5 ± 0.5 mm [35] in the center and cut them into 15 cm long pieces. Afterwards, each twig piece was saturated for at least 65 h in a plastic bag totally filled with demineralized water and sealed without any trapped air. After saturation, a subsample of 5 cm long was taken to measure twig density and water holding capacity, leaving the remaining 10 cm length as the drying sample. Twig density (ρ) (mg/cm^3) was calculated as:

$$\rho = \frac{1000 \times m_{(oven-dried)}}{V} \tag{1}$$

where, $m_{(oven\text{-}dried)}$ is the oven-dried (70 °C , 72 h) mass (g) and V is the saturated volume (cm^3) of the subsample.

The saturated volume of the subsample was measured by the water displacement method. Saturated twigs were immersed into a plastic container filled with water loaded on a top-loading electronic balance. The twigs were pressed below the water surface with the aid of a needle of negligible volume compared to twig volume. The volume of the twig was read on the balance as the mass of the displaced water [36]. Twig water holding capacity (WHC) was calculated as:

$$\mathrm{WHC} = \frac{m_{(saturated)} - m_{(oven-dried)}}{m_{(saturated)}} \tag{2}$$

where $m_{(saturated)}$ is the saturated mass (g) and $m_{(oven\text{-}dried)}$ is the oven-dried (70 °C , 72 h) mass (g) of the subsample. Following saturation, we gently blotted dry any surface water of the subsample and sample with tissue paper before measuring their saturated mass and/or beginning the drying experiment.

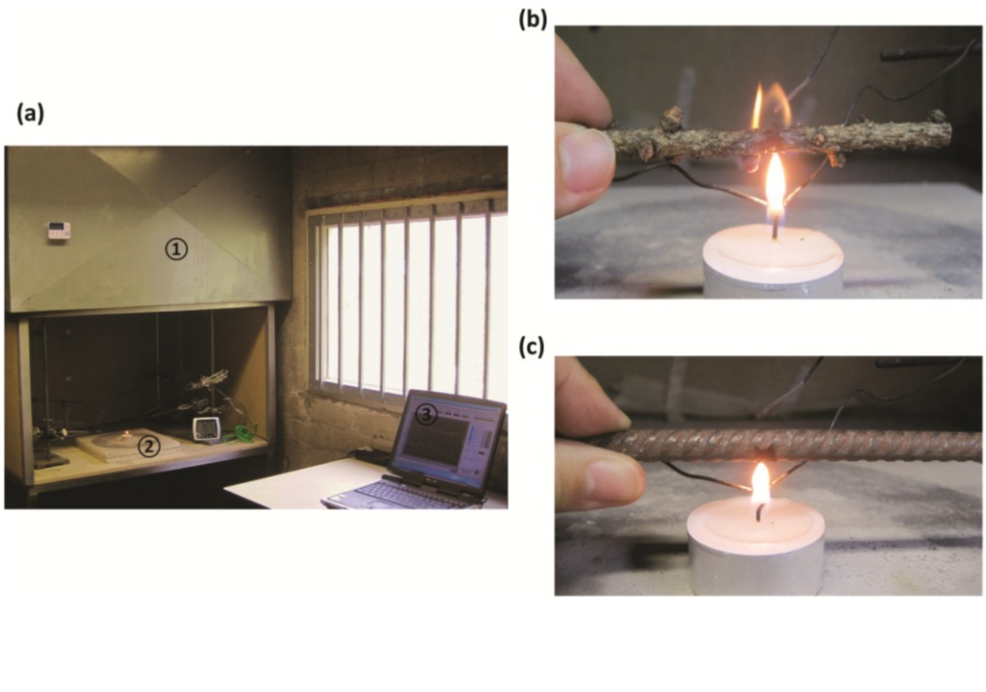
In the drying experiment, each saturated sample was air-dried on a petri-dish lid (91.5 mm in diameter) at a constant temperature of 17 °C (16.3~17.7) and air humidity of 70% (63.2~72.8) in a climate controlled room. The weight of the sample was measured at the start of the drying (0 h, totally saturated) and after 1, 2, 4, 8, 12, 24, 36, 48, 72, 96, 174, 198 and/or 222 h (174 h for *Betula pendula* and *Larix kaempferi*, 198 h for *Quercus robur*, 222 h for *Populus* × *canadensis*) until twig water loss was negligible. Time until 50% water loss was determined as the time saturated samples needed to lose half of their water (water content when saturated).

2.3. Air Dry Twig Flammability

After the drying experiment, a selection of air-dried twigs of each of the four species (20 twigs for *L. kaempferi*, 25 twigs for *P.* × *canadensis*, 24 twigs for B. pendula, and 27 twigs for *Q. robur*) with the smallest difference in diameter (most very close to 5.5 mm) and the biggest variance in density were used to determine air dry twig flammability.

The fire experiment was carried out in the Fire Laboratory of Amsterdam for Research in Ecology (FLARE) located at VU University Amsterdam, The Netherlands during January–March 2013. All burnings were conducted under a fume hood on a solid fire-resistant plate (Figure 2a). The fume hood was ventilated at a constant speed and the air drawn in from outside by the extractor fan was first warmed to room temperature [20]. Prior to each burn, the fume hood was turned on and the experiment started when room temperature was 21.4 ± 4 °C.

Figure 2. (**a**) the Fire Laboratory of Amsterdam for Research in Ecology (FLARE); ①Fume hood, ②fire resistant plate, and ③laptop running TC Meas program for temperature data recording; (**b**) Twig burning. Three thermocouples were placed: one was approximately 1.5 cm above the source flame tip and the other two were at the sides of the source flame; (**c**) Background burning with a metal bar. Three thermocouples were placed: one was approximately 1.5 cm above the source flame tip and the other two were at the sides of the source flame.



Just before burning, each twig was re-measured for diameter three times at the middle point to get a reliable estimate of the real diameter of the section exposed to the source flame. Afterwards the twigs were held by hand in a fixed position at the tip of a tea-light flame, making slight contact with the flame (Figure 2b). The reason why we held the twigs by hand is that we found this the easiest way to keep the twigs constantly at the tip of the source flame during burning. The tip of the source flame provided a constant temperature of 800 °C (authors' data not shown). Three thermocouples (1 mm thick type K thermocouple, TC Direct, Uxbridge, UK) were placed: one was approximately 1.5 cm above the source flame tip and the other two were at the sides of the source flame (Figure 2b). The thermocouples could measure temperatures up to 1100 °C and temperature data was analyzed with TC Meas, a program written by the Electronic Engineering Group Bèta VU in Labview (Figure 2a). Temperature was recorded every second during each burning. The two thermocouples at the sides of the flame measured the source flame temperature to compare constancy between burnings. The thermocouple above the twig measured the twig flame temperature to determine the twig flammability parameters.

Following Anderson (1970), we define flammability in terms of ignitability, sustainability, and combustibility. In our experiment, ignitability and sustainability was measured as the time until ignition and the time until twig breaking (burning time), respectively. Combustibility is characterized by twig heat release and maximum flame temperature. First, the time until ignition was determined as the time from the twig making contact with the source flame tip (at the same time, start the temperature recording) to the twig flame temperature reaching 500 °C. Second, time until twig breaking (burning time) was measured as the time from twig ignition to twig breaking. As only the middle part of the twig was exposed to the source flame, when this part was burned down, the twig would break into two pieces. The time of twig breaking was also the end of the burning. We used a stopwatch to record the time to twig breaking. We started the time recording when the twig made contact with the source flame. The time recording was stopped when we saw the twig had broken into two pieces. Third, a proxy for twig heat release was calculated with the following formula:

$$\text{Sum of heat release} = \sum_{i=1}^{n}(Tn - 371\ {}^{\circ}\text{C}) \tag{3}$$

(n = 1, 2, 3, 4 … … t, where t is the burning time in seconds)

The temperature Tn (°C) measured each second was calibrated by the average baseline temperature of 371 °C and the sum of these calibrated temperatures represented our proxy. To calculate the baseline temperature, we did four background burnings separately. For the background burning, the set-up was the same as the twig burning except we replaced the twig with a metal bar of 8 mm in diameter to mimic the physical heat banning effect of twigs in real burning (Figure 2c). Each background burning lasted 10 min. We use the temperature recorded by the thermocouple above the metal bar to calculate the baseline temperature. The baseline temperature was the measured average temperature of all background burnings. Fourth, the maximum flame temperature was measured as the maximum twig flame temperature reached during the burning.

2.4. Interactions between Water Dynamics and Flammability

To understand interactive effects of decomposition and water dynamics on twig flammability in depth, an additional water dynamics experiment was done with *Q. robur*. At first 127 twigs of *Q. robur* with a diameter 6.5 ± 0.5 mm [35] in the center were chosen and cut into 15 cm long pieces. Afterwards each twig piece was saturated (details see above) and after saturation a subsample of 5 cm long was taken to measure the twig density, leaving the remaining 10 cm length as candidate drying samples. After knowing the twig density, 92 twigs were finally chosen as real drying samples, divided into four batches of 23 twigs each with the same range of densities, and randomly dried these four batches for 1, 24, 48, or 72 h after saturation (for details see "Water holding capacity and time until 50% water loss" section).

Twigs of each of the four batches were burned immediately after drying for 1, 24, 48, or 72 h. To determine twig flammability parameters, we used the same methods as described in the "Air-dry twig flammability" section, except for ignition time, which was determined as the time between the start of the source flame and twig flame temperature making a jump of within one second greater than 10 °C because many wet twigs were incapable of igniting or reaching 500 °C during burning.

2.5. Twig Chemical Properties

To determine whether effects of decomposition stage on flammability were due to changes in structure or key chemical properties, *Q. robur* twig subsamples for the 72 h treatment of the water dynamics experiment (for details see the "Interactions between water dynamics and flammability" section) were measured for lignin and cellulose concentration, using a standard protocol. Lignin was determined following Poorter and Villar (1997) [37]: in short, after several extraction steps to ensure that only cellulose and lignin made up the composition of the residue of the sample, the C and N concentrations of this residue were used to calculate the lignin and cellulose concentration, based upon the difference in carbon content between cellulose and lignin.

2.6. Data Analysis

For the effects of decomposition stage on water dynamics and air dry twig flammability, an analysis of covariance (ANCOVA) was performed with species as a factor and density and diameter as covariates. Furthermore, multiple linear regressions were performed with water or flammability parameters as dependent variables and species, density and diameter as independent variables. We chose the best model by Akaike Information Criterion (AIC) in a stepwise algorithm. The interaction between species and density was also taken into account. As the twig diameter was highly controlled to a certain range for all four species when we selected the twigs, we did not consider the interaction between species and diameter.

For the effects of decomposition stage on flammability of twigs during drying, an analysis of covariance (ANCOVA) was performed with drying time as a factor and density and diameter as covariates. Drying time was considered to be an ordered factor, because it represents an ordinal variable. Furthermore, a multiple linear regression was performed with flammability parameters as dependent variables and time, density and diameter as independent variables. We chose the best models by Akaike

Information Criterion (AIC) in a stepwise algorithm. The interaction between time and density was also taken into account. As the twig diameter was highly controlled to a certain range for all twigs with different drying time when we selected them, we did not consider the interaction between time and diameter.

To test the relative strength of structural *versus* chemical effects of decomposition on flammability, an analysis of covariance (ANCOVA) was performed with density as a factor and cellulose: lignin ratio and diameter as covariates. Furthermore, a multiple linear regression was performed with flammability parameters as dependent variables and cellulose: lignin ratio, density and diameter as independent variables. We chose the best models by Akaike Information Criterion (AIC) in a stepwise algorithm. The interaction between cellulose: lignin ratio and density was also taken into account. Because the twig diameter was highly controlled to a certain range for all decomposition stage twigs, we didn't consider the interaction between density and diameter. A simple linear regression was performed to test the correlation between decomposition stage and twig chemical variables.

For all analyses, all variables were normally distributed and homogeneous in variances, therefore no transformation was necessary. R software version 2.15.1 was used to perform the statistical analyses [38].

3. Results

3.1. Water Holding Capacity and Time until 50% Water Loss

Partly decomposed twigs (for brevity called "decomposed twigs" hereafter) with lower density absorbed more water after saturation compared to fresh (undecomposed) twigs, resulting in a higher water holding capacity (WHC) (Table 1, Figure 3a). WHC was different among species: *Larix kaempferi* showed lower WHC compared to other species, while *Populus* × *canadensis* showed a less strong relation between density and WHC compared to other species.

Decomposed twigs held more water when saturated and also released water faster than fresh twigs (Table 1, Figure 3b). Again, *Larix kaempferi* showed a different pattern compared to other species, as its time until 50% water loss ($t_{(50\%WL)}$) was considerably longer. The relation between density and time until 50% water loss was species-specific, with no relation found in *Betula pendula* and *Populus* × *canadensis* twigs. Altogether, decomposed twigs had both a higher WHC and a longer $t_{(50\%WL)}$ with some variation among species for $t_{(50\%WL)}$.

3.2. Air Dry Twig Flammability

The density of air-dried twigs was positively related to time until ignition (Table 1, Figure 4a). The strength of this relation varied among species, with the strongest relationship for the *Populus* × *canadensis* twigs. Density was also strongly related to the burning time (time until twig breaking) except for *Larix kaempferi* (Table 1, Figure 4b). Nevertheless, *L. kaempferi* showed longer burning time compared to other species. Overall the results showed that, in dry conditions, decomposed twigs were more flammable compared to fresh twigs. However, the twig heat release proxy showed no relation with density, as the net heat release was similar between decomposed and fresh twigs (Table 1, Figure 4c). Similarly, maximum flame temperature was not related to density (Table 1, Figure 4d).

Figure 3. Density *versus* water holding capacity (**a**) and time until 50% water loss (**b**) of single twigs of all four species; Only significant relationships within species are shown as regression lines (Table 1).

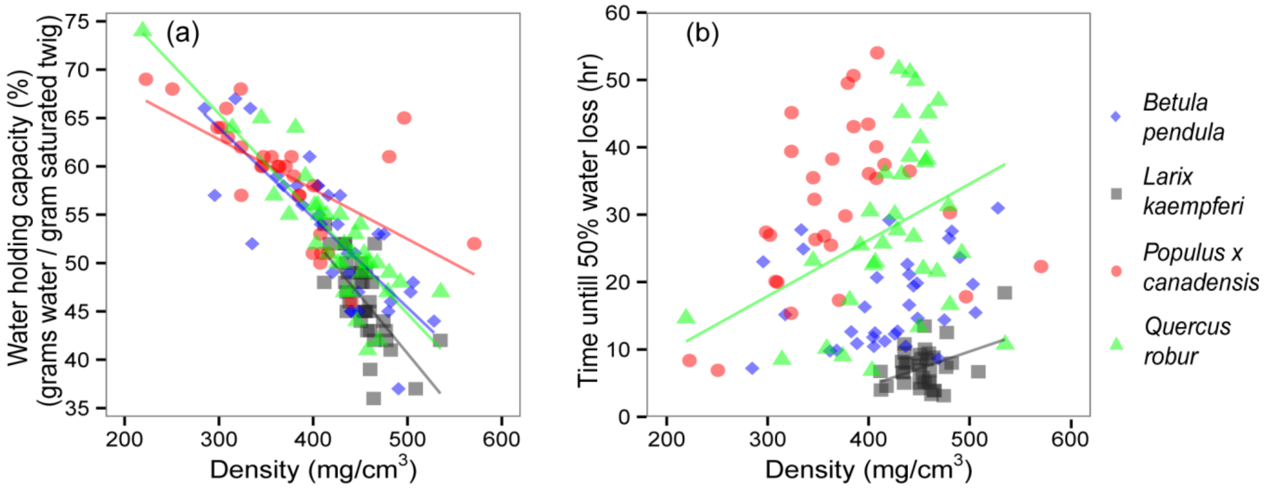


Table 1. Summary of statistics of linear models for water holding capacity (WHC), time until 50% water loss ($t_{(50\%WL)}$) and air dry twig flammability with species, density, and diameter as independent variables; The interaction between species and density was also taken into account; We chose the best model by Akaike information criterion (AIC) in a stepwise algorithm; The best model (the smallest AIC) does not include all factors, as it removed factors that do not contribute significantly to the model.

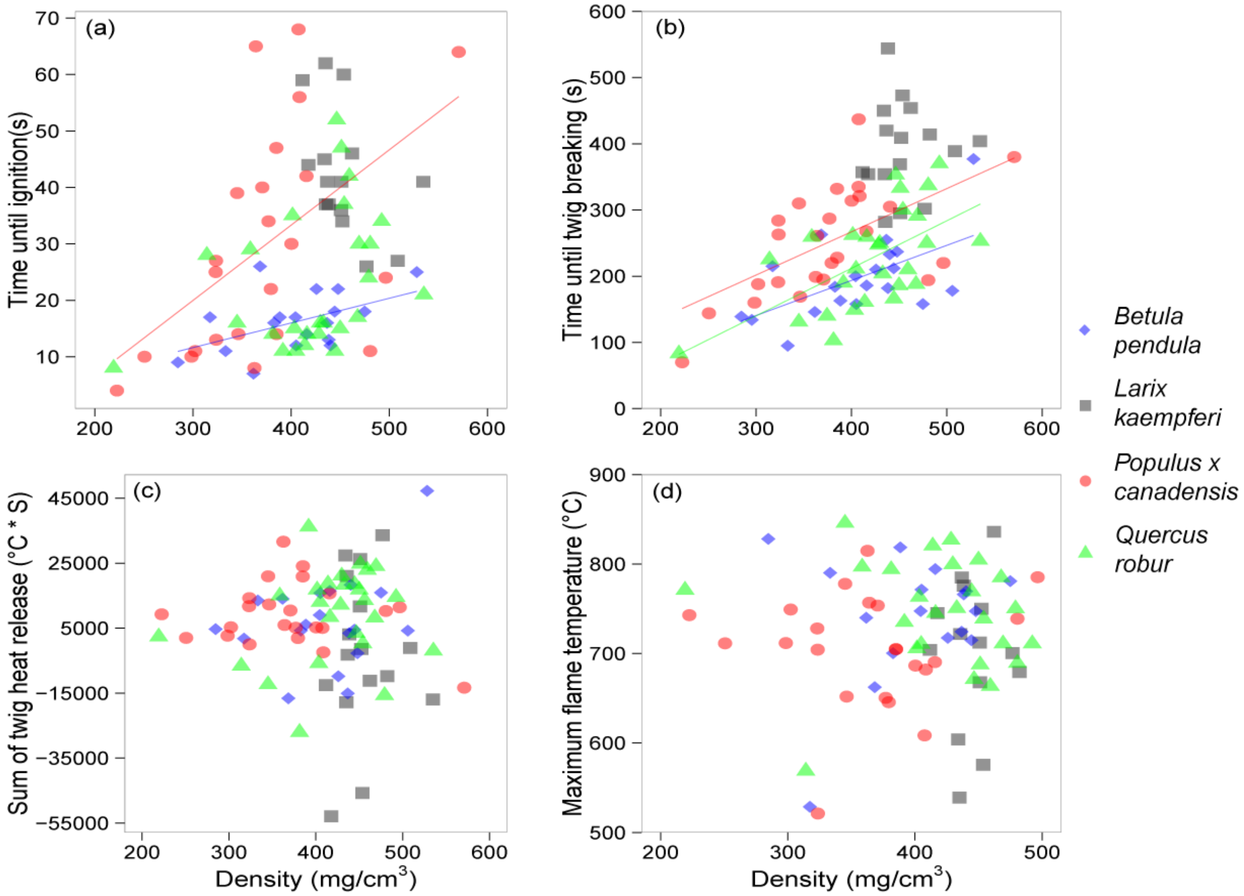
		Water dynamics variables		Flammability variables			
	Measures	**WHC**	$t_{(50\%WL)}$	**Time until ignition**	**Time until twig breaking**	**Sum of twig heat release**	**Max flame temperature**
Species	*Df*	3	3	3	3	3	3
	F	63.8	48.0	13.2	33.1	2.7	3.0
	P	$<2.2 \times 10^{-16}$ ***	$<2.2 \times 10^{-16}$ ***	5.8×10^{-7} ***	4.0×10^{-14} ***	0.05	0.03 *
Density	*Df*	1	1	1	1	-	-
	Coef	−0.091	0.050	0.043	0.627	-	-
	SE	0.012	0.015	0.054	0.111	-	-
	F	171.3	13.4	12.2	32.4	-	-
	P	$<2.2 \times 10^{-16}$ ***	3.77×10^{-4} ***	8.14×10^{-4} ***	1.92×10^{-7} ***	-	-
Diameter	*Df*	1	1	1	1	1	-
	Coef	2.670	−3.269	−0.237	11.18	-1.779×10^{4}	-
	SE	1.153	2.721	6.094	28.36	6.780×10^{3}	-
	F	5.4	1.4	0.1	0.2	6.9	-
	P	0.02 *	0.23	0.75	0.70	0.01 *	-

Table 1. *Cont.*

		Water dynamics variables		Flammability variables			
	Measures	**WHC**	$t_{(50\%WL)}$	**Time until ignition**	**Time until twig breaking**	**Sum of twig heat release**	**Max flame temperature**
Species * Density	*Df*	3	3	3	-	-	-
	F	5.1	0.6	2.6	-	-	-
	P	2.472×10^{-3} **	0.61	0.06	-	-	-
The Best Model	*Df*	123	126	73	82	79	80
	R^2	0.76	0.54	0.39	0.59	0.16	0.07
	SE	3.854	9.146	12.52	6.273	15130	67.20
	F	47.9	31.8	7.5	26.4	3.7	3.1
	P	$<2.2 \times 10^{-16}$ ***	$<2.2 \times 10^{-16}$ ***	3.17×10^{-7} ***	8.63×10^{-16} ***	0.008 **	0.03 *

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 4. Density *versus* flammability variables of air-dried twigs of all four species: (**a**) time until ignition, (**b**) time until twig breaking, (**c**) sum of twig heat release and (**d**) maximum flame temperature; Only significant relationships within species are shown with regression lines (Table 1).



3.3. Interactions between Water Dynamics and Flammability

Decomposed *Quercus robur* twigs lost their water faster and became flammable more rapidly compared to fresh twigs. One hour after saturation, none of the twigs ignited. In contrast, all twigs dried for 72 h ignited within 25 seconds with the low density twigs showing especially quick ignition. A significant relationship between time until ignition and density existed after twigs had dried for 48 h or longer (Table 2, Figure 5a). Drying affected burning time (time until twig breaking) even more strongly than ignition time. The relation between density and burning time steepened as the twigs became drier (Table 2, Figure 5b). In other words, density had a stronger relation with twig flammability as the drying time increased. As twigs became drier, their net heat release increased and a slight negative relation between density and heat release arose in twigs that had dried for 48 and 72 h (Table 2, Figure 5c). No relation between maximum flame temperature and density existed (Table 2, Figure 5d).

Figure 5. Interactive effects of density and water dynamics on flammability variables of *Quercus robur* twigs: (**a**) time until ignition, (**b**) time until twig breaking, (**c**) sum of twig heat release, and (**d**) maximum flame temperature. Points with different shapes and colours represent different drying periods of *Quercus robur* twigs before burning; Only significant relationships within a certain drying period are shown as regression lines (Table 2).

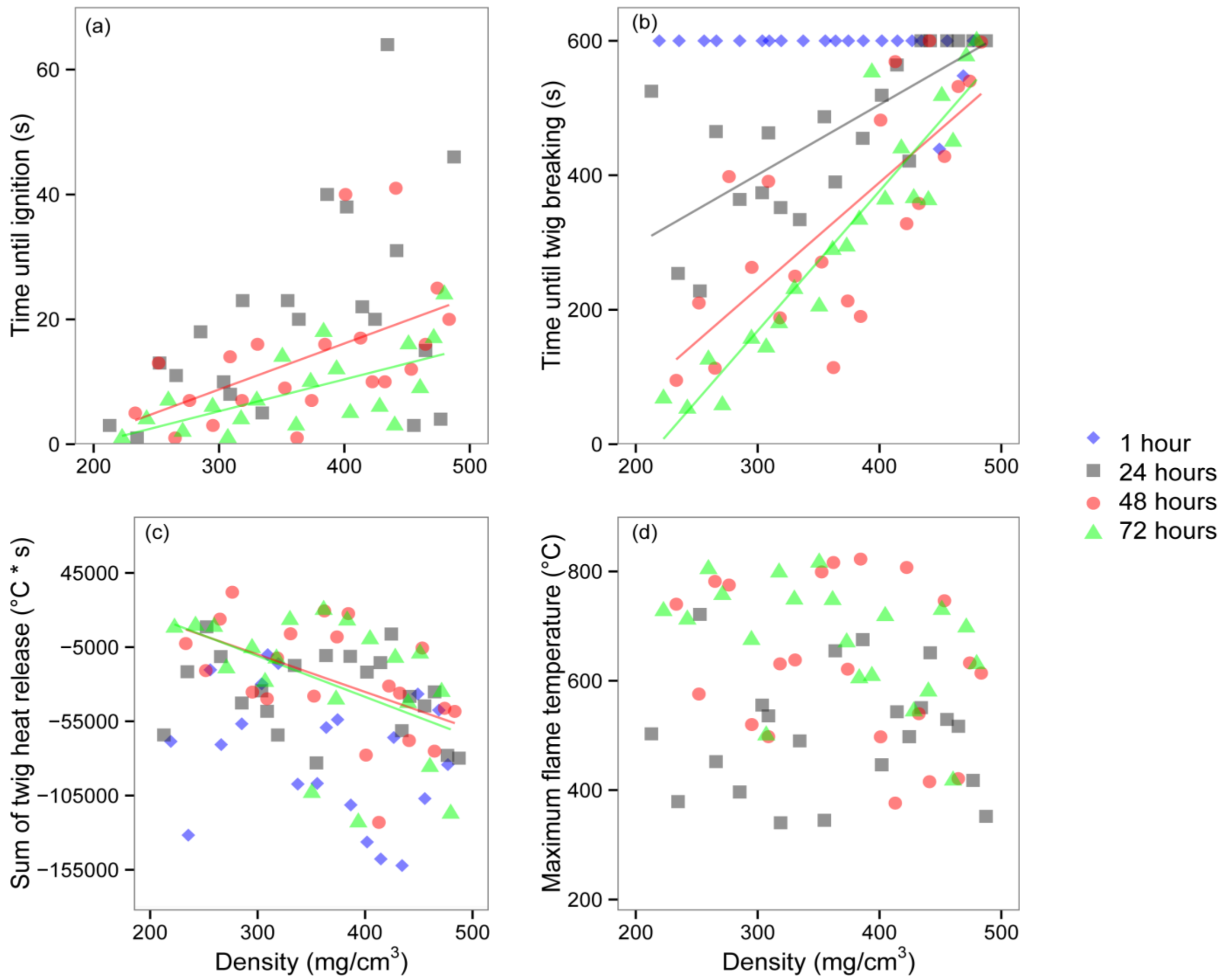


Table 2. Summary of statistics of linear models for flammability variables of *Q. robur* twigs during drying with time, density, and diameter as independent variables; The interaction between time and density was also taken into account; We chose the best model by Akaike information criterion (AIC) in a stepwise algorithm; The best model (the smallest AIC) does not include all factors, as it removed factors that do not contribute significantly to the model.

		Flammability variables			
	Measures	**Time until ignition**	**Time until twig breaking**	**Sum of twig heat release**	**Max flame temp**
Time	*Df*	2	2	3	2
	F	5.2	19.4	8.1	12.3
	P	8.1×10^{-3} **	2.95×10^{-7} ***	8.25×10^{-5} ***	3.17×10^{-5} ***
Density	*Df*	1	1	1	1
	Coef	0.056	1.444	−188.15	−0.268
	SE	0.015	0.126	46.96	0.172
	F	15.0	137.0	17.8	3.0
	P	2.64×10^{-4} ***	$<2.2 \times 10^{-16}$ ***	6.1×10^{-5} ***	0.09
Diameter	*Df*	-	-	-	-
	Coef	-	-	-	-
	SE	-	-	-	-
	F	-	-	-	-
	P	-	-	-	-
Time*Density	*Df*	-	2	-	-
	F	-	3.8	-	-
	P	-	0.03*	-	-
The Best Model	*Df*	63	62	85	63
	SE	10.6	90.2	38610	122.2
	R^2	0.29	0.75	0.33	0.30
	F	8.5	36.7	10.5	9.2
	P	8.39×10^{-5} ***	$<2.2 \times 10^{-16}$ ***	5.61×10^{-7} ***	4.01×10^{-5} ***

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3.4. Twig Chemical Properties

The cellulose concentration was positively related to density (Figure 6a), while the lignin concentration was negatively related (Figure 6b). In other words, as decomposition progressed twigs contained increasingly less cellulose and more lignin, resulting in lower cellulose: lignin ratios (Figure 6c). For all flammability variables except sum of twig heat release, the variance of flammability was mostly explained by their variance in density (structure) instead of their chemical change (Table 3).

Figure 6. Chemical properties of *Quercus robur* twigs selected from the 72 h treatment in the water dynamics experiment. Density has a significantly positive relationship with (**a**) cellulose ($F_{1, 21} = 42.11$, $p < 0.001$, $R^2 = 0.65$) and a significantly negative relation with (**b**) lignin concentration ($F_{1, 21} = 32.32$, $p < 0.001$, $R^2 = 0.59$). Overall, (**c**) the cellulose: lignin ratio is positively related to density ($F_{1, 21} = 53.91$; $p < 0.001$; $R^2 = 0.71$).

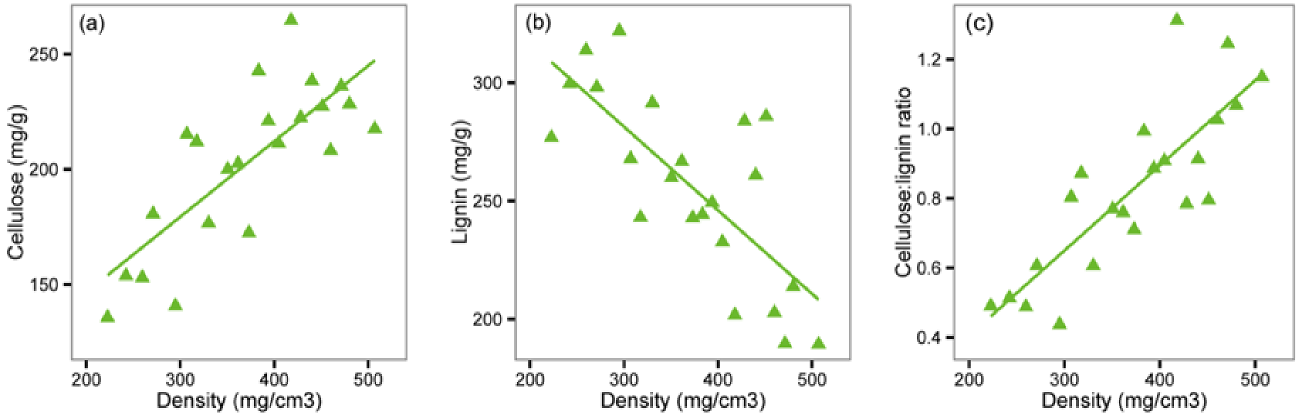


Table 3. Summary of statistics of linear models for flammability variables of *Q. robur* twigs dried 72h from saturation with cellulose: lignin ratio, density and diameter as independent variables; The interaction between cellulose: lignin ratio and density was also taken into account; We chose the best model by Akaike information criterion (AIC) in a stepwise algorithm; The best model (the smallest AIC) does not include all factors, as it removed factors that do not contribute significantly to the model; For the flammability variable "sum of twig heat release", all independent variables we described above were not included in the model with the smallest AIC, so we didn't present any statistics related to this variable in the table.

		Flammability variables			
	Measures	**Time until ignition**	**Time until twig breaking**	**Sum of twig heat release**	**Max flame temp**
Cellulose: Lignin	*Df*	1	1	-	-
	Coef	−17.8	−595.8	-	-
	SE	21.6	284.6	-	-
	F	0.8	0.4	-	-
	P	0.39	0.52	-	-
Density	*Df*	1	1	-	1
	Coef	−0.025	0.597	-	−253.3
	SE	0.042	0.535	-	104.5
	F	15.9	149.2	-	5.9
	P	9.52×10^{-4} ***	1.92×10^{-10} ***	-	0.02 *

Table 3. *Cont.*

		Flammability variables			
	Measures	**Time until ignition**	**Time until twig breaking**	**Sum of twig heat release**	**Max flame temp**
Diameter	*Df*	1	-	-	-
	Coef	−13.72	-	-	-
	SE	8.226	-	-	-
	F	2.2	-	-	-
	P	0.16	-	-	-
Cellulose: Lignin *Density	*Df*	1	1	-	-
	Coef	0.067	1.679	-	-
	SE	0.050	0.675	-	-
	F	1.8	6.2	-	-
	P	0.19	0.02 *	-	-
The Best Model	*Df*	17	19	-	20
	SE	4.750	64.74	-	4.368×10^4
	R^2	0.444	0.874	-	0.189
	F	5.2	51.9	-	5.9
	P	6.45×10^{-3} ***	2.39×10^{-9} ***	-	0.02 *

Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

Decomposition had a range of direct and indirect effects on single twig flammability. As twigs decompose, their woody material is metabolized by invertebrates, fungi, and bacteria [6,30,31]. During this process, wood density decreases and porosity increases [33], with this change affecting flammability both directly and indirectly via the water dynamics of twigs. Consistent with our hypothesis (Figure 1), the change in structure during decomposition is the main factor influencing twig water properties and flammability. In this discussion, we first consider the indirect effects of decomposition through influencing twig water dynamics and then the direct effects of decomposition on twig flammability and the relative strength of those direct and indirect effects.

4.1. Indirect Effects of Decomposition on Flammability via Twig Water Dynamics

During wood decomposition, *i.e.*, density loss, there is an increase in the proportion of internal empty spaces, which may be filled with water during wet periods, thereby increasing twig water holding capacity (Figure 3a). However, fire is not likely to occur shortly after rain, and our experiments showed that this increased water content is quickly lost (Figure 3b), so the increased water holding capacity of decomposed twigs is unlikely to be a major factor in wildfires.

The progression of decomposition likely allows water to evaporate faster owing to the increased contact between air and water inside twigs and also possibly owing to damage to the sealing properties of bark [39]. These two processes are highly dependent on decomposition stage and have a considerable influence on the flammability of twigs. In our experiment, more decomposed twigs became more flammable in a shorter period (Figure 5). In natural environments, partly decomposed woody materials may become flammable sooner after the last rain event compared to fresh materials. In our experiment, this effect lasted for roughly seven to nine days, but this timeframe is dependent on both the specific temperature and humidity of the drying conditions and the diameter of the twigs used. For larger diameter woody debris in cooler and/or more humid conditions, this non-flammable period likely lasts longer.

4.2. Direct Effects of Decomposition on Flammability

A decrease in density also has a direct effect on flammability. Within a partly decomposed, low-density twig, surface-to-volume ratio and fuel-air interaction are higher, both factors that correlate strongly in other fuel types with quicker ignition and faster fire spread [17,19,40]. Our data show that twig ignition and burning time are considerably affected by decomposition: decomposed twigs ignite and burn faster after a certain time of wetting event or at given water content (Figures 3 and 5).

Flammability is a comprehensive term that consists of multiple specific fire measures contributing to fire dynamics in distinct ways. Ignition and burning time of twigs affect fire spread, because a quick ignition and burning may relate to the fast spread of fire, while maximum flame temperature and heat release may be subscribed more to the intensity of fire. We found no effect of decomposition on heat release or maximum flame temperature; this contrasts with our expectation that undecomposed twigs would release more heat due to higher fuel quantities per unit fuel bed volume [41]. This surprising result may be explained by the higher fuel quantity being counter-balanced by negative effects of high density and moisture content of fresh twigs: fresh plant litters may need more energy input to evaporate water before they contribute to fire compared to more decomposed ones [42,43]. In addition, the lack of a relationship between density and flame temperature suggests that decomposed twigs may promote fire more in the phase of fuel ignition and early fire spread.

Decomposition changes not only twig structure but also chemical properties. Our data is consistent with previous evidence that cellulose is broken down faster than lignin, which reduces the cellulose: lignin ratio through decomposition (Figure 6) [44]. This lower cellulose: lignin ratio might be expected to reduce flammability, because lignin requires higher temperatures for volatilization during combustion than cellulose [45,46]. However, the increase in flammability of decomposed compared to fresh *Q. robur* twigs in our study suggest that the change in structure is the driving factor for the increased flammability and exceeds the possible negative effects of the reduction in the cellulose: lignin ratio (Table 3).

4.3. Interactions between Direct and Indirect Effects of Decomposition on Flammability

One hour after saturation none of the twigs were able to ignite or burn. However, after a longer period of drying, a stronger relation appeared between density and ignition and burning time (Figure 5), suggesting a strong interaction between the direct effect of structure (density) and its indirect effect via twig water dynamics (water loss) on twig flammability. Therefore, the hypothesis that the indirect effect of structure through water dynamics is less than direct effects of structure should probably be altered: the effect sizes appear to be close to equal especially during the after-rain drying period.

4.4. Importance of Decomposing Twigs during Fires

The effect shown here, that decomposed twigs are generally more flammable than fresh twigs, should be interpreted in light of fuel architecture. As twigs decompose, they become more flammable, which could be important in early stage fires, because fine surface fuels (leaves and twigs (diameter < 6 mm)) are the most flammable fuel type, easily consumed by fire and therefore, contribute to spreading and forward movement of fires [22,47,48]. Thus, decomposed twigs could be important for the easier and faster transition from a small fire of leaves and fine twigs to large fires that include coarse wood and living parts of plants. However, our single twig fire results alone cannot be scaled up to stand level fire properties without also considering the effects of fuel bed depth and structure. Large amounts of tightly packed fine litter may in some circumstances inhibit ignition and early fire spread owing to lack of oxygen supply to the fuel [16]. The extent to which such a smothering effect of fine litter packing might be lessened by the more porous structure of the partly decomposed fuel particles themselves would be a relevant next focus of study.

Decomposed twigs as a ground fuel mainly contribute to horizontal fire spread, while dead branches and twigs attached to the tree may support fire spread up trees and allow expansion from surface to crown fires [40]. The fact that no effects of decomposition on maximum flame temperature and heat release were found in our experiments, may suggest that decomposed woody material has a small influence on fire intensity, but could play an important role in the horizontal and vertical spread of fire.

In semi-arid shrublands and woodlands, during rainless seasons, photodegradation instead of microbial decomposition could be a dominant control on above-ground litter decomposition due to the open canopy and intense solar radiation [21,49–51]. Ultraviolet radiation can increase litter lignin loss [50] and this change in photodegraded litter may also greatly increase litter flammability and influence fire behaviors in those highly flammable systems.

5. Conclusions

In conclusion, our data suggest that partly decomposed twigs are more flammable than freshly senescent, undecomposed twigs: they ignite quicker and burn faster. The increased flammability of decomposed twigs is mainly due to their lower density and therefore increased fuel-air interactions. Our results suggest that when lying on the ground, partly decomposed fine woody fuels may promote horizontal spread of surface fires, while still attached to the plant, fine woody fuels can act as a fuel ladder that allows a surface fire to reach the canopy. The interaction between decomposition and twig flammability shown in our study adds a brand-new dynamic to our understanding of fire behaviors of woody ecosystems, albeit a dynamic that needs to be confirmed in field experiments. To further our understanding of decomposition effects on fires and its underlying mechanisms, it would be essential to extend the results from burns of single twigs in controlled conditions to other fuel types like branches and to single and mixed fuel types in a variety of architectures. However, we believe that our findings add conceptual and empirical knowledge towards a better understanding of forest carbon storage and release.

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Author Contributions

Weiwei Zhao, Luke G. Blauw, William K. Cornwell, and Johannes H. C. Cornelissen designed the experiments. Weiwei Zhao, Luke G. Blauw, and Richard S. P. van Logtestijn prepared and carried out the experiments. Weiwei Zhao, Luke G. Blauw, William K. Cornwell, and Johannes H. C. Cornelissen analyzed and interpreted the data. Weiwei Zhao, Luke G. Blauw, Richard S. P. van Logtestijn, William K. Cornwell, and Johannes H. C. Cornelissen prepared the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

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