



Soil heating during wildfires and prescribed burns: a global evaluation

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ABSTRACT

Background. Fires can alter soil properties via downward heat transfer. Numerous studies have examined effects of wildfires and prescribed burns on soils, yet knowledge of the soil temperatures and durations reached is limited. This can lead to erroneous assumptions regarding fire impacts, especially when laboratory heating results are extrapolated to field conditions. **Aims and methods.** We compiled new and published data on maximum temperatures and heating durations for mineral soils during wildfires and prescribed burns in forests, shrublands and grasslands around the globe, and compared these with data from laboratory heating experiments.

Key results. Most fires heated only the uppermost centimetres of the soil, rarely exceeding 300°C below 0.5 cm depth. Where 300°C was exceeded at the soil surface, heat pulses were shorter (<500 s) than those often applied in laboratory studies (30 min to 1 h). The highest soil-surface temperature occurred in a shrubland wildfire (~964°C), and longest heating durations in forests with deep duff layers (>3 h above 60°C). **Conclusions and implications.** Most fires, except in deep smouldering fuels, generate short and shallow soil heating. Laboratory studies with long heating durations rarely represent field conditions. When investigating fire effects on soil, inclusion of shallow near-surface layer samples is recommended.

Keywords: burn severity, fire effects belowground, flame temperature, heat transfer, heating duration, mineral soils, soil heating, soil organic matter, soil temperature, thermocouples.

Introduction

Downward heat transfer from the combustion of live and dead fuels during vegetation fires can change the physical, chemical and biological characteristics of soils (DeBano *et al.* 1979; Certini 2005). The magnitude of these changes is conditioned by the amount of heat transferred, which is often expressed in the form of maximum temperature thresholds exceeded. For example, mortality of soil biota (microbes, fungi, invertebrates) as well as cambium cells, roots and seeds has been suggested to occur above a threshold of ~60°C, a complete loss of free soil water is associated with temperatures above 100°C, and organic matter combustion becomes prevalent above 300°C (see reviews by Certini 2005; Santín and Doerr 2016). The maximum temperatures reached and the duration for which the soil exceeds a specific threshold during a fire will depend on several factors related to fire behaviour, soil type and environmental conditions. Fire behaviour, and more specifically the rate and total of heat energy released at a given point, are determined by fuel characteristics, weather and topography (Keeley 2009). Importantly, estimates of heat release such as fireline intensity (Keeley 2009) or fire radiative power and fire radiative energy (Wooster *et al.* 2005), or measures of temperatures recorded by devices placed in flames reached above ground, do not necessarily reflect downward heat transfer and associated potential changes of soil properties (Hartford and Frandsen 1992; Stoop *et al.* 2013). Owing to its porous structure, soil is a poor conductor of thermal energy, limiting downward heat transfer (DeBano 2000). A high water content

Received: 1 May 2025

Accepted: 24 October 2025

Published: 27 November 2025

Cite this: Doerr SH *et al.* (2025) Soil heating during wildfires and prescribed burns: a global evaluation. *International Journal of Wildland Fire* **34**, WF25103.

[doi:10.1071/WF25103](https://doi.org/10.1071/WF25103)

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increases a soil's thermal conductivity and facilitates deeper heat penetration, but the temperature at a given point in the soil will not exceed 100°C until the local soil water has evaporated (Campbell *et al.* 1995; Stoop *et al.* 2011; Robichaud *et al.* 2025). Moreover, in addition to temperatures reached, several studies, including those examining the extreme case of stationary slash pile burns that can lead to substantial and deep soil heating (e.g. Massman *et al.* 2010), have demonstrated that the duration of heating is also critical in determining its effect on the underlying soil. Thus, slow-moving low-intensity fires can often have a greater effect on soil than fast-moving fires with high fire intensities (Hartford and Frandsen 1992; Doerr *et al.* 2010; Girona-García *et al.* 2019).

The findings on the effects of wildland fires on *in situ* soils in the field and of heat treatments applied to soil in the laboratory, including the temperature thresholds above which specific effects are suggested to occur, have been the subject of a series of reviews (Giovannini 1994; Doerr *et al.* 2000; Certini 2005; Neary *et al.* 2005; Shakesby and Doerr 2006; Mataix-Solera *et al.* 2011; Santín and Doerr 2016; Certini *et al.* 2021). However, a comprehensive evaluation of actual temperatures reached in mineral soils and their duration during wildland fires has been lacking to date. As a result, it remains unclear how closely heat treatments applied in the laboratory and the associated thresholds reported match the actual temperatures and heating durations reached in wildland fires.

To address this research gap, we evaluate published and new data on maximum soil temperatures reached (T_{\max}) and heating duration above the widely used threshold temperatures of 60, 100 and 300°C recorded in the field during prescribed burns and wildfires for a wide range of ecosystems globally. Given that fire behaviour (e.g. smouldering vs flaming, burn duration or residence time, energy and heat release rates), downward heat transfer and the resulting fire impacts on soil (i.e. soil burn severity; Parsons *et al.* 2010) can vary substantially within a burned area (Keeley 2009), we focus here on the recorded temperature extremes and associated heating durations above critical threshold temperatures to provide insights into the upper limits that might be expected under the different types of fires examined. Thus, we provide, to our knowledge, the first comprehensive compilation and analysis of maximum temperatures and durations above commonly used threshold temperatures obtained from wildland and prescribed fires. These are grouped into major fuel types and specific soil depths, and also compared with those applied in laboratory heating experiments in previous studies used to examine fire effects on soils.

Methods and data

We compiled and examined soil temperature data collected in the field at the mineral soil surface and at specific mineral

soil depths during wildland fires around the world (Table 1; Fig. 1). These include both prescribed burns in unmodified fuels (e.g. ecological burns, fuel reduction burns, underburns, broadcast burns) and wildfires (natural, human-caused and experimental) as specified below. Contextual data such as dominant vegetation (i.e. main fuel type including dominant plant species) and, where provided, fuel consumption (or fuel load) ($t\ ha^{-1}$), flame length (m), soil moisture (%) and maximum temperatures measured by thermocouples in the litter layer or above ground (e.g. sometimes termed 'fire temperatures' (Bova and Dickinson 2008)) were also extracted (Supplementary Table S1). Fuel moisture content (%) and fireline intensity ($kW\ m^{-1}$) were rarely stated and hence not compiled.

A series of detailed studies have been conducted under field conditions on pile burns or other artificial fuel beds (e.g. Massman *et al.* 2010; Busse *et al.* 2013), but these were excluded from the present study as they are not representative of the spatially more extensive wildland fire fuels. Studies examining temperatures in organic instead of mineral soils, which often burn as smouldering ground fires consuming entire soil layers (e.g. Grau-Andrés *et al.* 2018), were also excluded.

We confined our analysis to data collected with thermocouples given that other data collection approaches, such as the use of different thermosensitive paints or other proxies, provide only broad temperature categories rather than more specific temperatures and do not offer temporally resolved data that reflect the duration of heating (Iverson *et al.* 2004; Bova and Dickinson 2008).

The data were categorised by fire type, vegetation type, maximum temperature and period above a specific threshold for a given soil depth as follows:

Fires were classified as (i) wildfires: including data from experimental wildfires in undisturbed natural fuels with fire behaviour comparable with that of an actual wildfire and, also, rare opportunistic data from actual wildfires collected by deploying thermocouple sensors in advance of a fire front; or (ii) prescribed burns: controlled fires carried out for management purposes, typically conducted under mild fire weather according to a specific burning prescription (Pausas and Keeley 2019).

The dominant vegetation types (i.e. fuels) were grouped into three categories: grass, shrub and forest. In addition to these three categories, on data inspection, the forest data showed a cluster of western USA conifer forest sites dominated by very long durations ($>15,000$ s) above 60°C. These sites were characterised by high to extreme surface fuel (i.e. the amount of plant material overlying the soil that acts as fuel) consumption, ranging from 28 to 306 $t\ ha^{-1}$ and composed mainly of duff (i.e. the fermentation and humus layers as defined in Robichaud and Miller (1999)), and downed fuels in a various fuel size classes. To facilitate data display and description, these western USA forest sites with substantial duff layers were therefore grouped into a separate forest subcategory called 'forest with deep duff'.

Table 1. Field studies using thermocouples to determine soil temperatures during wildfires and prescribed burns in natural fuel beds. Studies are grouped by fire and dominant vegetation type (F, forest; FD, forest with deep duff; S, shrubs; G, grass). NF, National Forest. n.s., no data or not stated. Pers. comm. refers to new unpublished data by members of the author team. Note: 3600 s equals 1 h; 14,400 s equals 4 h; 72,000 s equals 20 h.

Fire type	Veg. group	Dominant vegetation	Max. soil temperature (°C)	Max. duration of near-surface temperature (s)			Soil depths monitored (cm)	Max. above-ground T (°C); (height above ground; cm)	Country/region	Province/location	Publication/source
				>60°C	>100°C	>300°C					
Wildfire and experimental wildfire	F	Eucalyptus (<i>E. dumosa</i>)	120	6900	1200	0	1–10	–	SE Australia	Yatong reserve	Bradstock <i>et al.</i> (1992)
	F	Eucalyptus (<i>E. gummifera</i>)	145	1080	0	0	0.5–12	–	SE Australia	Blue Mountains	Bradstock <i>et al.</i> (1992)
	F	<i>Abies concolor</i> , <i>Pinus lambertiana</i>	106	22,200	5400	0	5–15	–	USA California	Lassen FF	Dickinson <i>et al.</i> (2024)
	F	<i>Pseudotsuga menziesii</i> , <i>P. ponderosa</i>	65	7800	0	0	5–15	–	USA California	Klamath NF	Dickinson <i>et al.</i> (2021)
	F	Mixed conifer (incl. <i>Pinus sabiniana</i>)	70	11,400	0	0	5–15	–	USA California	Klamath NF	Dickinson <i>et al.</i> (2020)
	F	Mixed dry eucalyptus	58	0	0	0	1	889 (2)	SE Australia	Warragamba	Doerr and Santin (pers. comm.)
	F	<i>Pinus banksiana</i> , <i>Picea mariana</i>	31	0	0	0	0.5	899 (6)	NW Canada	Ft Providence	Doerr and Santin (pers. comm.)
	F	<i>Pinus banksiana</i> , <i>Populus tremuloides</i>	380	400	300	170	0	320 (20)	E Canada	Ontario	Smith and Sparling (1966)
	F	<i>Pinus banksiana</i> , <i>Picea mariana</i>	85	900	0	0	0.5	698 (2)	NW Canada	Fort Smith	Doerr and Santin (pers. comm.)
	FD	<i>Pinus ponderosa</i>	85	58,800	0	0	10–15	–	USA California	Plumas NF	Dickinson <i>et al.</i> (2019)
	FD	<i>Tsuga heterophylla</i>	87	113,400	0	0	5–15	–	USA California	Willamette NF	Dickinson <i>et al.</i> (2023)
	FD	<i>Pinus contorta</i>	123	10,695	1980	0	1–4	–	W USA	Little Hogback	Robichaud <i>et al.</i> (2018)
	FD	<i>Pinus contorta</i>	185	15,900	8175	0	1–4	–	W USA	Lolo peak	Robichaud <i>et al.</i> (2018)
	FD	<i>Tsuga heterophylla</i>	61	210	0	0	2–4	–	W USA	Strychnine	Robichaud <i>et al.</i> (2018)
	FD	<i>Pseudotsuga menziesii</i>	196	25,269	11,499	0	1–4	–	W USA	Cougar	Robichaud <i>et al.</i> (2018)
	S	<i>Rosmarinus officinalis</i>	710	4200	1200	0	0	–	E Spain	Ayora	Baeza <i>et al.</i> (2014)
	S	Mixed shrub (<i>Rhamnus lycioides</i>)	677	n.s.	n.s.	n.s.	0	–	E Spain	Valencia	Gimeno-García <i>et al.</i> (2004)
	S	Mediterranean shrub	702	1320	480	300	0–5	–	E Spain	Alicante	Mataix-Solera (1999)
	S	<i>Ulex parviflorus</i> , <i>Rosmarinus officinalis</i>	450	n.s.	2100	n.s.	0.5	–	E Spain	Valencia	Molina and Llinares (2001)
	S	<i>Ulex parviflorus</i> , <i>Rosmarinus officinalis</i>	350	n.s.	1800	n.s.	0.5	–	E Spain	Valencia	Molina and Llinares (2001)
	S	Chaparral (<i>Adenostoma fasciculatum</i>)	964	2400	900	300	0–2	–	USA California	Vandenberg Air Force Base	Odion and Davis (2000)
	S	<i>Cistus albidus</i> , <i>Rosmarinus officinalis</i>	78	120	0	0	1	–	E Spain	Valencia	Santana <i>et al.</i> (2011)
	S	<i>Erica umbellata</i> , <i>E. cinerea</i>	800	234	n.s.	114	0	–	Portugal	Valtorto	Stoof <i>et al.</i> (2013)
	S	<i>Quercus coccifera</i>	250	n.s.	n.s.	0	0–5	700 (100)	S France	St Gély-du-Fesc	Trabaud (1979)
	G	<i>Aristida</i> spp.	135	1000	420	0	0.5	–	USA Florida	Olustee exp. Forest	Heyward (1938)
	G	<i>Hyparrhenia hirta</i> , <i>Ampelodesmos mauritanicus</i>	480	n.s.	300	n.s.	0	–			Novara <i>et al.</i> (2013)
	G	<i>Themeda triandra</i> , <i>Urochla mosambicensis</i>	53	0	0	0	1	560 (2)	South Africa	Satara	Santin and Doerr (pers. comm.)
	G	<i>Hyperthelia dissoluta</i> , <i>Themeda triandra</i>	93	40	31	0	1	780 (2)	South Africa	Mooniplas	Santin and Doerr (pers. comm.)
	G	<i>Bothriochloa radicans</i>	269	218	50	0	1	780 (2)	South Africa	Mopane	Santin and Doerr (pers. comm.)
	G	<i>Prosopis glandulosa</i>	240	325	n.s.	0	0	–	USA Texas	Rolling plains	Stinson and Wright (1969)
	G	<i>Spinifex</i> spp.	366	2820	n.s.	n.s.	0–4	–	NW Australia	Haast Bluff	Wright and Clarke (2008)

(Continued on next page)

Table 1. (Continued)

Fire type	Veg. group	Dominant vegetation	Max. soil temperature (°C)	Max. duration of near-surface temperature (s)			Soil depths monitored (cm)	Max. above-ground T (°C); (height above ground; cm)	Country/region	Province/location	Publication/source
				>60°C	>100°C	>300°C					
Prescribed burn	F	<i>Quercus frainetto</i>	27	0	0	0	2	720 (–)	S Italy	Rugia	Carra et al. (2021)
	F	<i>Pinus pinaster</i>	23	0	0	0	2	712 (–)	S Italy	Calamacia	Carra et al. (2021)
	F	<i>Castanea sativa</i>	29	0	0	0	2	645 (–)	S Italy	Orgaro	Carra et al. (2021)
	F	Mixed dry eucalyptus	238	30	20	3	0	–	SE Australia	Upper Yarra	Cawson et al. (2016)
	F	<i>Pinus palustris</i>	224	604	278	0	0	–	SE USA	Eglin Air Force Base	Dickinson (pers. comm.)
	F	Mixed dry eucalyptus	50	0	0	0	1	898 (520)	W Australia	Manjimup	Doerr and Santin (pers. comm.)
	F	<i>Pinus pinaster, Juniperus oxycedrus</i>	26	0	0	0	0	149 (30)	SE Spain	Albacete	Fajardo-Cantos et al. (2023)
	F	<i>Pinus ponderosa</i>	200	5000	n.s.	0	2	750 (15)	California	Kings Canyon NP	Keeley and McGinnis (2007)
	F	<i>Pinus pinaster</i>	104	n.s.	29	0	0	–	Central Spain	–	Merino et al. (2019)
	F	<i>Pinus nigra</i>	47	0	0	0	0	–	Central Spain	–	Merino et al. (2019)
	F	<i>Pinus pinaster, Pinus halepensis</i>	42	0	0	0	0	160 (2)	Spain	Castilla-La Mancha	Plaza-Álvarez et al. (2021)
	F	<i>Shorea obtusa, S. siamensis</i>	373	678	300	n.s.	0–5	–	Thailand	Huay Kha Khaeng	Wanthonchai et al. (2008)
	FD	<i>Sequoiadendron giganteum</i>	113	64,800	0	0	5–46	–	USA California	Kings Canyon	Haase and Sackett (1998)
	FD	<i>Pinus lambertiana</i>	369	93,600	n.s.	n.s.	5–46	–	USA California	Kings Canyon	Haase and Sackett (1998)
	S	<i>Echinospartum horridum</i>	397	1500	1300	0	0	–	NE Spain	Huesca	Armas-Herrera et al. (2016)
	S	<i>Echinospartum horridum</i>	812	1319	950	450	1–2	–	NE Spain	Huesca	Alfaro-Leranuz et al. (2023)
	S	Quercus spp. shrubs	628	2100	1200	180	0–2	–	USA Florida	Ocala	Carrington (2010)
	S	Quercus spp. shrubs	621	900	360	60	0–2	–	USA Florida	Archbold	Carrington (2010)
	S	Barrens (<i>Pinus banksiana</i> understory)	438	162	186	100	0	–	USA Wisconsin	Moquah Barrens	Dickinson and Miesel (pers. comm.)
	S	Barrens (<i>Populus tremoides</i> understory)	132	200	66	0	0	–	USA Wisconsin	Moquah Barrens	Dickinson and Miesel (pers. comm.)
	S	Barrens (<i>P. banksiana</i> understory)	75	80	0	0	0	–	USA Wisconsin	Moquah Barrens	Dickinson and Miesel (pers. comm.)
	S	<i>Erica umbellata</i>	209	0	0	0	0–5	625 (2)	NW Spain	Dòzon	Fernández et al. (2008)
	S	<i>Erica australis</i>	46	0	0	0	0–2	765 (90)	NW Spain	Orense	Fernández et al. (2013)
	S	<i>Pterospartum tridensatum</i>	53	0	0	0	0–2	814 (60)	NW Spain	Orense	Fernández et al. (2013)
	S	<i>Cystus oromediterraneus</i>	151	n.s.	n.s.	0	0–2	908 (91)	Central Spain	Avila	Fernández et al. (2018)
	S	<i>Echinospartum horridum</i>	768	905	560	325	0–3	–	NE Spain	Asin de Bronto	Girona-García et al. (2019)
	S	<i>Echinospartum horridum</i>	438	1650	750	150	0–3	–	NE Spain	Buisan	Girona-García et al. (2019)
	S	<i>Echinospartum horridum</i>	595	310	230	90	0–4	–	NE Spain	Yebra de Basa	Girona-García et al. (2019)
	S	<i>Cistus oromediterraneus</i>	151	n.s.	n.s.	0	0–2	–	Central Spain	n.s.	Merino et al. (2019)
G		<i>Festuca altaica</i>	44	0	0	0	1	292 (20)	Canada	Saskatchewan	Archibald et al. (2003)
G		<i>Heteropogon contortus</i>	250	120	100	0	0–4	–	E Australia	SE Queensland	Tothill and Shaw (1968)

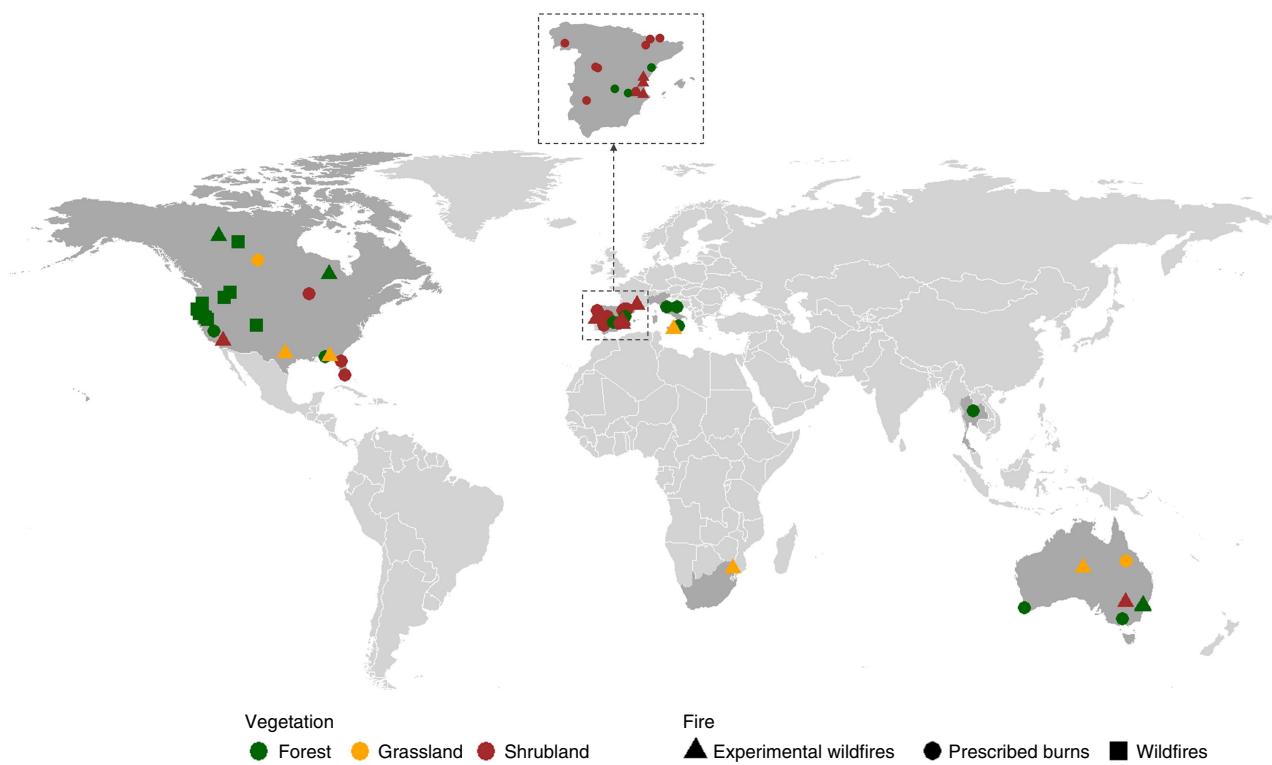


Fig. 1. Location of the fires included in this study ($n = 55$), indicating vegetation (fuel) type burned (colour of the markers) and type of fire (shape of the marker). Darker-shaded countries represent those for which data were available. Spain is enlarged to allow better representation of data location.

Regarding temperature, we extracted maximum temperature (T_{\max} or mean T_{\max} where only the latter was given) for a given soil depth and, where available, the maximum duration for which the temperature remained above a specific threshold. The thresholds were 60°C (notable biological damage), 100°C (vaporisation of soil water) and 300°C (organic matter combustion becomes prevalent) as discussed in Santín and Doerr (2016) and outlined in the introduction.

Soil depth data were grouped to the nearest 0.5 cm from the mineral soil surface (0 cm) to 5 cm depth. One study (Haase and Sackett 1998) in the 'forest with deep duff' category reported data only from depths below 5 cm, but reaching down to 47 cm. These results were included but are discussed separately given they cover greater depths.

The resulting wildland fire dataset is a combination of all published data we were able to identify and new unpublished data (Table 1). The full dataset is available in Supplementary Table S1. All values from published data were extracted directly from the text or tables, or estimated from graphs in a consistent manner insofar as possible. New data presented here include data collected by some of the authors of this study that have not been published explicitly in the peer-reviewed literature. Locations, fire and site characteristics are summarised in Table 1. These include experimental wildfires in forest (Australia, Canada), savanna grasslands (South Africa), Mediterranean shrubland (Spain), wildfires in forest

and shrubland (western USA) and prescribed fires in eucalyptus (Australia) and pine forest (western USA). In each of these studies, arrays of high-temperature thermocouples were placed at specific depths in the mineral soil and the temperature was recorded using heat-protected dataloggers.

In addition, to examine how heat pulses from actual fires compare with those generated in laboratory experiments, we also performed a thorough review of laboratory studies published in the peer-reviewed literature that aimed at simulating the heating effects of fire on soil. We classified these experiments in two major groups: (i) experiments heating the sample homogeneously mainly in muffle furnaces, ovens, or stoves (e.g. Badía and Martí 2003a, b; García-Corona *et al.* 2004; Stoof *et al.* 2010); and (ii) those involving surface heating using tools such as blowtorches, lamps, or burners (e.g. Fox *et al.* 2007; Zavala *et al.* 2009; Badía *et al.* 2017; Pereira *et al.* 2023). For each study and heat treatment, we extracted the temperature ranges applied (minimum and maximum) and their durations, as well as the depth (i.e. thickness) of the soil sampled in the field for these experiments (Table 2).

Results

The dataset compiled includes information from a total of 55 fires, 35 from published data, with the first one published

Table 2. Characteristics of heating treatments carried out in published laboratory studies aimed at simulating the effect of wildland fire on soil (heating from above: $n = 26$; heating the entire sample: $n = 51$). Where more than one heating temperature and duration value was stated in a given study, the ranges (maximum and minimum values) are given. Soil depth is the depth over which the sample used was taken in the field. A single depth range indicates that a sample representative of that depth was used. Multiple depth ranges for a given study mean that samples from those depths were heated separately. n.s., not stated.

Heating treatment	Heating method	Temperatures applied (°C)	Duration of heating (s)	Soil sample depths used (cm)	Publication
Heating the soil surface	Blowtorch	n.s.	900	0–6.5	Badía et al. (2017)
	Blowtorch	n.s.	>3600	0–15	Badía-Villas et al. (2014)
	Blowtorch	132	3600	n.s.	Escobedo et al. (2024)
	Blowlamp	n.s.	180–540	0–15	Kupka et al. (2022)
	Blowlamp	n.s.	60–120	0–8	Llovet et al. (2008)
	Burning litter on surface	n.s.	>3600	0–20	Busse et al. (2010)
	Burning litter on surface	250–300	900	Bulk sample 5 cm deep	Keesstra et al. (2014)
	Burning needles on surface	150	n.s.	Bulk sample 4 cm deep	Fox et al. (2007)
	Combustion wind tunnel	n.s.	n.s.	0–25	Merino et al. (2018)
	Digital heating gun	200–500	2400	0–10	Wieting et al. (2017)
	Electric radiant heater	100–450	2400	0–7	Zavala et al. (2010)
	Heat lamps	100–600	150–558	0–10	Brucker (2023)
	Infrared lamps	100–400	n.s.	Bulk sample 4 cm deep	Barreiro et al. (2020)
	Infrared lamps	200–434	n.s.	0–15	Cancelo-González et al. (2012)
	Infrared lamps	100–400	n.s.	Bulk sample 4 cm deep	Cancelo-González et al. (2014)
	Infrared lamps	n.s.	900	0–10	DeBano and Klopatek (1988)
	Infrared lamps	94	900	Bulk sample 10 cm deep	Klopatek et al. (1988)
	Infrared lamps, propane torch and radiant propane heater	n.s.	>3600	0–30	Reardon et al. (2007)
	Insulated manifold	n.s.	960–1200	0–5, 5–10, 10–15	Pattinson et al. (1999)
	Mass loss calorimeter	337	120	0–10	Johnson et al. (2024)
	Propane burner	n.s.	300	Bulk sample 2.5 cm deep	Stoof et al. (2010)
	Propane heater	100	n.s.	0–15.5	Campbell et al. (1995)
	Propane torch	n.s.	n.s.	0–10	Abdulraheem et al. (2021)
	Propane torch	n.s.	15	Bulk sample 8 cm deep	Hatten and Zabowski (2010)
	Radiant propane heater	100–500	>3600	0–30	Robichaud and Hungerford (2000)
Homogeneous sample heating	Furnace	250–850	1500	0–1	Tuhy et al. (2021)
	Muffle furnace	100–200	2700	0–10	Adkins and Miesel (2021)
	Muffle furnace	25–500	1800	0–15	Badía and Martí (2003a)
	Muffle furnace	150–500	1800	0–15	Badía and Martí (2003b)
	Muffle furnace	150–450	7200	1–5	Bahureksa et al. (2022)
	Muffle furnace	50–500	1800	0–10	Bárcenas-Moreno and Bååth (2009)
	Muffle furnace	100–500	300–1800	0–5	Blank et al. (1994)
	Muffle furnace	220–500	120	0–5	Campo et al. (2011)
	Muffle furnace	225–500	7200	0–5	Cawley et al. (2017)
	Muffle furnace	160–380	1800	0–10	Choromanska and DeLuca (2002)
	Muffle furnace	300–900	300–1200	n.s.	DeBano and Krammes (1966)
	Muffle furnace	250–400	300–2400	0–2.5	Doerr et al. (2004)
	Muffle furnace	200–850	7200	0–2.5	Fajković et al. (2022)

(Continued on next page)

Table 2. (Continued)

Heating treatment	Heating method	Temperatures applied (°C)	Duration of heating (s)	Soil sample depths used (cm)	Publication
	Muffle furnace	200–600	7200	0–5	Filimonenko <i>et al.</i> (2024)
	Muffle furnace	170–460	1800	0–5	García-Corona <i>et al.</i> (2004)
	Muffle furnace	100–500	120–900	0–10	Glass <i>et al.</i> (2008)
	Muffle furnace	200–500	10,800	O horizon	Gorbach <i>et al.</i> (2022)
	Muffle furnace	200–600	120	n.s.	Guerrero <i>et al.</i> (2001)
	Muffle furnace	100–700	900	0–1.5	Guerrero <i>et al.</i> (2005)
	Muffle furnace	225–499	7200	0–5	Hohner <i>et al.</i> (2019)
	Muffle furnace	300–700	1200	0–2.5	Jiménez-Pinilla <i>et al.</i> (2016)
	Muffle furnace	100–700	600	A horizon	Kiersch <i>et al.</i> (2012)
	Muffle furnace	50–300	900	0–2	Lombao <i>et al.</i> (2021)
	Muffle furnace	180–500	1200	0–2.5	Lozano <i>et al.</i> (2016)
	Muffle furnace	100–500	300–3600	0–5	Marcos <i>et al.</i> (2007)
	Muffle furnace	100–500	1800	0–5	Marcos <i>et al.</i> (2018)
	Muffle furnace	300–900	7200	0–30	Martínez <i>et al.</i> (2022)
	Muffle furnace	250–500	1800	0–5	Miotliński <i>et al.</i> (2023)
	Muffle furnace	100–300	1800	A horizon	Negri <i>et al.</i> (2021)
	Muffle furnace	300–500	1800	n.s.	Rascio <i>et al.</i> (2022)
	Muffle furnace	170–700	1800	0–5	Soto <i>et al.</i> (1991)
	Muffle furnace	100–500	1800	0–2.5	Stoof <i>et al.</i> (2010)
	Muffle furnace	50–900	1200	0–5	Šurda <i>et al.</i> (2023)
	Muffle furnace	200–500	3600	0–7.5	Terefe <i>et al.</i> (2008)
	Muffle furnace	250–650	180–900	0–5	Thomaz and Fachin (2014)
	Muffle furnace	250–650	180–900	0–5	Thomaz (2017)
	Muffle furnace	170–460	1800	0–5	Varela <i>et al.</i> (2010)
	Muffle furnace	170–460	1800	0–5	Varela <i>et al.</i> (2015)
	Muffle furnace	100–625	900–21,600	0–7	Webster (2015)
	Muffle furnace	300–500	n.s.	0–4	White <i>et al.</i> (1973)
	Muffle furnace	150–550	n.s.	0–10	Wilkerson and Rosario-Ortiz (2021)
	Muffle furnace	250–300	1800	0–5	Wu <i>et al.</i> (2022)
Oven	Oven	30–90	n.s.	n.s.	Campbell <i>et al.</i> (1995)
Oven	Oven	100–300	1800	0–5	Costa <i>et al.</i> (2025)
Oven	Oven	150–490	1800	0–5	Fernández <i>et al.</i> (1997)
Oven	Oven	45–75	n.s.	n.s.	Izzo <i>et al.</i> (2006)
Oven	Oven	45–70	n.s.	0–3, 3–6, 6–9	Kipfer <i>et al.</i> (2010)
Oven	Oven	20–60	3600–43,200	0–12	Malmström (2008)
Oven	Oven	65–70	600–900	n.s.	Peay <i>et al.</i> (2009)
Oven	Oven	100	n.s.	0–7.5	Terefe <i>et al.</i> (2008)
Oven	Oven	175–350	900	0–2	Verdes and Salgado (2011)
Oven	Oven	50–200	n.s.	0–4	White <i>et al.</i> (1973)
Overall ranges (min.–max.)		20–900	15–43,200	0–30	

in 1966 and the most recent in 2024, and 20 fires from unpublished data. The fires include 27 wildfires and 28 prescribed burns. They cover a range of ecosystems in nine countries, including all continents except Antarctica,

although it is important to note that most records originate from Western countries. Some fires provided data for more than one fuel type, resulting in an overall total of 31 datasets for wildfires ($n = 7$, 9 and 15 for grass, shrub and forest,

respectively) and 31 for prescribed burns ($n = 22, 15$ and 14 for grass, shrub and forest, respectively) (Fig. 1; Table 1).

Maximum temperatures reached during wildfires and prescribed burns

The maximum temperatures reached during wildfires and prescribed burns for grass, shrub and forest sites grouped together are summarised in Fig. 2. The average maximum temperature values at the soil surface (0 cm) were 544°C for wildfires (range: 240 – 964°C) and 304°C (range 26 – 812°C) for prescribed burns. At 1 cm depth, reported average maximum temperatures already declined sharply (wildfires: 129°C , range 19 – 450°C ; prescribed burns 158°C , range 31 – 397°C). There is large variability across the data, especially at 0 and 1 cm depth. Temperatures exceeding $60, 100$ and 300°C at any soil depth were observed in $24, 18$ and 9 of the 31 wildfire datasets, and in $20, 20$ and 10 of the 31 prescribed burn datasets, respectively. It is also worth noting that below 1 cm depth, temperatures exceeding 300°C were only reported in one study, a prescribed burn in shrubland (Carrington 2010). Regarding vegetation type, the highest soil surface temperatures were reported from shrublands for wildfires ($\sim 964^{\circ}\text{C}$) as well as prescribed burns ($\sim 812^{\circ}\text{C}$), followed by wildfires in grasslands (480°C) and then forests (380°C) (Fig. 3a, b).

Across all studies in which also aboveground thermocouple (i.e. 'flame') temperatures (but no duration data) were available (seven wildfires and eight prescribed burns

identified in Table 1), maximum temperatures above ground ranged from less than 200°C to nearly 900°C , with no clear relationship between the maximum temperature measured above ground and the maxima recorded at or below the soil surface (0–5 cm depth; Fig. 4).

Temperature residence time during wildfires and prescribed burns

Data from those wildfires and prescribed burns where heating durations above the $60, 100$ and 300°C temperature thresholds were recorded respectively are shown in Fig. 3c–j. Where temperatures exceeded 60°C at 0–2.5 cm depth, excluding forest sites with deep duff, this was sustained for periods from a few seconds up to 7000 s (> 1 h) for both wildfires and prescribed burns (Fig. 3c, d). Below 2.5 cm depth, durations fell sharply to < 1 min. In contrast, at the forest sites with deep duff layers consumed during the fires, $> 60^{\circ}\text{C}$ was maintained for extremely long periods of $> 15,000$ s (> 4 h) down to 4–5 cm soil depth (Fig. 3i, j). One study (Haase and Sackett 1998) monitored soil temperatures below 5 cm to a depth of 47 cm during prescribed burns in Californian giant sequoia mixed conifer stands with extremely high surface fuel loads of up to 306 t ha^{-1} . Here, temperatures $> 60^{\circ}\text{C}$ were recorded for more than $60,000$ s (~ 17 h) down to 20 cm depth and exceeding $39,500$ s (~ 11 h) up to 47 cm depth (not shown in Fig. 3).

Where temperatures exceeded 100°C , again excluding forest sites with deep duff, this was sustained for periods between 10 and 3600 s (1 h) to depths up to 2 cm, with shrubland again exhibiting the longest durations for both wildfires and prescribed burns (Fig. 3e, f). In forest and grassland wildfires, most values remained below 100 s at all depths. In prescribed burns, only three studies reported temperatures $> 100^{\circ}\text{C}$ at 1–2 cm depth, with durations ranging from a few seconds to 1300 s. At the forest sites with deep duff, $> 100^{\circ}\text{C}$ was maintained for periods of $> 11,000$ s (> 3 h) at 1 cm to > 5000 s (> 80 min) down to 5 cm soil depth (Fig. 3i, j).

Temperatures over 300°C (Fig. 3g, h) were recorded in 19 of the 55 fires, with maximum durations reaching up to 420 s (7 min) at the soil surface and 130 s (~ 2 min) at 0.5 cm depth in forest wildfires, and up to 325 s (5.4 min) at the soil surface in prescribed burns in shrublands.

Heating temperatures and durations used in laboratory experiments

We found a total of 77 laboratory soil heating experiments, published between 1966 and 2025 (Table 2), using field soil sampled to depths up to 30 cm. Most studies ($n = 51$) involved heating the entire soil sample using muffle furnaces or ovens to temperatures ranging from 20 to 900°C and for overall durations between 120 and $43,200$ s

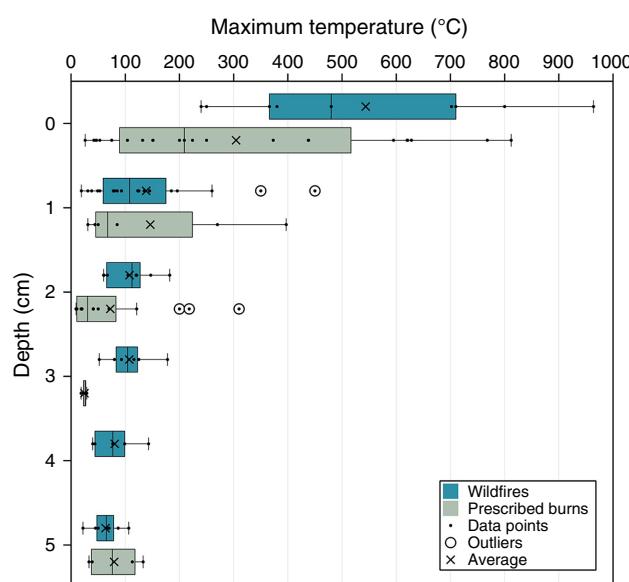


Fig. 2. Maximum temperatures reached during wildfires (experimental and actual) and prescribed burns at the mineral soil surface (0) and 1, 2, 3, 4, and 5 cm soil depths for forest, shrubland and grassland combined ($n = 50$). Measured soil depths were rounded to the nearest centimetre for better visualisation. Outliers were identified with the 1.5 interquartile range. Error bars indicate the 95% confidence interval.

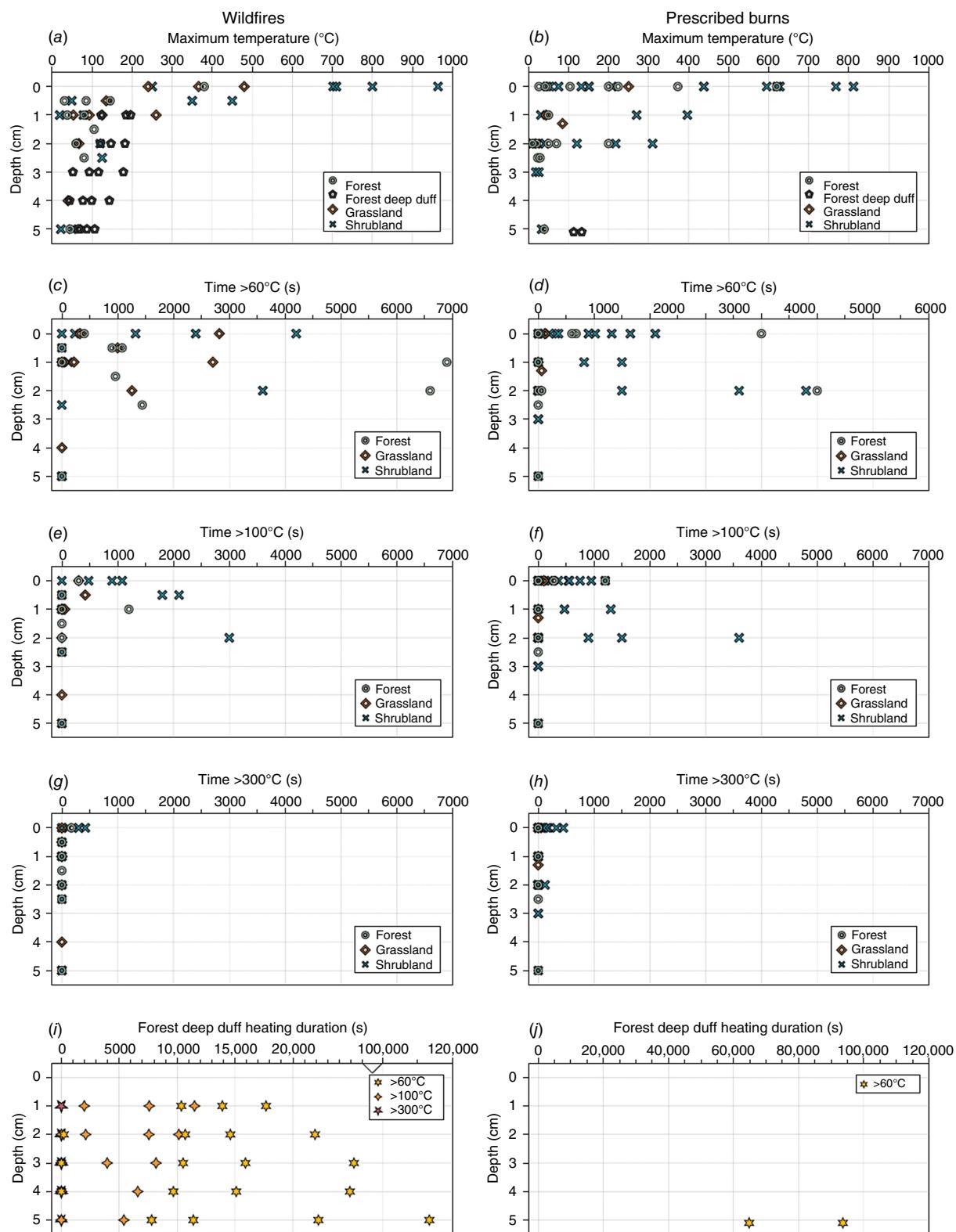


Fig. 3. (a–j) Maximum soil temperature (a, b) and duration of temperature maintained above 60, 100 and 300°C (c–h) at different soil depths up to 5 cm measured during wildfires and prescribed burns for forest, shrubland and grassland. Heating duration recorded for forest fires with deep duff layers are presented separately (i, j) to allow better visualisation given their longer heating durations (see Methods section). Note: 3600 s equals 1 h; 14,400 s equals 4 h; 72,000 s equals 20 h.

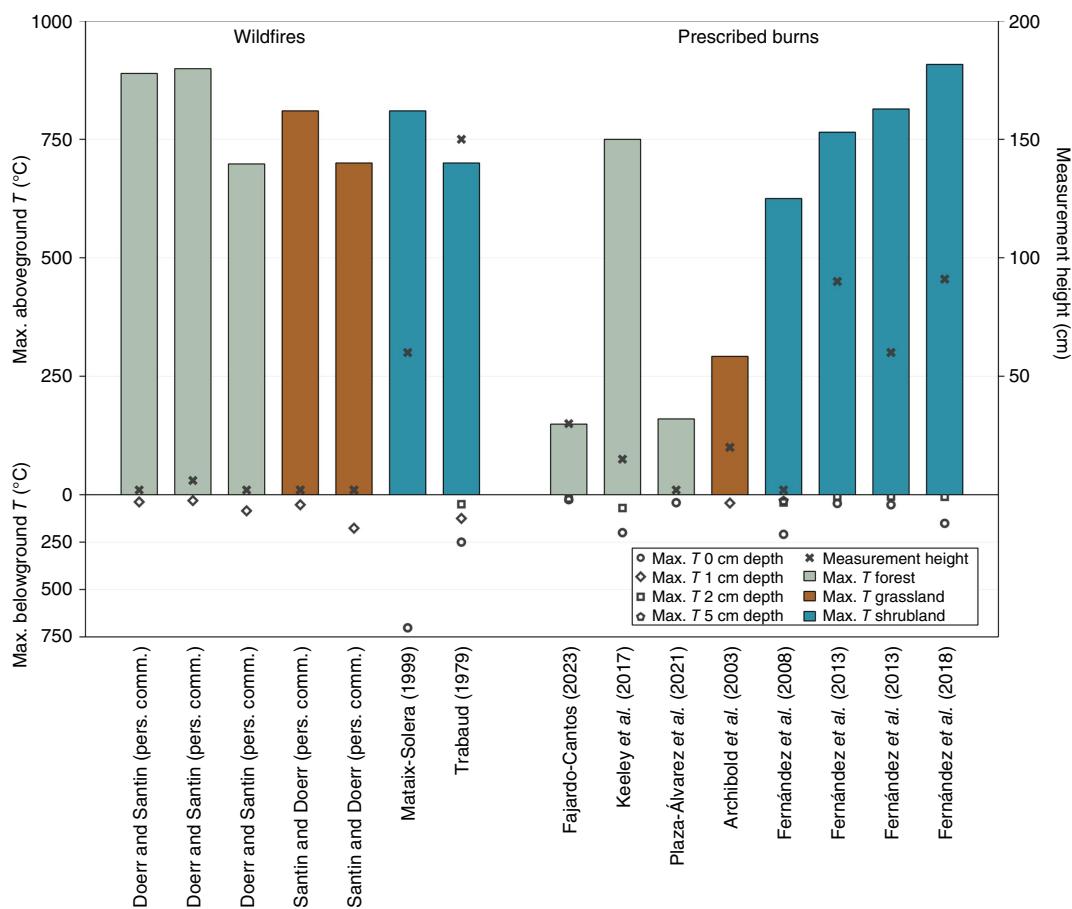


Fig. 4. Maximum thermocouple temperatures recorded simultaneously below and above ground. Note that this is a subset of the full below-ground dataset of Fig. 3 as associated aboveground temperatures are only available from 15 fires. None were available for the 'forest with deep duff' category. Data are displayed separately for each study as aboveground thermocouple temperatures are not directly comparable among studies if they are of different diameters and are deployed at different heights. Measurement height indicates the height (cm) at which the aboveground temperature measurement was recorded. pers. comm., personal communication (i.e. new unpublished data).

(2 min to 12 h), excluding ramp time where applied (Fig. 5 and Table 2). In the remainder, heat was applied from above ($n = 26$), using blowtorches, radiant heaters, infrared lamps or burning leaf litter. This generated temperatures in the range of 94–600°C with overall durations ranging from 15 to 35,640 s (~10 h; Fig. 5 and Table 2). Overall, the heating durations above the upper temperature thresholds studied here (300°C) were often notably longer (≥ 1800 s; ≥ 30 min) than those recorded in the field, where such temperatures were only reported at the soil surface or within the first centimetres in a few cases for < 500 s (~8 min; Fig. 3). In contrast, the maximum durations exceeding the 100°C threshold reported from the field were captured well by laboratory studies, whereas the maximum durations exceeding 60°C used in laboratory experiments fell far short (by over an order of magnitude) of those observed in the field (Fig. 3).

Discussion

Maximum temperatures reached during wildfires and prescribed burns

The highest soil surface temperatures as well as the highest overall averages of the data compiled here were found under wildfires. This is expected given that most prescribed burns are designed to have a minimal impact on soil (i.e. produce low soil burn severity). They typically burn under higher fuel and soil moisture contents, and under less severe fire weather (i.e. lower ambient air temperature and higher relative humidity) than wildfires (Fernandes 2015). Indeed, the difference in soil temperature extremes between most wildfires and prescribed burns is likely to be even greater than the data compiled here suggest (Fig. 2). Although it has been possible to collect data across a wide range of prescribed burns, data from more extreme wildfires

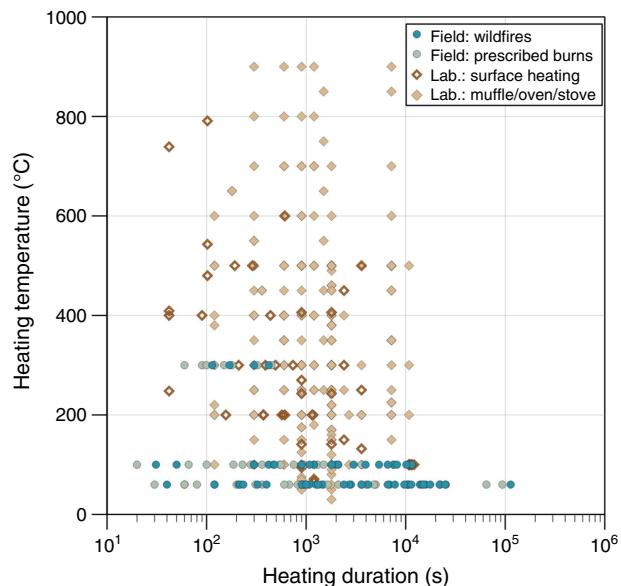


Fig. 5. Heating temperatures and durations used in laboratory studies ($n = 77$, Table 2) compared with field-measured temperature duration data (duration >60 , >100 and $>300^\circ\text{C}$; soil depths 0–5 cm) during wildfires and prescribed burns ($n = 50$, Table 1). '0' values are not shown owing to the logarithmic scale of the x-axis.

is more challenging to collect, owing to obvious logistical constraints like unpredictable occurrence, accessibility and safety concerns, and thus they are likely to be underrepresented in the data compiled here.

Notwithstanding the above, it is notable that most wildfires and prescribed burns only heated the first few centimetres of the mineral soil, with temperatures exceeding 300°C being rare, especially below 1 cm depth. It should be reiterated here that these temperatures are the highest recorded at each of the fires studied; i.e. when more than one temperature value was obtained per site, only the highest value is presented here. This supports the generally very shallow heat penetration highlighted previously in studies examining individual fires (e.g. Hartford and Frandsen 1992, Doerr *et al.* 2010; Stoof *et al.* 2013; Girona-García *et al.* 2019). It is also clear from the data presented in Fig. 4 that 'flame temperatures' measured above the ground bear no meaningful relationship to temperatures reached in the mineral soil. This is not at all surprising considering that soil temperature reached is dependent on the cumulative heat flux into the soil (Neary *et al.* 2005) rather than the maximum temperature recorded in a flame at a specific position above the ground. Also, when present, the soil organic layer insulates the soil when it is not consumed by fire but it heats the underlying soil when it burns (Hartford and Frandsen 1992). An additional issue of data comparability arises when different thermocouples are being used in flames, or when thermocouples are exposed at the soil or fuel surface. Thicker thermocouples reach lower maximum temperatures than thinner ones when exposed to the same

flames (Walker and Stocks 1968), whereas the good thermal contact between thermocouples and soil allows quite accurate measurement of soil temperatures (e.g. Brady *et al.* 2022). Calibrating devices to provide estimates of standard fire behaviour descriptors that can be compared among studies is a partial solution to this problem (Bova and Dickinson 2008). Time-integrated measurements of fire behaviour, such as fuel consumption and total energy released may be better predictors of soil heating than rates (e.g. fireline intensity) given the dependence of soil heating on cumulative heat flux into the soil (Neary *et al.* 2005).

In this study, we have not included data from sustained stationary burning of wood or slash piles, downed trees or large branches as they have very specific burning conditions that are not representative of how most landscapes burns. However, it is important to note that these high accumulations of woody fuels can lead to very substantial, if localised, heating of the mineral soil and associated changes in its properties up to tens of centimetres within the mineral soil (Massman *et al.* 2010; Busse *et al.* 2013). For example, instrumenting a series of wood pile burns, Busse *et al.* (2013) found temperatures $>300^\circ\text{C}$ at 5 cm, and $>200^\circ\text{C}$ at 10 cm soil depth to be sustained for more than 40 h, which by far exceeds the heat penetration depths and the durations recorded under the natural fuels examined in the current study.

The data collated here support the notion that, overall, the impacts of prescribed burns in natural fuel beds are likely to be spatially limited and tend to be confined to the first few centimetres of soil. The same is likely to apply to most wildfires within the range of those represented here, although it is clear from indirect soil burn severity indicators such as total organic matter loss, fine root consumption and changes in soil water repellency, colour or mineralogy, that some wildfires can lead to substantial alterations to soil beyond the top few centimetres (Certini 2005; Parsons *et al.* 2010). It is also important to consider that the top few centimetres are usually the most fertile and organic-rich layer, as well as those most exposed to wind and water erosion (Shakesby and Doerr 2006), and hence they disproportionately determine many soil functions.

Irrespective of fire type, another noteworthy finding is that the highest soil temperatures were reported from shrub and some grass fires. This may seem surprising given that grass and shrub fires tend to have greater rates of spread and lower residence times, as well as lower energy release rates and totals than forests fires (e.g. Stavi 2019). Shrub and grass fires are reasonably well represented in our dataset ($n = 23$ and 9 respectively) and this general finding appears to be not driven by a particular shrub or grassland type (see Table 1). However, an important zone of fuel consumption and thus energy release in many forest fires will be well above the ground, whereas the dominant zone of energy release in many shrub and grass fires will be closer to the soil, and soils here are often bare of an insulating organic layer, which could explain the comparatively high soil surface temperatures found here. An exception in forests are

fires burning through deep duff layers (Fig. 3*i, j*), where combustion of this forest floor fuel layer can occur in direct contact with the mineral soil, which can continue long after the main flaming front has passed (Frankman et al. 2012).

Temperature residence time during wildfires and prescribed burns

The maximum temperature reached in the soil is a widely used parameter linked to established thresholds above which specific changes to the soil are expected to occur. However, we argue here that the duration for which a threshold has been exceeded may be a more important parameter for soil impacts. For example, Pingree and Kobziar (2019) reviewed the widely used threshold of 60°C (when applied for at least 1 min, irrespective of soil moisture content) for soil biota mortality and found that in no single study and for no group of organisms was this threshold consistently evidenced. What could be inferred was that mortality of soil biota is likely to occur at lower temperatures when duration of heating is longer and *vice versa* (Pingree and Kobziar 2019), a relationship also highlighted previously in a study on heat-induced cambium cell mortality by Dickinson and Johnson (2004). Heating duration has also been found to substantially change the temperature threshold at which soil water repellency is eliminated (270–400°C; DeBano 2000; Doerr et al. 2004; García-Corona et al. 2004), with thresholds under oxygen-limited conditions ranging by as much as 200°C for heating durations between 120 and 10,800 s (Bryant et al. 2005). What is clear from the data on temperature and duration maxima compiled here is that heat pulses in most wildfires and prescribed burns are not only shallow but are also of relatively short duration. Where 60 or 100 °C was exceeded, values clustered below 3000 s, and for >300°C durations, were all below 500 s (Fig. 3*c–f*). The exceptions here are again the forest fires with deep duff where temperatures exceeding 60°C were not only sustained for 1–2 orders of magnitude longer but also penetrated to much greater depths (Fig. 3*i, j*). The study by Haase and Sackett (1998) in which temperatures were monitored only below 5 cm, but down to 47 cm (Supplementary Table S1) supports these findings and shows that where surface fuel loads are extreme and burning can last several days, heating durations at least exceeding 60°C can approach those usually confined to log pile burns. Deep duff layers and heavy surface fuels combined with a dry climate in fire-suppressed forests, such as those widespread across the western US, can be expected to contribute to fires that can create such high and prolonged soil heating.

Implications for laboratory soil heating studies

Our comparison of the maximum temperatures, heating durations and heat penetration depths between laboratory

heating experiments and field measurements highlights important limitations of the laboratory experiments. First, when using laboratory heating experiments with the aim to simulate the effects of wildfires or prescribed burns on soils, the majority of studies have heated the sample homogeneously rather than applying heat from the surface. The steep vertical temperature gradient shown in the field data compiled here supports the principle that heating a sample from above is more realistic to simulate the thermodynamic processes occurring in wildland fires. Although the number of surface heating experiments have increased in the past 15 years (17 out of 25 studies published since 2010), homogeneous heating experiments still comprise the majority of studies (29 out of 52 studies published since 2010). Second, regarding heating duration, many laboratory studies use fixed times of 1800 s (30 min; Table 2). The field data compiled here indicate that this duration is unlikely to be representative of most wildfires and prescribed burns. Although it captures the maximum durations reported for the 100°C threshold, it far exceeds the durations above the 300°C threshold but does not capture the longest durations above the 60°C threshold (see Fig. 5). Applying heat from the surface and including a range of durations and with a focus on temperature maxima below 500°C will likely be more realistic where studies are aimed at being representative of wildfires and prescribed burns.

Implications for wildland fire impacts on soil

The data compiled here suggest that the typically shallow and short heat pulses during most prescribed burns and wildfires can be expected to have only limited direct impacts from heat transfer on deeper (>2–3 cm) soil layer properties. This contrasts the deep and prolonged heat transfer under the more spatially confined pile and log burns. This should, for example, be considered when sampling soil after wildland fires with the aim to examine heat-induced impacts. For example, Parsons et al. (2010) indicate sampling in the top few centimetres for soil structural changes and fine root consumption as being important. Where possible, shallow sampling of the near-surface layers at centimetre or even sub-centimetre scale is most likely to allow detection of impacts. Bulk sampling of thicker layers such as the top 5 cm is likely to dilute any impact on soil given the often limited heating below the top 1–2 cm (Santín and Doerr 2016).

Exceptions can be expected where deep duff layers and heavy surface fuels combined with long dry periods and associated low fuel and soil moisture levels as can occur, for example, in some western USA regions, lead to fires that generate prolonged soil heating over larger spatial scales (e.g. Robichaud et al. 2018). In contrast, in the mesic boreal forests, which are also characterised by high forest floor fuel loads and long fire return intervals, the typically higher soil moisture content will often result in patchy duff combustion that would limit heat transfer into soil (Miyanishi and

Johnson 2002). It is, however, important to remember that even where the direct impact of heat penetration on soil is negligible, the loss of litter and vegetation cover and the resulting enhanced erosion risk can nevertheless lead to substantial and often delayed impacts on soil in the post-fire period (see reviews by Neary *et al.* 1999; Shakesby and Doerr 2006). For example, a reduction in soil organic matter, nutrient content or biological activity found weeks, months or even years after fire can be the result of accelerated post-fire erosion rather than direct heat impact (Shakesby *et al.* 2015; Girona-García *et al.* 2019; Alfaro-Leranoz *et al.* 2023).

Limitations and suggestions for future research

The data compiled here aim to cover as many relevant fires as possible in a consistent manner. We focused on recorded temperature extremes, and the findings should therefore be considered in context of potential upper limits, rather than being typical of soil temperatures reached during wildland fires. That noted, the data available to date, especially for wildfires, are limited; extreme fires with high rates of energy release may be underrepresented here, and the available data are biased towards fires in Western countries. Further research, in particular across a wider range of wildfires, will be valuable in enabling a fuller understanding of soil temperatures reached during fires. This will be particularly relevant considering increasing fire intensity and fuel consumption due to climate change, observed especially in boreal and temperate regions (Jones *et al.* 2022; Cunningham *et al.* 2024; Parks *et al.* 2025). When examining the relationship between thermal impacts of fire on soil, it may also be insightful to focus not only on specific temperatures and exposure durations, but also to consider measures of cumulative thermal exposure such the heat flux density integral over the exposure duration as applied previously to the charring of wood (Mathieu *et al.* 2023).

Conclusions

We have compiled a comprehensive dataset of available published and new data on maximum temperatures reached in the mineral soil and heating durations above widely used temperature thresholds during wildfires and prescribed burns from a range of regions and ecosystems in five continents and compared these with those applied in published laboratory soil heating studies. Key findings are:

- Heat penetration during wildfires and prescribed burns was largely shallow, often affecting only the first 0–2 cm of the mineral soil. At 1 cm depth, the temperature rarely exceeded 300°C. Heating durations >300°C did not exceed 500 s.
- Very long heating durations where 60°C was exceed for over 4 h down to 4–5 cm were observed at forest sites with deep duff layers consumed. For all other fires, 60°C was

exceeded for periods between a few seconds up to more than 1 h at 0–2.5 cm depth for both wildfires and prescribed burns, whereas below 2.5 cm depth, the durations >60°C fell sharply to <1 min.

- Soil surface temperatures and overall average maximum temperatures were lower in prescribed burns than wildfires. This is expected as the former are typically conducted under higher fuel moisture conditions and milder fire weather. However, owing to the logistical difficulty in monitoring real wildfires, their range is likely to be under-represented in this study. Irrespective of the type of fire, the highest soil temperatures were reported for shrub and grass fires.
- When comparing the maximum temperatures and heating durations from field measurements with those from laboratory heating experiments, which primarily use muffle furnaces, ovens and, less frequently, surface burning (i.e. blowtorch or heaters), the laboratory heating durations often not represent those observed under natural fuel beds in wildland fires.
- Our data support the notion that aboveground temperatures recorded by a range of devices at different heights (often reported as 'flame' or 'fire temperatures') are not a useful indicator of underlying soil heating for a variety of reasons. We urge researchers to measure and report fire behaviours such as fireline intensities, fuel consumption (including of duff), radiation (Fire Radiative Power and Fire Radiative Energy) and relate them to soil heating. Currently, reported measurements of fire characteristics are often inconsistent across studies, which prevents a thorough review of their relationships with soil heating.
- Although the direct impact of wildland fire on soil from heat penetration will often, but not always, be rather limited to shallow depths, it is important to highlight that the loss of litter (duff) and vegetation cover results in enhanced erosion risk.
- Further research assessing soil heating in more extreme wildfires and in currently underrepresented regions (e.g. Africa, Central and South America, south and east Asia) will be useful in providing a more comprehensive understanding of the relationships between heat transfer and soil impacts in various ecosystems.

Supplementary material

Supplementary material is available online.

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Data availability. The full dataset examined in this study is available in Supplementary Table S1.

Conflicts of interest. Stefan H. Doerr is one of the Editor-in-Chiefs of *International Journal of Wildland Fire* but was not involved in the peer review or decision-making process for this paper. The authors declare no other conflicts of interest.

Declaration of funding. This study was supported by Leverhulme Trust Grant (RPG-2014-095) (CS, SHD), Leverhulme Trust Fellowship (RF-2016-456\2) (SHD), NERC grant IDEAL FIRE (NE/X005143/1) (SHD), European Commission H2020 project no. 101003890 (FireUrisk) (SHD, CS), Grant RYC2021-031262-I funded by MICIU/AEI/10.13039/501100011033 and European Union NextGenerationEU/PRTR (AG), Grant PID2023-146991NA-I00 funded by MICIU/AEI/10.13039/501100011033 and by 'ERDF/EU' (AG).

Acknowledgements. The authors are grateful to the following organisations and individuals that supported field data collection during fire: Canada: FPInnovations, Government of the Northern Territories; South Africa: SANParks; Australia: WaterNewSouthWales, USA: USDA Forest Service. We are also grateful for the useful reviewer comments that improved this manuscript.

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