IMPACT OF THERMAL STRESS ON *PINUS LARICIO:* DETERMINING TOLERANCE LEVELS TO PRESCRIBED BURNING THROUGH FIELD EXPERIMENTATION

Lila Ferrat,[1] Frédéric Morandini, Isabelle Baconnais, Xavier Silvani, Liliane Berti, and Vanina Pasqualini
University of Corsica, Faculty of Sciences, UMR 6134 CNRS, B.P. 52, 20250 Corte, France

ABSTRACT

In the Mediterranean area, forest fires represent an important and periodic threat to the environment, to socioeconomic activities, and to human beings. In Corsica (France), in order to prevent large-scale fires and to protect forests, low-intensity prescribed burning, or high-intensity thermal pruning, are conducted within increasingly young Corsican pine (*Pinus nigra* ssp. *laricio* (Poir.) Maire var. *corsicana* (Loud.) Hyl.) forests. However, resistance to thermal stress has only been empirically assessed so far through comparisons that do not give any insight into underlying mechanisms. The recommended approach requires the characterization of tolerance levels of pines to experimental fires of various intensities. Experimental prescribed burns with increasing fuel loads (0, 250, 500, 750, and 1000 g m^{-2} pine needle beds) were performed under young Corsican pine (5 years old) in a departmental nursery at Ajaccio during May 2008. For each fireline intensity reflecting respective fuel loadings, the heat stress was thermodynamically characterized. To this end, temperatures were measured in the soil and in the canopy. The impact of fire was then evaluated on 1) photosynthesis, through measurements of chlorophyll fluorescence (Fv/Fm); 2) lipid peroxidation (malonedialdehyde contents); and 3) morphological parameters (burned foliage, death percentage) before the prescribed burn, followed by measurements 24 hours, 48 hours, and 1 week after burning. Thermal stress was detected 24 hours after burning and increased with fuel load, with a strong alteration of photosynthetic efficiency, an increase in oxidative damage, and a high level of chlorotic foliage (75%) for 750 and 1000 g m^{-2}. One week after burning, physiological parameters tended to return to pre-burn values, except for the 1000 g m^{-2} fuel load. We conclude that Corsican pine can be directly affected by heat transfer to needles during burning, and can also be affected by the loss of integrity of xylem vessels (embolism). These results will help to provide recommendations for monitoring of ecosystems through prescribed burning practice.

Keywords: chlorophyll fluorescence, Corsica, experimental, fuel load, lipid peroxidation, *Pinus laricio*, prescribed burning.

Citation: Ferrat, L., F. Morandini, I. Baconnais, X. Silvani, L. Berti, and V. Pasqualini. 2010. Impact of thermal stress on *Pinus laricio:* determining tolerance levels to prescribed burning through field experimentation. Pages 133–140 *in* K.M. Robertson, K.E.M. Galley, and R.E. Masters (eds.). Proceedings of the 24th Tall Timbers Fire Ecology Conference: The Future of Prescribed Fire: Public Awareness, Health, and Safety. Tall Timbers Research Station, Tallahassee, Florida, USA.

INTRODUCTION

Anthropogenic disturbances have increasingly engendered dramatic ecological consequences on Mediterranean forests, including atmospheric pollution, deforestation, forest fragmentation, overgrazing, biological invasion, and fires (Quézel and Médail 2003). Forest fires constitute one of the major perturbations for Mediterranean ecosystems, notably for pine (*Pinus* spp.) forests (Leone and Lovreglio 2004). Each year, almost 35,000 ha of forest are burned by wildfire in the French Mediterranean region (Hubert et al. 1991). Between 1994 and 2004, the annual impact of fires is estimated at 900 forest and shrubland fires covering 88,435 ha (DRAF 2007). The repetition of these fires constitutes a major factor of disturbance in ecosystems, representing a real human, economic, and ecological hazard.

Corsican pine (*Pinus nigra* ssp. *laricio* (Poir.) Maire var. *corsicana* (Loud.) Hyl.) is an ecologically and economically important species, as it is exploited for timber production under the control of the Office National des Forêts (ONF) for use in France and for export to Italy and Spain. Endemic to Corsica, it grows up to 50 m high, has a straight trunk, and occurs on mountainous terrain at altitudes of 900–1,800 m (Gamisans and Marzocchi 1996), forming forests covering 45,000 ha.

The vulnerability of Corsican pine to fire constitutes an important threat for the conservation of plantations containing this species. Mediterranean pines are well known for their flammability and their susceptibility to natural fires (Leone and Lovreglio 2004). In Corsica, in order to preserve forests and young plantations from large-scale fires, prescribed burns of low intensity, or thermal pruning of strong intensity, have been applied under increasingly young Corsican pine forests.

Although some studies have investigated the effects of prescribed burning on other pine species in the region (Fernandes and Botelho 2004, Fernandes and Rigolot 2007), resistance of Corsican pine to thermal stress has only been empirically assessed so far, through comparisons that do not give insight into the underlying mechanisms. Prescribed burning is used in forests to reduce fuel buildup and fire risk, but it could have a negative impact if conducted under conditions resulting in excessive fireline intensity. A scientific framework is thus necessary to help guide this management practice. Specifically, it is essential to answer the following question: Up to which fuel load is prescribed burning sustainable for Corsican pine? Past studies have investigated the effects of localized heating of trunk and branches of Aleppo pine (*Pinus halepensis*) with an electrical heating system (Ducrey et al. 1996) or application of a blowtorch to

---

[1] Corresponding author (ferrat@univ-corse.fr).

maritime pine (*Pinus pinaster*) (Alonso et al. 2002). These experiments allowed the understanding of some important mechanisms of response of these species to thermal stress, but they are not necessarily representative of a real prescribed burn.

The aim of this study is to characterize the short-term physiological impact of prescribed burning at different burning intensities on very young specimens of Corsican pine. Physiological and biochemical parameters are of particular interest as they are involved in the response to environmental stress, whether they are of biotic or abiotic origin (e.g., water deficit, temperature, nutrient deficiency, polluting agents, attacks by pathogens). This characterization will be determined through descriptors of vitality, including photosynthesis activity, and descriptors of damage, including lipid peroxidation. Photosynthesis is a good indicator of the adaptation of plants to their environment because it varies in plants according to adversity of conditions (Maksymiec et al. 2006). Lipid peroxidation reflects stress undergone by plants. Indeed, stress can result in production of disturbance of dioxygen in chloroplasts, generating free radicals (Jouili and El Ferjani 2003), which are highly reactive and damaging to cell molecules (Dorey et al. 1999). Photosynthetic efficiency and lipid peroxidation have already been used as thermal stress biomarkers (Ali et al. 2005) and could constitute reliable markers of thermal stress in Corsican pine.

Our approach involves characterization of tolerance levels of pines to experimental fires conducted with different fuel loads. For each fuel load and associated fireline intensity, the thermal stress will be thermodynamically characterized, as this will allow linking the physiologic response of the pines to a given thermal constraint. Then the impact of fire on photosynthesis will be through measurements of photosynthetic capacity, and oxidative damage will be indicated through measurements of lipid peroxidation. The originality of this work is that it links physiological, biochemical, and physical parameters in order to characterize levels of tolerance of pines to fires of various intensities. The results should allow the understanding of the physiological responses of Corsican pine to thermal stress, in order to obtain reliable descriptors of plant sensitivity, determine tolerance levels, and furnish recommendations for application of prescribed burning.

MATERIALS AND METHODS

Experimental Procedure

Experiments were carried out on young Corsican pine (5 years old; Table 1) planted in the administrative nursery of Castelluccio in Ajaccio commune, Corsica (France). Soil comprised a homogeneous mix of blond turf and tuff.

Table 1. Morphological characteristics of 5-year-old Corsican pine (±95% standard deviation), June 2008, Corsica.

Characteristic	Measurement
Total length (cm)	148.4 ± 5.9
Trunk length (cm)	50.1 ± 2.2
Trunk diameter (at 20 cm above soil, cm)	18.4 ± 0.9
Length of 2007 principal branch (cm)	29.5 ± 2.0

The experimental design consisted of five plots with 15 pines each. The dimensions of each plot were 0.8 m × 2 m. A Corsican pine dry needle bed was homogeneously sprinkled throughout each plot (except for the control) to provide varying fuel loads among plots (0, 250, 500, 750, and 1000 g m^{-2}). The pine needles were oven-dried at 60°C for 24 hours and their fuel moisture content was 5%. Wind conditions were low during the burns (<1 m s^{-1}). In plots containing fuel, fire was lit along one edge of each plot using alcohol and the fire spread across the pine needle bed, which was $>95\%$ consumed. The fireline intensity, which represents the heat released per unit time per unit length of flame front, was estimated by the Byram equation (Byram 1959). Fireline intensity is defined as the product of the fuel consumed (kg m^{-2}), the rate of spread (m s^{-1}), and the heat of combustion, which is assumed to be 18,000 kJ kg^{-1} for most vegetal fuels (Byram 1959).

Temperature measurements at the height of plant tissue are more useful than the Byram relation for characterizing thermal stress to plants caused by fire. Thus, the temperature of the air and the ground was measured at two locations 1 m apart at the center of each plot using K-type thermocouples with 250-μm-diameter grounded junctions. These options were chosen to guarantee a good compromise between

Figure 1. Fire spreading across a bed of pine needles under a young stand of Corsican pine during a prescribed burn experiment, June 2008, Corsica.

Table 2. Properties of the fire spread experiments in a 5-year-old stand of Corsican pine, June 2008, Corsica.

	Fuel load (kg m^{-2})			
Property	0.25	0.50	0.75	1.00
Flame height (m)	0.23	0.31	0.37	0.44
Rate of spread (m s^{-1})	0.004	0.012	0.012	0.013
Fireline intensity (kW m^{-1})	16	112	162	234
Maximum temperature (°C)				
−0.01 m (subsurface)	53	67	66	154
0 m (soil surface)	625	715	767	695
0.50 m (tree canopy)	124	192	286	372
1.00 m (tree canopy)	59	205	120	307
1.50 m (tree canopy)	40	88	120	97
2.00 m (tree canopy)	49	67	73	104

accuracy and resistance. At each measurement location, thermocouples with insulated cables were attached to a vertical pole at heights of 0.5, 1.0, 1.5, and 2.0 m. The soil surface and subsurface temperatures were also measured at 0 and −1 cm, respectively. The timing of fire progress from one pole to the other allowed determination of the rate of spread of the fire. The thermocouples were connected to a data logger located near the experimental plots and data measurements were taken at 1-second intervals. In order to obtain accurate observations of the fire spread, digital video and infrared cameras were used to record the side view of the fire spread. These recordings provided information on the rate of spread of the flame front and on its geometric properties, namely the flame height and the tilt angle.

Sampling Strategy

Sampling was conducted on branches that grew in 2007 for each tree of each plot. The principal vertical branch was used for measurements of photosynthetic efficiency and the lateral branches were used to sample for lipid peroxidation analyses. For all the parameters analyzed in this study, a reference state on all stands was measured before prescribed burning on 27 May 2008 (time point T0). Prescribed burns were applied on 3 June 2008 and follow-up measurements were taken 24 hours (T1), 48 hours (T2), and 1 week (T8) after burning. Trunk scorching and the percentage of chlorotic foliage (needles with yellow-brown color; Ducrey et al. 1996) were also described at each sampling time.

Photosynthetic Efficiency

Chlorophyll fluorescence (Fv/Fm) of photosystem II (PSII) was measured according to Cornic (2007) using a PAM chlorophyll fluorometer (PAM-2100; Walz, Effeltrich, Germany). Needles were placed in the dark for 20 min, followed by measurement of minimal fluorescence (F0) and maximal fluorescence (Fm) under a saturated pulse.

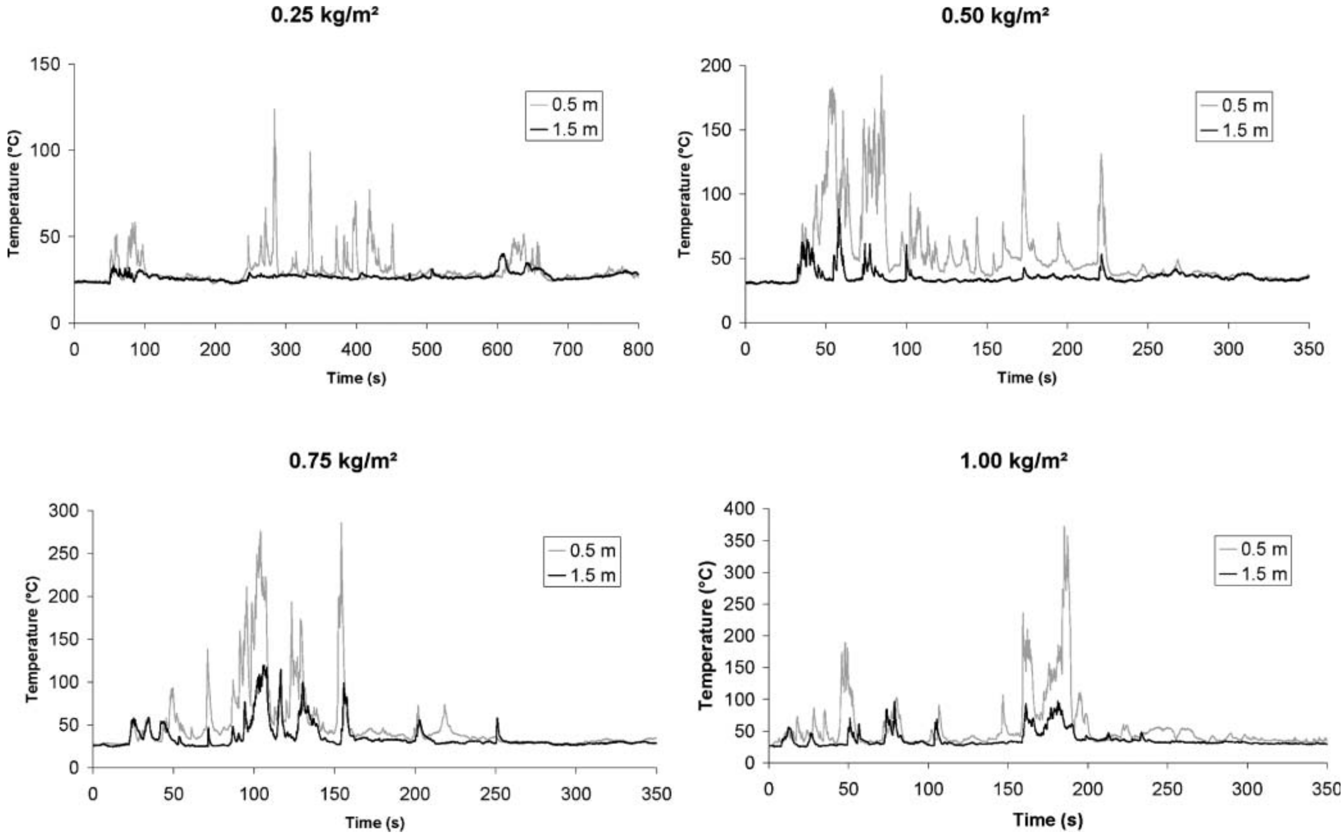

Figure 2. Temperature at the upper and lower edges of the tree canopy for the different fuel load treatments in a 5-year-old stand of Corsican pine during a prescribed burn experiment, June 2008, Corsica.

Lipid Peroxidation

Lipid peroxidation was measured as the content of total 2-thiobarbituric acid (TBA) reactive substances and expressed as equivalents of malonedialdehyde (MDA), as described in Tang and Newton (2004). One gram of needles was homogenized in 3 mL of 20% (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 5,000 rpm for 20 minutes. One milliliter of 20% TCA containing 0.5% (w/v) TBA and 100 µL 4% (w/v) butylated hydroxytoluene (BHT) in ethanol was added to 1 mL of the aliquot of the supernatant. The mixture was heated at 95°C for 30 min and then quickly cooled on ice. The contents were centrifuged at 10,000 × *g* for 15 minutes and the absorbance was measured at 532 nm. The value for nonspecific absorption at 600 nm was subtracted. The concentration of thiobarbituric acid–reactive species (TBARS) was calculated by the method of Groppa et al. (2001).

Statistical Analysis

Indicators of plant stress were compared among fuel load treatments using analyses of variance (ANOVA) when the conditions of application were satisfied (homogeneity of variance and normality). Otherwise, nonparametric tests of median comparisons were made (Kruskal–Wallis; Zar 1984). The software Statgraphics for Windows (Statistical Graphics Corporation, Warrenton, VA) was used for these various tests.

RESULTS

Thermodynamical Measurements

Following ignition, fire spread across the bed of pine needles and fire fronts remained linear during spread in each burn (Figure 1). Flames were approximately vertical, and the smoke plume rose through the canopy of the pines, indicating the location of increased air temperature in the canopy. Details about the fire properties are reported in Table 2. As expected, fireline intensity corresponded to fuel load among the plots. The varying fuel loads led to a relatively wide range of fireline intensities, specifically from 16 to 234 kW m^{-1}. Flame height ranged from 0.23 to 0.44 m. The temperatures recorded at the upper and lower edges of the canopy during fire spread across the four beds of pine needles are provided in Figure 2. The maximum temperatures measured at soil level were consistently around 700°C. The maximum temperatures reached within soil and canopy were significantly different among the four experiments, with highest temperatures for the highest fuel loads (Table 2). The residence times of temperatures above 60°C exhibited increasing values with increasing fuel load (Figure 3).

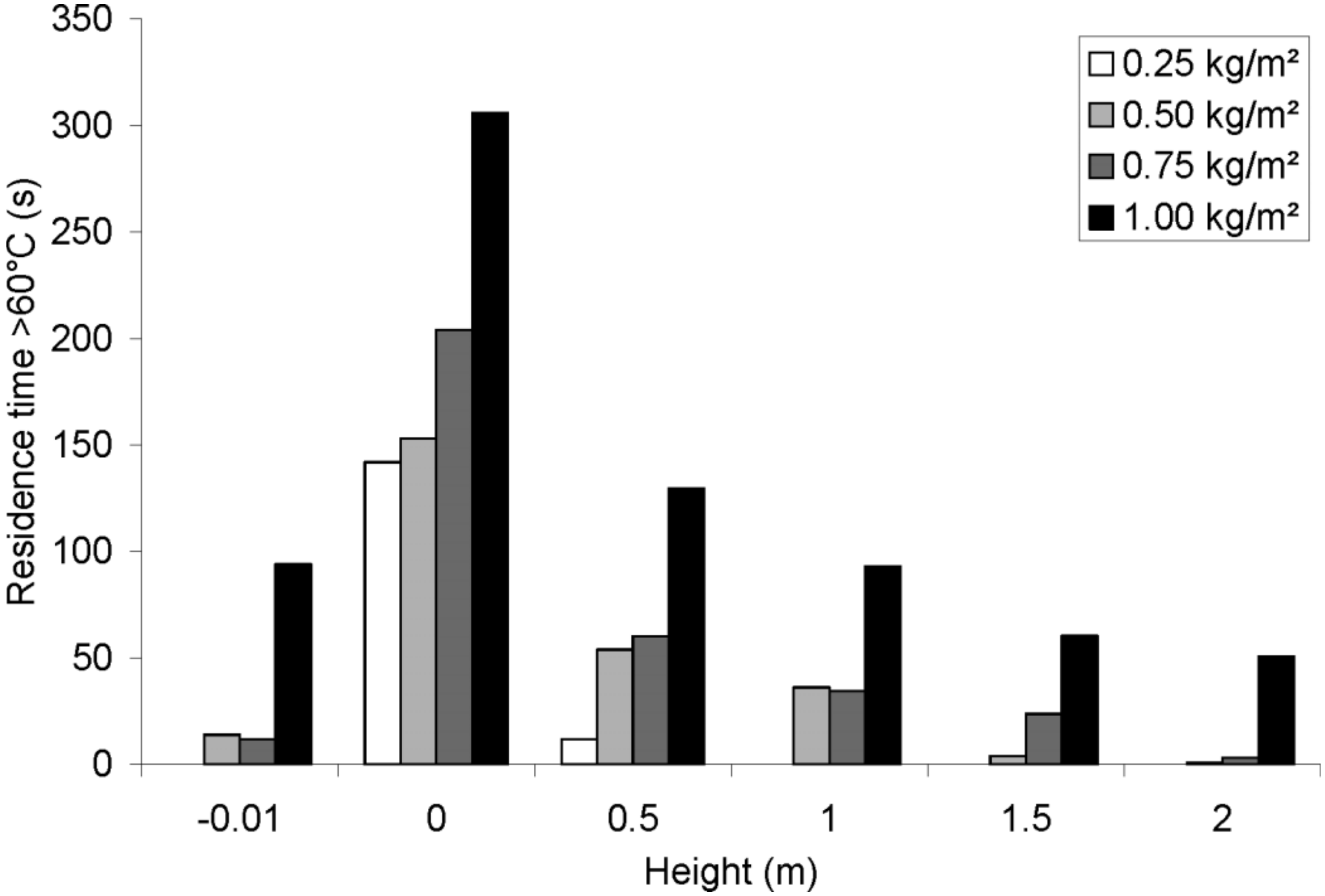

Figure 3. Residence time above 60°C at different heights for the different fuel load treatments in a 5-year-old stand of Corsican pine during a prescribed burn experiment, June 2008, Corsica.

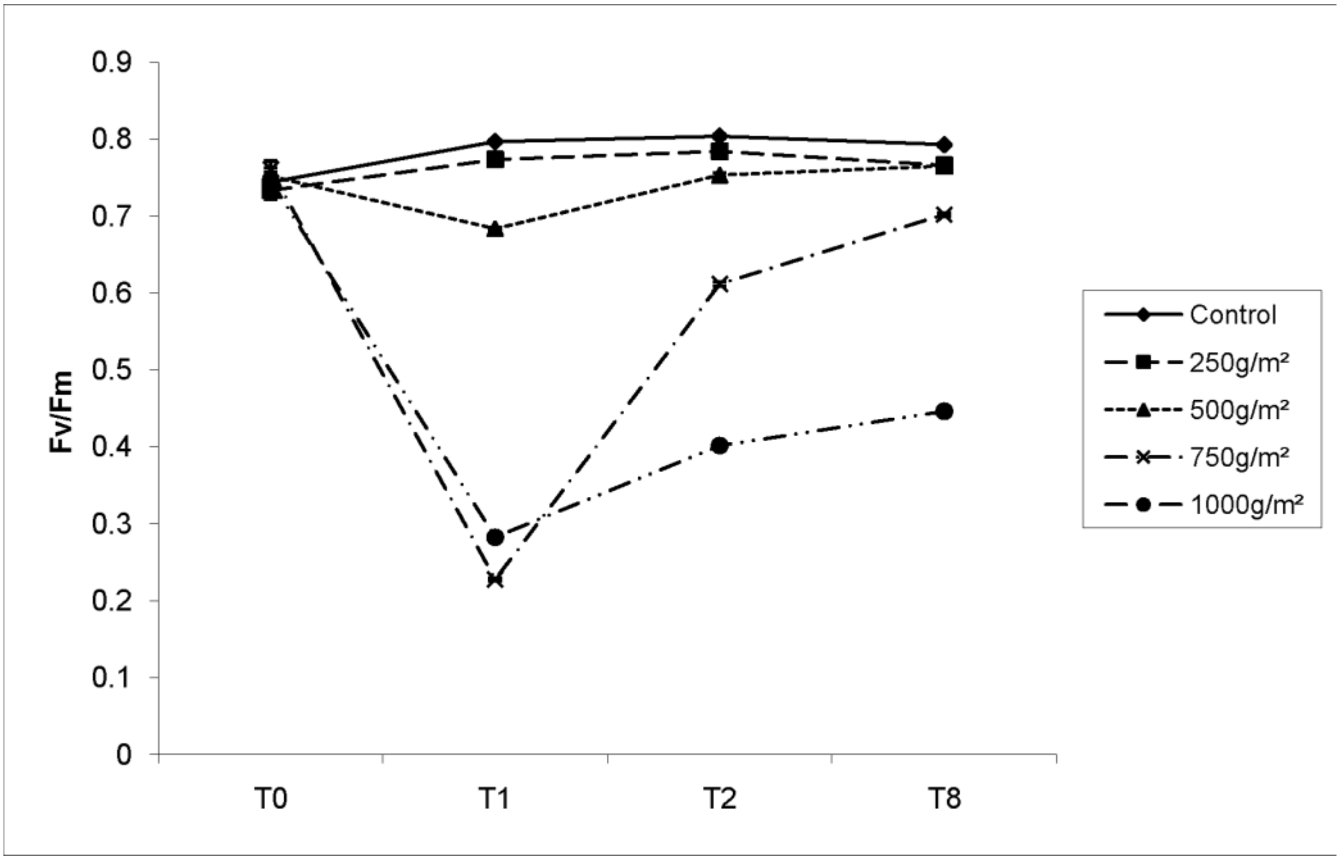

Figure 4. Chlorophyll fluorescence (Fv/Fm) as a function of fuel load from time T0 to T8 on 5-year-old Corsican pine during a prescribed burn experiment, June 2008, Corsica. T0, measurements taken before the prescribed burn; T1, T2, and T8, measurements taken 24 hours, 48 hours, and 1 week, respectively, after the prescribed burn.

Morphological Parameters

Trunk scorching was 20 cm on average and did not reveal any significant variation among burned plots (ANOVA; $P = 0.5436$). The percentage of chlorotic foliage increased significantly as a function of the fuel load. Plots with 250 g m^{-2} fuel load had 5–25% chlorotic foliage, plots with 500 g m^{-2} fuel load had 25–50% chlorotic foliage, and plots with 750 and 1000 g m^{-2} fuel loads had 75–100% chlorotic foliage. There was little mortality of trees immediately after burning (T1). One pine died in the 750 g m^{-2} fuel load plot and three pines died in the 1000 g m^{-2} plot. There was no additional mortality from T1 to T8.

Chlorophyll Fluorescence

Before burning (T0), all the stands presented a statistically homogeneous Fv/Fm (ANOVA; $P = 0.4604$) with an average of 0.74 (Figure 4). The control plot presented a slight increase between T0 and T1 (Kruskal–Wallis; $P = 0.0013$), then remained stable during the rest of the experiment (Fv/Fm = 0.80 on average). The 250 g m^{-2} plot, like the control, showed a slight increase in Fv/Fm between T0 and T1 (Kruskal–Wallis; $P = 0.0013$), then remained stable during the rest of the experiment (Fv/Fm = 0.80 on average). In contrast, plots burned with 500, 750, and 1000 g m^{-2} showed a considerable decrease of Fv/Fm (0.7, 0.29, and 0.23, respectively) compared to the control plots. The magnitude and duration of these decreases corresponded to the level of fuel loading (Figure 4). The lowest levels were immediately after burning (T1; Kruskal–Wallis; $P = 0.0009$) followed by increases in photosynthetic efficiency at T2 and T8. Recovery was weak for high fuel loads and strong for low fuel loads (Figure 4).

Lipid Peroxidation

Before burning (T0), all the plots presented a statistically homogeneous MDA content (30 nmol g^{-1}; ANOVA; $P = 0.4212$; Figure 5). MDA content of the control plot remained stable during the experiment (ANOVA; $P = 0.6846$). All the burned plots presented an average increase in MDA of 60% at T1 compared to T0 (Kruskal–Wallis; $P = 0.0094$). A return to initial values of MDA was demonstrated at T2 for pines burned at 250 and 500 g m^{-2}, but not for those burned at 750 and 1000 g m^{-2}, of which the latter had twice the MDA of the initial value.

DISCUSSION

The temperatures measured at soil level and in the air are in agreement with laboratory measurements across similar

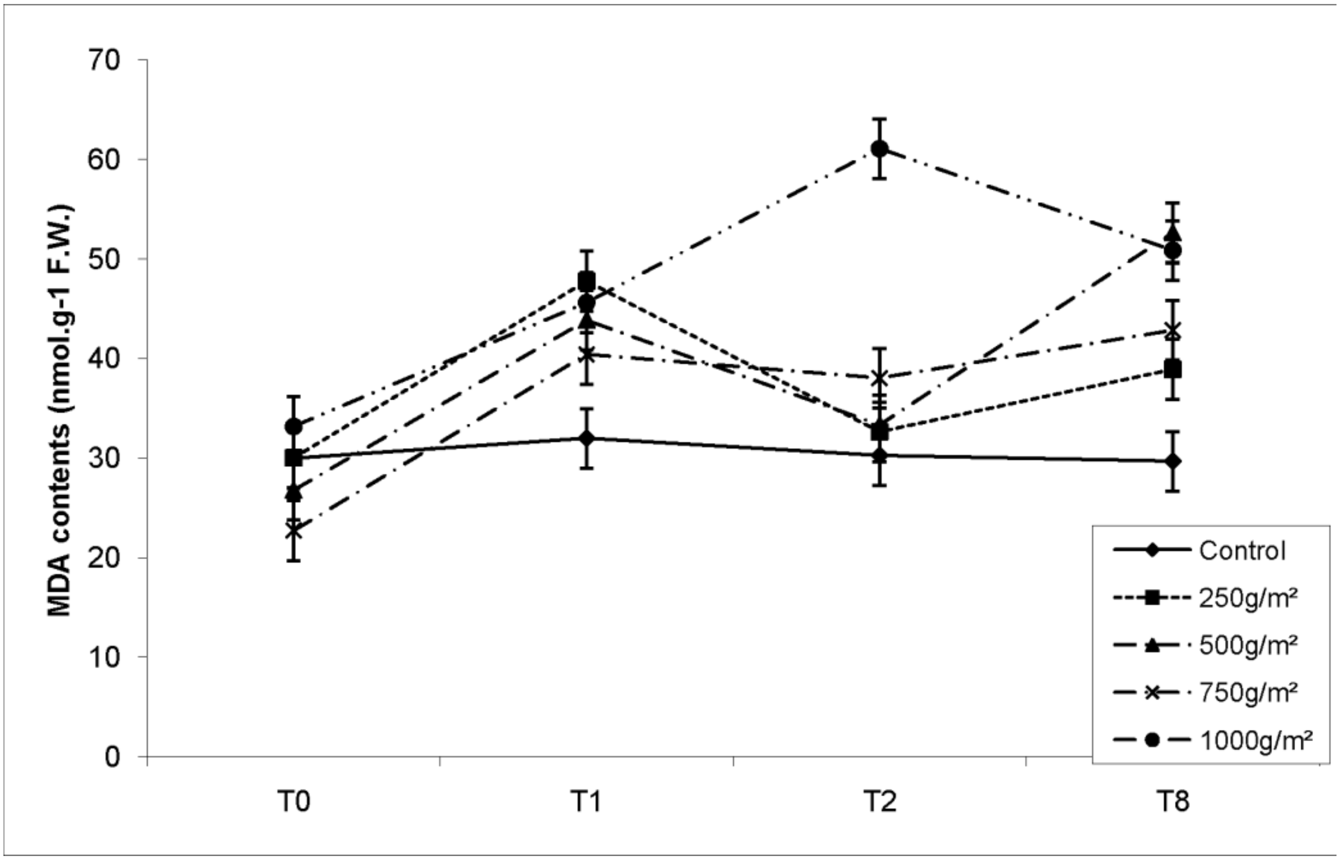

Figure 5. Malonedialdehyde (MDA) contents (nmol g^{-1} fresh weight [F.W.]) as a function of fuel load from time T0 to T8 on 5-year-old Corsican pine during a prescribed burn experiment, June 2008, Corsica. T0, measurements taken before the prescribed burn; T1, T2, and T8, measurements taken 24 hours, 48 hours, and 1 week, respectively, after the prescribed burn.

beds of pine needles (Mendes-Lopes et al. 2003). It should be noticed that the maximum temperatures reached do not provide the best estimate of fire severity because such temperature levels occur only during a few seconds. The characterization of the burn is better related to the exposure times of the canopy and soil to heat. Residence time above a given temperature provides a better estimation of potential damage to trees (Pérez and Moreno 1998). The impact of fire on trees can therefore be estimated from residence time above 60°C. At this threshold temperature, heat-induced biochemical changes of organic matter start to occur (Valette et al. 1994) and lethal tissue damage occurs after 60 seconds of exposure (Kayll 1963, Ducrey et al. 1996).

It appears clear that stress to pines increases significantly with fuel load. The applicability of these experiments is increased by their being carried out under natural weather conditions with natural fuels. This study represents the first in which chlorophyll fluorescence and lipid peroxidation were used to measure stress on Corsican pine, such that the only comparisons of those measurements available in the literature were on different species. For holly oak (*Quercus ilex*), Fv/Fm values between 0.75 and 0.85 were considered as normal for correctly hydrated plants (Fleck et al. 1996), suggesting that the control in our study did not suffer from any stress during the experiment. Dash and Mohanty (2001) showed a thermal post-stress decrease of Fv/Fm on wheat (*Triticum aestivum*) subjected to 40°C, then a return to pre-stress values in 24 hours, similar to our findings. According to Ali et al. (2005) and Fracheboud (2008), the decrease of Fv/Fm indicates that a portion of PSII reactional centers were damaged. Dash and Mohanty (2001) suggest in their study that thermal stress inhibits the accumulation of chlorophylls and carotenoids (electron carriers), provoking a decrease of chlorophyll *a* fluorescence and photosynthesis. A decrease in fluorescence observed for barley (*Hordeum vulgare*) at temperatures >44°C was linked to the irreversible inactivation of PSII. This inactivation is apparently due to changes in the structure of PSII in the electron transport chain, which would prevent the recombination of the different charges for chlorophyll excitation (Čajánek et al. 1998).

During our experiment, the variations of Fv/Fm were proportional to the fuel load, indicating proportional thermal stress. Heat increases the number of damaged reactional centers and the inhibition of PSII in thylakoids. Photoinhibition, and thus the number of damaged reactional centers, appeared to approach irreversibility around fuel loads of 750 and 1000 g m^{-2}.

A significant increase of MDA (60%) was seen between T0 and T1 for all fuel loads. Dash and Mohanty (2001) similarly measured an increase of 46% on wheat subjected to thermal stress. The authors explain that this increase is due to the oxidative lipid degradation of cells due to the thermal stress. The presence of TBARS confirms that important products of lipid peroxidation have been liberated from damaged membranes (Tang and Newton 2004). For this parameter, oxidative damages also approached irreversibility for the fuel load of 1000 g m^{-2}, as MDA content approximately doubled. At this level, plants may not be able to counteract oxidative damages through antioxidative defense systems (Dash and Mohanty 2001, Tang and Newton 2004).

These analyses of physiological and biochemical parameters are in agreement with our morphological observations, with percentages of chlorotic foliage increasing steeply with increases in fuel loading. The probability of survival of a given percentage of chlorotic foliage depends on tree species. Rigolot (2004) showed that Aleppo pine survives below 75% of chlorotic foliage, but that Italian stone pine (*Pinus pinea*) survives up to 90% of chlorotic foliage if the trunk is $<30\%$ burned.

The observation of the impact of fire on tree trunks shows that the heat received by the needles is not the only factor to take into account while studying the mechanisms of response to thermal stress. Indeed, Ducrey et al. (1996) explained that a significant heat exposure of the trunk or roots leads to the destruction of phloem tissues, interrupting translocation of carbohydrates and nutrients in the plant. Also, cavitation in xylem tracheids (embolism) can lead to irreversible losses of hydraulic conductance, provoking a strong and rapid hydric stress (Cochard 2006). The vertical distribution of temperatures showed that temperature was highest at the level of the litter and trunk. It is thus probable that the phenomenon of cavitation was caused during our experiment. Indeed, Fleck et al. (1996) showed that a decrease of Fv/Fm can cause a decrease of the hydric potential of a plant.

This preliminary study shows that prescribed burning induces damage for 5-year-old pines for fuel loads of 750 g m^{-2} or greater. These results relate to field conditions in that this fuel load corresponds to 2–3 years of litter accumulation under Corsican pine (Cannac et al. 2009). It remains to be determined whether or not prescribed burning under young trees of Corsican pine will have a net benefit, although it can be inferred that reduction of fuel loads to <750 g m^{-2} will help protect young trees from subsequent fire. It would also be informative to study the response of pines over a longer period, in order to follow their post-burn resistance to summer and winter climatic conditions. It will also be important to develop a protocol of embolism measurement (Fernández et al. 2001), a study of heat shock protein involvement (ubiquitous protective polypeptides whose expression is induced when cells are subjected to heat; Wahid et al. 2007), and to monitor the growth of the trees, to guide appropriate forest management using prescribed burning.

LITERATURE CITED

Ali, M.B., E.J. Hahn, and K.Y. Paek. 2005. Effects of temperature on oxidative stress defence systems, lipid peroxidation and lipoxygenase activity in *Phalaenopsis*. Plant Physiology and Biochemistry 43:213–223.

Alonso, M., M.J. Rozados, J.A. Vega, P. Pérez-Gorostiaga, P. Cuinas, M.T. Fonturbel, and C. Fernandez. 2002. Biochemical responses of *Pinus pinaster* trees to fire induced trunk girdling and crown scorch: secondary metabolites and pigments as needle chemical indicators. Journal of Chemical Ecology 28:687–700.

Byram, G.M. 1959. Combustion of forest fuels. Pages 61–89 *in* K.P. Davis (ed.). Forest fire control and use. McGraw-Hill, New York.

Čajánek, M., M. Štroch, I. Lachetová, J. Kalina, and V. Spunda. 1998. Characterization of the photosystem II inactivation of heat-stressed barley leaves as monitored by the various parameters of chlorophyll *a* fluorescence and delayed fluorescence. Journal of Photochemistry and Photobiology B: Biology 47:39–45.

Cannac, M., V. Pasqualini, T. Barboni, F. Morandini, and L. Ferrat. 2009. Phenolic compounds of *Pinus laricio* needles: a bioindicator of the effects of prescribed burning in function of season. Science of the Total Environment 407:4542–4548.

Cochard, H. 2006. Cavitation in trees. Comptes Rendus Physique 7:1018–1026.

Cornic, G. 2007. L'émission de fluorescence chlorophyllienne. Régulation de l'activité du PSII et estimation du flux d'électrons dans les thylacoïdes sur des feuilles intactes. Guide pratique de l'utilisation de l'émission de la fluorescence chlorophyllienne. www.ese.u-psud.fr/IMG/pdf/Emission_de_la_fluorescence_chlorophyllienne--Mesure_et_utilisation.pdf [accessed 24 Aug 2010]. [In French.]

Dash, S., and N. Mohanty. 2001. Evaluation of assays for the analysis of thermo-tolerance and recovery potentials of seedlings of wheat (*Triticum aestivum* L.) cultivars. Journal of Plant Physiology 158:1153–1165.

Dorey, S., M. Kopp, P. Geoffroy, B. Friting, and S. Kauffman. 1999. Hydrogen peroxide from the oxidative burst is neither necessary nor sufficient for hypersensitive cell death induction, phenylalanine ammonia lyase stimulation, salicylic acid accumulation, or scopoletin consumption in cultured tobacco cells treated with elicitin. Journal of Plant Physiology 121:163–172.

DRAF. 2007. Plan de Protection des Forêts et des Espaces Naturels contre les Incendies en Corse 2006–2012. Direction Régionale de l'Agriculture et de la Forêt, Ajaccio, France. [In French.]

Ducrey, M., F. Duhoux, R. Huc, and E. Rigolot. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. Canadian Journal of Forest Research 26:1366–1374.

Fernandes P., A.M., and H.S. Botelho. 2004. Analysis of the prescribed burning practice in the pine forest of northwestern Portugal. Journal of Environmental Management 70:15–24.

Fernandes P., A.M., and E. Rigolot. 2007. The fire ecology and management of maritime pine (*Pinus pinaster* Ait.). Forest Ecology and Management 241:1–13.

Fernández, J.E., M.J. Palomo, A. Díaz-Espejo, B.E. Clothier, S.R. Green, I.F. Girón, and F. Moreno. 2001. Heat-pulse measurements of sap flow in olives for automating irrigation: tests, root flow and diagnostics of water stress. Agricultural Water Management 51: 99–123.

Fleck, I., D. Grau, M. Sanjose, and D. Vidal. 1996. Influence of fire and tree-fell on physiological parameters in *Quercus ilex* resprouts. Annals of Forest Science 353(2–3):337–348.

Fracheboud, Y. 2008. Using chlorophyll fluorescence to study photosynthesis. Unpublished report. Institute of Plant Sciences, ETH, Zürich, Switzerland.

Gamisans, J., and J.F. Marzocchi. 1996. La flore endémique de la Corse. Edisud, Aix-en-Provence, France. [In French.]

Groppa, M.D., M.L. Tomaro, and M.P. Benavides. 2001. Polyamines as protectors against cadmium or copper-induced oxidative damage in sunflower leaf discs. Plant Science 161:481–488.

Hubert, B., E. Rigolot, and T. Turlan. 1991. Les incendies de forêts en région méditerranéenne: nouveaux enjeux pour la recherche. Science Technique Technologie 18:8–15. [In French.]

Jouili, H., and E. El Ferjani. 2003. Changes in antioxidant and lignifying enzyme activities in sunflower roots (*Helianthus annuus* L.) stressed with copper excess. Comptes Rendus Biologies 326: 639–644.

Kayll, A.J. 1963. Heat tolerance of Scots pine seedling cambium using tetrazolium chloride to test viability. Canada Department of Forestry Publication 1006, Forest Research Branch, Ottawa, ON, Canada.

Leone, V., and R. Lovreglio. 2004. Conservation of Mediterranean pine woodlands: scenarios and legislative tools. Plant Ecology 171: 221–235.

Maksymiec,W., M. Wójcik, and Z. Krupa. 2006. Variation in oxidative stress and photochemical activity in *Arabidopsis thaliana* leaves subjected to cadmium and excess copper in the presence or absence of jasmonate and ascorbate. Chemosphere 66:421–427.

Mendes-Lopes, J.M.C., J.M.P. Ventura, and J.M.P. Amaral. 2003. Flame characteristics, temperature–time curves, and rate of spread in fires propagating in a bed of *Pinus pinaster* needles. International Journal of Wildland Fire 12:67–84.

Pérez, B., and J.M. Moreno. 1998. Methods for quantifying fire severity in shrubland-fires. Plant Ecology 139:91–101.

Quézel, P., and F. Médail. 2003. Ecologie et biogéographie des forêts du bassin méditerranéen. Elsevier (Collection Environnement), Paris, France. [In French.]

Rigolot, E. 2004. Predicting postfire mortality of *Pinus halepensis* Mill. and *Pinus pinea*. Plant Ecology 171:139–151.

Tang, W., and R.J. Newton. 2004. Increase of polyphenol oxidase and decrease of polyamines correlate with tissue browning in Virginia pine (*Pinus virginiana* Mill.). Plant Science 167:621–628.

Valette, J.C., V. Gomendy, J. Marechal, C. Houssard, and D. Gillon. 1994. Heat-transfer in the soil during very low-intensity experimental fires—the role of duff and soil-moisture content. International Journal of Wildland Fire 4:225–237.

Wahid, A., S. Gelani, M. Ashraf, and M.R. Foolad. 2007. Heat tolerance in plants: an overview. Environmental and Experimental Botany 61:199–223.

Zar, J.H. 1984. Biostatistical analysis. Second edition. Prentice-Hall International Edition, Englewood Cliffs, New Jersey.