



Tree Physiology 36, 967–982
doi:10.1093/treephys/tpw044



Research paper

Impacts of prescribed fire on *Pinus rigida* Mill. in upland forests of the Atlantic Coastal Plain

Nicholas J. Carlo¹, Heidi J. Renninger^{2,3}, Kenneth L. Clark⁴ and Karina V.R. Schäfer^{1,2,5}

¹Department of Earth and Environmental Sciences, Rutgers University, 101 Warren St, Newark, NJ 07102, USA; ²Department of Biological Sciences, Rutgers University, 195 University Ave., Newark, NJ 07012, USA; ³Department of Forestry, Mississippi State University, Thompson Hall, Box 9681, Mississippi State, MS 39762, USA; ⁴Silas Little Experimental Forest, USDA Forest Service, 501 Four Mile Road, New Lisbon, NJ 08064, USA; ⁵Corresponding author (karinavr@andromeda.rutgers.edu)

Received September 30, 2015; accepted April 18, 2016; handling Editor Roberto Tognetti

A comparative analysis of the impacts of prescribed fire on three upland forest stands in the Northeastern Atlantic Plain, NJ, USA, was conducted. Effects of prescribed fire on water use and gas exchange of overstory pines were estimated via sap-flux rates and photosynthetic measurements on *Pinus rigida* Mill. Each study site had two sap-flux plots, one experiencing prescribed fire and one control (unburned) plot for comparison before and after the fire. We found that photosynthetic capacity in terms of Rubisco-limited carboxylation rate and intrinsic water-use efficiency was unaffected, while light compensation point and dark respiration rate were significantly lower in the burned vs control plots post-fire. Furthermore, quantum yield in pines in the pine-dominated stands was less affected than pines in the mixed oak/pine stand, as there was an increase in quantum yield in the oak/pine stand post-fire compared with the control (unburned) plot. We attribute this to an effect of forest type but not fire per se. Average daily sap-flux rates of the pine trees increased compared with control (unburned) plots in pine-dominated stands and decreased in the oak/pine stand compared with control (unburned) plots, potentially due to differences in fuel consumption and pre-fire sap-flux rates. Finally, when reference canopy stomatal conductance was analyzed, pines in the pine-dominated stands were more sensitive to changes in vapor pressure deficit (VPD), while stomatal responses of pines in the oak/pine stand were less affected by VPD. Therefore, prescribed fire affects physiological functioning and water use of pines, but the effects may be modulated by forest stand type and fuel consumption pattern, which suggests that these factors may need to be taken into account for forest management in fire-dominated systems.

Keywords: forest disturbance, forest fire, gas exchange, sap-flux, water use.

Introduction

Fire plays a major role in many forest ecosystems around the globe such as the fynbos in South Africa (van Wilgen et al. 2010, van Wilgen 2013), the prairies in the American Midwest (Grimm 1984, Hobbs et al. 1991, Briggs and Knapp 1995) and the Pine Barrens in New Jersey and Long Island (Forman and Boerner 1981, Little 1998). Fire adaptations in the New Jersey Pinelands include serotinous cones of the pines, thick bark and epicormic sprouting after fire (Givnish 1981, Schwilk and Ackerly 2001, He et al. 2012). The pitch pines (*Pinus rigida* Mill.) require a stand-replacing wildfire for seed dispersal and seedling

establishment (Forman and Boerner 1981, Little 1998, Landis et al. 2005). However, due to fire suppression or decreased fire frequency (Abrahamson and Abrahamson 1996), oaks have become established and the ecological force of fire to reset succession in the New Jersey Pinelands is diminishing (Little and Moore 1949, Little 1973, 1998, Clark et al. 2014b). Short-term studies of post-fire ecosystem responses have found both positive and negative or no changes in individual tree productivity or growth (Busse et al. 2000, Reich et al. 2001, Keeling and Sala 2012). These include increases in growth following fire (Boerner et al. 1988, Gilbert et al. 2003, Battipaglia et al. 2014), increased or transient changes in photosynthesis

(Gilbert et al. 2003, Sala et al. 2005, Renninger et al. 2013), increases in water use (Renninger et al. 2013), transient responses in water use (Clinton et al. 2011), a decrease in water use (O'Brien et al. 2010), changes in nutrient supply dynamics (Neary et al. 1999, Reich et al. 2001, Gray and Dighton 2006, Lavoie et al. 2010) or no changes in soil nutrients (Richter et al. 1982). Complicating tree responses to fire are also the prevailing meteorological conditions during fire as heat and higher spatially explicit vapor pressure deficit (VPD) could lead to cavitation in branches with subsequent mortality (Kavanagh et al. 2010). These changes in physiological and abiotic responses can be attributed to a variety of factors. For example, mortality of the understory increases resources such as water, therefore decreasing resource competition, and combustion of litter increases nutrient availability for overstory trees (Abrahamson 1984, Peterson and Ryan 1986, Ryan and Reinhardt 1988, Covington and Sackett 1992, Abrahamson and Abrahamson 1996, Bova and Dickinson 2005, Certini 2005, Gray and Dighton 2006, 2009, Rozas et al. 2011).

The physical extent of a fire's effect on biological processes can also extend belowground, including tree root–fungal interactions and belowground microbial processes (Smith et al. 2004, Hart et al. 2005b, Gray and Dighton 2006, 2009, Mikita-Barbato et al. 2015). For example, low-intensity surface fires can smolder and burn organic matter causing severe root damage, lowering the amount of water and nutrients the tree is capable of acquiring (Ahlgren and Ahlgren 1960, Hart et al. 2005a, Varner et al. 2009, O'Brien et al. 2010). However, Clark et al. (2015) found that most fires from 2004 to 2010 in the New Jersey Pinelands on the Atlantic Coastal Plain did not burn the organic horizon, where most shallow fine roots would be located (Clark et al. 2015). Furthermore, an intense fire can have severe impacts on soil microbial communities by altering their composition and biomass for a number of years (Mabuhay et al. 2003, Certini 2005), curtailing nutrient release and thus affecting photosynthesis. Taken together, this could create a more nutrient-poor soil and thus lower forest growth and thereby productivity (Busse et al. 2000, Lavoie et al. 2010).

Due to the inherent variability of fire behavior (Hiers et al. 2009, Loudermilk et al. 2012, 2014), and the many variables that can affect the consumption of fuels during a fire, it is obvious that prescribed fires do not act uniformly across spatial scales, forest types and meteorological conditions (Ryan et al. 2013). While meteorological conditions such as VPD and wind-speed (Moritz et al. 2010), as well as fuel moisture and temperature, are large drivers of fire behavior (Hiers et al. 2009, Loudermilk et al. 2012, 2014), total fuel loading, fuel arrangement and small-scale variations in fuel characteristics have also been shown to contribute to fire severity (Anderson 1982, Thaxton and Platt 2006, Loudermilk et al. 2012, 2014). A low-intensity fire that burns mainly forest floor materials aids in greater soil fertilization (Gray and Dighton 2006, 2009), whereas

a higher intensity fire will burn shrub stems, which effectively reduces competition for water and nutrients (Mkhabela et al. 2009). Therefore, even in similar forest types, fires and their associated effects can vary due to large-scale meteorological differences (Westerling et al. 2006, Meyn et al. 2010, Daniau et al. 2012), microclimate and fuel characteristics (Boring et al. 2004, Thaxton and Platt 2006, Loudermilk et al. 2012, Brewer et al. 2013). It is, therefore, important to study multiple fire events across different forest types to better understand how fire behavior affects physiological processes (DeSouza et al. 1986, Sala et al. 2005, Keeley 2009, Varner et al. 2009).

This study seeks to test the effects of prescribed fires on overstory pines across multiple forest types. By measuring leaf-level photosynthesis rates at both control (unburned) and burned plots before and after each fire, the hypothesis that photosynthesis of overstory pines is more increased after fire in burned vs control (unburned) plots will be tested. By monitoring sap-flux and meteorological data at all of these sites both before and after fire, the hypothesis that water use is increased is tested, which may then subsequently also increase either stomatal conductance, photosynthesis or leaf area. In a previous study, it was demonstrated that after an initial decrease in water use following the fire, there was an increase in water use persisting until the late summer (Renninger et al. 2013). Thus, by replicating this experiment across two more fires at different forest stand types, this study aims to build upon our previous study to assess whether these results are generalizable across the dominant forest types that are subject to prescribed fire in this region, which are dominant (pure) pine forests or oak/pine forests consisting of predominantly oaks with a smaller fraction of pines in the stand.

Materials and methods

Site descriptions

The New Jersey Pine Barrens (Pinelands) is a globally unique ecosystem, located in the coastal plains of southern New Jersey. It is generally a *P. rigida* (pitch pine) and *Quercus* spp. (oak) dominated forest ecosystem, characterized by frequent disturbance regimes of both wildfire and prescribed burns (Scheller et al. 2011, Clark et al. 2015). These prescribed burns are conducted by the New Jersey Forest Fire Service (NJFFS) with a goal of burning over 8000 ha annually within a designated area. The three study sites were located within the Pinelands National Preserve, which is a forested coastal plain ecosystem, covering 450,000 ha in central and southern New Jersey. The soils at all sites are generally composed of well-drained, acidic, nutrient-poor sands, with a characteristic low water holding and cation exchange capacity (Schäfer 2011). The topography is relatively flat, with a mean elevation of 33 m above sea level. Each study site was composed of one control (unburned) plot and one burned plot where pine sap-flux and pine photosynthesis

measurements were conducted. For the 3 years of the study, 2011, 2012 and 2013, mean annual temperatures were 13.0, 13.1 and 11.9 °C, with 1358, 997 and 1085 mm annual rainfall, respectively. Due to the proximity of each coupled control (unburned) and burned plot, the meteorological differences between fire and control (unburned) plots for each respective site were assumed to be negligible (Renninger et al. 2015).

The oak/pine site was located within the Rutgers Pinelands Research Field Station (also known as Silas Little Experimental Forest, SL), in Pemberton, NJ, USA (Clark et al. 2012, Schäfer et al. 2014a, 2014b). The SL control (unburned) plot was located at 39°55'0"N, 74°36'0"W and its associated burned plot was located 350 m to the west within the NJFFS area to be burned. This study site was composed of a mixed oak/pine forest, with an oak understory. The species composition included *Quercus prinus* L. (chestnut oak), *Quercus velutina* Lam. (black oak), *Quercus alba* L. (white oak) and *P. rigida* (pitch pine, Table 1).

One of the pine-dominated sites (see Table 1) was located in the Brendan T. Byrne State Forest (BTB), in New Lisbon, NJ, USA (39°53'27.66"N, 74°34'46.63"W). The BTB burned plot within the NJFFS area to be burned was located 250 m north-west of the BTB control plot.

The second pine-dominated site was located near the Cedar Bridge Fire Tower (CB), in Lacey Township, NJ, USA (39°84'21"N, 74°37'77.92"W), which had already been burned previously in 2008 (Clark et al. 2015). The control plot for CB was located 800 m south-southeast of the CB burned plot, which was within the NJFFS area to be burned. Table 1 shows species composition, stand density and tree sizes, along with the measurement plot size and the date each site was burned.

Fire treatment

The NJFFS is charged to burn ~8000 ha each year with a fire frequency of about 5–10 years. The primary purpose of these prescribed burns is to lower fuel loading and forest floor litter buildup in order to prevent or curtail catastrophic wildfires that can damage life and property (<http://www.nj.gov/dep/parksandforests/fire/aboutus.html> or www.njwildfire.org). These fire treatments in the Northeast USA commenced after research conducted by Silas and Moore (Little and Moore 1945, 1949) in the late 1940s to affect economically viable maintenance of pitch and shortleaf pines in the New Jersey Pine Barrens and reduce wildfire risk. The last wildfires in the experimental plots were in 1963 for SL and BTB and in 1995 for CB. The prescribed fire interval for SL and BTB is 8–12 years and for CB every 5 years (see also Table 1). The prescribed fires take place in the late winter/early spring between January and March when air temperature does not exceed 16 °C and the relative humidity is between 30 and 50% so as to avoid too dry conditions but have no snow cover and dormant conditions (Little and Moore 1945, 1949, Little et al. 1948). In addition, the fuel moisture should be between 5 and 10% of dry weight and the fuel loading (built up index) between 6 and 40. The best wind conditions are when the direction is NW, W, SW, North or South and the speed between 2.2 and 4.5 m s⁻¹, which were met during these fires. The fire is set by drip fuel torches along the edges and the internal firebreaks as backing fires (see Figure 1) that through wind facilitates a low-intensity burning of the area against the wind with low flame length (Clark et al. 2014b). In general, these forest fires have small first-order effects on overstory trees such as crown scorching, stem or phloem damage (Skowronski et al. 2007, 2014), but can have an effect on forest floor nutrient cycling (Gray and Dighton 2006, 2009).

Table 1. Stand species composition and density of the three sites for the control (unburned) and burned plots. Diameter at breast height with standard error of the mean in parenthesis for all the trees in the measurement plot. CB, Cedar Bridge; SL, Silas Little; and BTB, Brendan T. Byrne site.

Site	Species composition (%)	Mean DBH (cm)	<i>P. rigida</i> measured	Plot size (ha)	Date burned
BTB Burned (2011)	<i>P. rigida</i> 100	18.2 (1.5)	10	0.030	20 March 2011
BTB Control (unburned) (2011)	<i>P. rigida</i> 64.5	19.6 (1.8)	9	0.030	NA
	<i>Q. alba</i> 22.6	10.7 (1.4)			
	<i>Q. velutina</i> 12.9	10.4 (1.1)			
	<i>Q. prinus</i> 20.5	9.1 (1.2)			
SL Burned (2012)	<i>P. rigida</i> 37.4	11.0 (1.5)	3	0.055	6 March 2012
	<i>Q. alba</i> 21.7	10.7 (0.8)			
	<i>Q. prinus</i> 20.5	9.1 (1.2)			
	<i>Q. velutina</i> 20.5	15.2 (0.9)			
SL Control (unburned) (2011)	<i>P. rigida</i> 0.7	5.5 (1.2)	3	0.302	NA
	<i>Pinus echinata</i> 8.4	9.3 (1.8)			
	<i>Q. alba</i> 6.9	7.8 (1.2)			
	<i>Quercus stellata</i> 3.7	6.1 (1.0)			
	<i>Q. prinus</i> 58.1	10.0 (0.5)			
	<i>Q. velutina</i> 14.8	13.4 (1.5)			
	<i>Quercus coccinea</i> 6.9	12.6 (1.8)			
	Unknown 0.5	10.9			
CB Burned (2013)	<i>P. rigida</i> 96.2	16.1 (1.3)	8	0.021	15 March 2013
	<i>Q. coccinea</i> 3.9	4.4			
CB Control (unburned) (2013)	<i>P. rigida</i> 100	16.4 (1.2)	10	0.025	NA



Figure 1. Image of the fire at Silas Little in 2012 (top image, photo courtesy K.V.R.S.) and at Cedar Bridge in 2013 (bottom image, photo courtesy N.J.C.).

Meteorological data

Each site was equipped with meteorological instruments that were connected to Campbell Scientific data loggers (CR3000 or CR1000, Campbell Scientific Inc., Logan, UT, USA), in which half-hourly averages or totals, based on the instrument, were calculated and stored. Soil moisture was measured with four 0–30 cm CS616 Water Content Reflectometers (Campbell Scientific Inc.), placed at the four cardinal directions from the center of each plot. At the two pine-dominated control plots, soil temperature was also measured using four Campbell Scientific Inc. model 107 soil temperature probes at ~15 cm depth. At both the oak/pine SL control plot and pine-dominated BTB control plot, a Licor LI190SB quantum sensor (LI-COR Biosciences Inc., Lincoln, NE, USA) was used to measure photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) in the understory below the canopy. Throughfall was measured at each control plot using a Texas Electronics TE525M tipping rain gauge (Texas Electronics, Dallas, TX, USA) and starting in March 2013, four 5 inch ClearVU Rain and Sprinkler Gauges (Taylor Precision Group, LLC, Oakbrook, IL, USA) were installed at each of the two CB plots, four were installed in June 2013 at each SL plot and all were measured weekly. Relative

humidity (%) and air temperature ($^{\circ}\text{C}$) (HMP45C, Vaisala Inc., Helsinki, Finland) were measured at two-thirds of mean canopy height in each control (unburned) plot, and data were used to calculate saturated vapor pressure and VPD according to an equation derived from Goff and Gratch (1946).

Understory and forest floor consumption

Fuel consumption during each fire was estimated from pre-fire and post-fire biomass loadings collected from 1-m² clip plots located throughout each burn unit. At all three stands that were burned, 20–30 1 m² clip plots were randomly located and biomass collected pre- and post-burn was separated into forest floor and shrubs. The forest floor materials comprised fine fuels, reproductive parts such as acorns and pine cones, and coarse wood fuels (see Figure 2). Understory vegetation was composed solely of standing dormant shrub stems because very little live foliage was present during the dormant season burns. Samples were separated, dried at 70 $^{\circ}\text{C}$ for a minimum of 72 h and then weighed. The amount of fuel consumed in each fuel class was estimated by comparing fuel loading before and after each fire.

Photosynthesis data

Along with meteorological and sap-flux data (see below), photosynthetic parameters were collected and compared both before and after the fires. Parameters were extracted from light response-net assimilation, as well as net assimilation to leaf

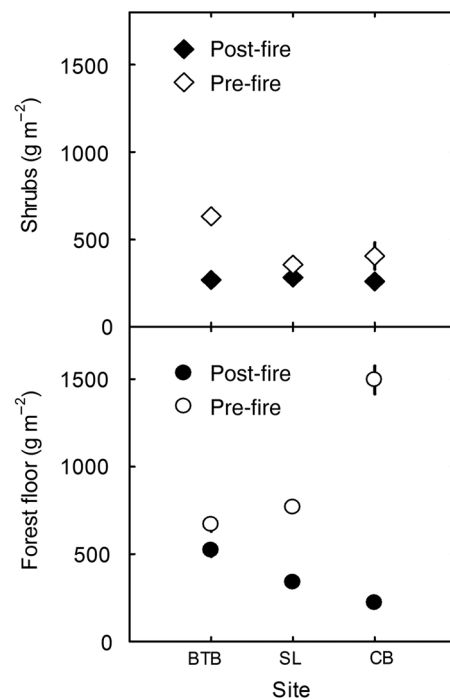


Figure 2. Shrub and forest floor biomass before and after the respective fires of the three sites: SL—Silas Little oak/pine forest, CB—Cedar Bridge pine forest and BTB—Brendan T. Byrne pine forest. Bars are standard error of the mean.

internal CO₂ concentration ($A-C_i$) curves that were measured using a Licor 6400 XT Portable Photosynthesis System (LI-COR Biosciences Inc.). The $A-C_i$ curves are measures of photosynthetic rates under a range of CO₂ concentrations within the leaf at saturating light levels ($1500 \mu\text{mol m}^{-2} \text{s}^{-1}$). Light response curves are measures of photosynthetic rates under a range of light intensities at ambient CO₂ concentration (set at 400 p.p.m.). Measurements were taken during each growing season on the current cohort of needles, as well as before and after each fire. To obtain each measurement, branches were cut from the tree using a pole pruner (Jameson LLC, Clover, SC, USA). The branches were then recut under water to ensure water flow resumed. Finally, after the measurements were complete, the needle material within the chamber was stored in sealed plastic bags until they were scanned using an Epson Perfection V30 flatbed scanner (Epson, Long Beach, CA, USA). By using Imaged (Scion Image, Frederick, MD, USA), needle areas were determined using threshold analysis and a 1-cm² reference square. The needle area estimates within the chamber were then used to area-correct the photosynthesis measurements in the chamber.

Deriving parameters from photosynthesis data

After collection of the photosynthetic data, photosynthetic parameters were inferred from the light response and $A-C_i$ curves (Farquhar et al. 1980). From the light response curves, exponential equations were fitted to the data, and maximum assimilation, quantum yield, light compensation point and dark respiration rate were calculated using Sigma Plot version 11.0 (Systat Software Inc., Chicago, IL, USA). For the $A-C_i$ curves, the same methods as for the light curve were used, extracting maximum assimilation and carboxylation efficiency, and CO₂ compensation point via linear curve fitting. In addition, maximum Rubisco-limited carboxylation rates ($V_{C_{\max}}$), maximum electron transport-limited carboxylation rates ($J_{\max}$) and carboxylation rates limited by triose phosphate utilization (TPU) were also obtained using nonlinear regressions (Farquhar et al. 1980, Sharkey 1985, Harley and Sharkey 1991) that were optimized via a best fit in an attempt to minimize the least sums of squares error between modeled and measured data (Sharkey et al. 2007). Measurements were made under a range of temperature conditions; thus, $V_{C_{\max}}$ and $J_{\max}$ were corrected to a standard temperature of 25 °C via equations derived from Campbell and Norman (1998) and Bernacchi et al. (2003), respectively. Finally, instantaneous leaf-level parameters including stomatal conductance, transpiration, water-use efficiency and internal to ambient CO₂ concentrations (C_i/C_a) were extracted from photosynthesis measurements taken at saturating light conditions (PPFD > $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) and ambient CO₂ chamber conditions (400 p.p.m.).

Leaf nutrient and isotope analysis

Needles from the same branch as the needle samples measured for photosynthesis were analyzed for internal concentrations of

nitrogen (N), phosphorus, potassium and magnesium. Furthermore, groups of currently senesced pine needles were collected from tree branches and forest floor (when sufficient amounts were not available on the branches) in the winter of 2013–14 to determine nutrient loadings of litter on the forest floor and the amount of nutrient re-translocation during leaf senescence. Three batches of pine needles were collected for each burned and control plot at the second pine stand (CB) and at the oak/pine stand (SL), totaling 12 pine samples. Extractable nutrient contents were determined by the University of Massachusetts, Amherst, Soil and Plant Tissue Testing Laboratory (Amherst, MA, USA). In addition, the needles measured for photosynthesis were sent to the University of California Davis, Stable Isotope Facility (Davis, CA, USA) for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic analysis. In some cases, extra samples from the same branch were added, in order to have enough material for analysis. Samples were dried in an oven at 60 °C for at least 72 h, ground to powder via a Spex Certiprep 80000 Mixer/Mill (Metuchen, NJ, USA), weighed into tin capsules and sent out to the laboratory for analysis. Nitrogen and carbon concentrations (C% and N%, respectively) were determined as well as C isotopic data of the needle ($\delta^{13}\text{C}$), which were used to calculate intrinsic water-use efficiency, the ratio between external and internal concentrations of CO₂ (C_i/C_a) and the discrimination factor of carbon ¹³C ($\Delta\text{‰}$).

Sap-flux measurements

To quantify the amount of water used by overstory pines, the thermal dissipation (TD) method was used (Granier 1987). Individual pines were selected to be a representative sample of the size distribution of the stand, while accounting for a large enough diameter at breast height (DBH; 1.35 m above ground, in cm) to accommodate the sensor lengths. At all sites, *P. rigida* individuals with a DBH > 10 cm were fitted with 2-cm-long sensors (Table 1), while individuals larger than 30 cm in DBH were fitted with two 2-cm-long sensors, one at the 0–2 cm sapwood depth range and another at the 2–4 cm range, to account for radial variation of sap-flux (Phillips et al. 1996). The calculated sap-flux density with the TD method was cross-validated with sap-flux derived by the heat balance method (Čermák et al. 1973) and found to be comparable (Renninger and Schäfer 2012); thus, the original calibration by Granier (1987) was deemed justifiable (Köstner et al. 1998, Steppe et al. 2010).

The TD sap-flux sensors were placed approximately at 1.3–1.5 m from the ground at azimuthal locations of 0°. The heated sensors were placed, on average, 10 cm above the reference sensors, to minimize influence of a temperature gradient along the trunk of the tree. The installation of the TD sensors is outlined by Renninger and Schäfer (2012). Sap-flux sensors were connected to AM16/32 multiplexers and relayed to dataloggers (Campbell Scientific Inc.). The dataloggers collected data every 30 s, and 30-min averages were stored. The raw, differential

voltage data were then converted to sap-flux rates (J_s ; $\text{kg m}^{-2} \text{s}^{-1}$; Eq. 1) using a modified matlab code (The Mathworks Inc., Natick, MA, USA) by Oishi et al. (2008) and the calibration equation originally devised by Granier (1987).

$$J_s = 0.119 \times \left[\frac{\Delta T_{\max}}{\Delta T} - 1 \right]^{1.23} \quad (1)$$

where the temperature difference ($\Delta T_{\max}$) is the greatest recorded difference between the heated and reference TD probes (i.e., when there was no water moving) and ΔT is the difference in temperature during sap-flux movement. In addition, to account for night-time transpiration, the criteria that VPD is <0.5 kPa for >2 h, PPFD is ~ 0 and temperature is not too low (greater than -5°C) to avoid frozen stems were applied to calculate the baseline for sap-flux conversion (Oishi et al. 2008).

Calculating sapwood depths

In order to scale sap-flux to whole tree and canopy transpiration, sapwood area is required. Thus, by analyzing 10 pitch pine core samples taken in 2011 using an increment borer (Haglof Inc., Madison, MS, USA, Table 2), linear regressions were devised to find relationships between DBH (1.3 m above the ground) and sapwood area (A_{SW}), sapwood depth (D_{SW}), heartwood depth (D_{HW}) and heartwood area (A_{HW}). The equations used to calculate these biometric parameters can be found in Table 2. Two separate relationships were devised and separated by diameter class. For individuals with a DBH <5.4 cm, it was assumed that the entire wood area was sapwood. To estimate bark depth (D_{BK}) for all trees, a section of the bark for 20 trees was carved out, and the D_{BK} was manually measured to the nearest 0.1 mm using a ruler. For the trees with a DBH <5.4 cm, a D_{BK} of 0.35 cm was assumed, as the linear relationship held true for the larger trees, and reached a minimum $D_{\text{BK}} \sim 0.35$ cm.

Scaling up sap-flux

In order to account for radial patterns in sap-flux rates in *Pinus* species, the ratios of inner sensor sap-flux rates (see Table 1) to outer sensor sap-flux rates were taken. It was found that, on

Table 2. Biometric equations for deriving sap wood areas (m^2) necessary for scaling up sap-flux measurements to total canopy conductance. The biometric parameters used were heart wood depth (D_{HW}), bark depth (D_{BK}), heart wood area (A_{HW}), sapwood depth (D_{SW}), sapwood area (A_{SW}) and total area (TA). All data are derived from this study (see text for details).

	DBH <0.054 (m)	DBH >0.054 (m)	R^2
D_{HW}	0	$0.5 \times \text{DBH} - D_{\text{BK}} - D_{\text{SW}}$	NA
D_{BK}	0.0035	$0.0909 \times \text{DBH} - 0.000484$	0.87
A_{HW}	0	$D_{\text{HW}}^2 \times \pi$	NA
D_{SW}	$\text{DBH}/2 - D_{\text{BK}}$	$\text{DBH} \times 0.2234 + 0.000484$	0.84
A_{SW}	$D_{\text{SW}}^2 \times \pi$	$\text{TA} - A_{\text{HW}}$	NA
TA	A_{SW}	$(\text{DBH}/2 - D_{\text{BK}})^2 \times \pi$	NA

average, inner sapwood was moving water at 0.55 ($\text{g H}_2\text{O m}^{-2}$ sapwood area s^{-1}) times the rate of the outer sensors, similar to the 0.6 rate found in other studies (Phillips et al. 1996, Renninger et al. 2013). By coupling sap-flux rates with stand-level biometric data such as tree density, A_{SW} and leaf area index (LAI in m^2 leaf area per m^2 ground area), half-hourly individual sap-flux rates were averaged across the sites, and scaled up to the canopy leaf-level transpiration (E_L). The DBH and stand densities were measured each year in the dormant season. The differences in these values were used to assume a linear increase in A_{SW} throughout the growing season (Schäfer 2011). The LAI was calculated using biometric equations developed by Whittaker and Woodwell (1968) for pitch pine. Using the same allometric relationships was justified by (i) the rain gauge data, as the SL burned and control plots were equal and the CB control plot had only slightly higher throughfall than its burned plot, suggesting similar LAIs and (ii) all fires were understory fires with no crown scorch within our experimental plots or very limited crown scorch outside our experimental plots (Clark et al. 2015) and, thus, there was no or only a small loss in overstory pine leaf area. However, since Whittaker and Woodwell (1968) calculated LAI by leaf perimeter, a correction factor between its needle perimeter and a two-dimensional plane was determined by measuring the cross-sectional 3D perimeter of 18 pine needles across the 6 plots (3 in each site) with a metric Vernier caliper (Scherr Tumico, St. James, MN, USA). The two-dimensional projection for *P. rigida* was determined to be 0.352 of the whole perimeter. A growth dynamic for loblolly pine needles, time shifted to match the region's seasonality, was applied to the LAI to account for changing leaf area over time (Kinerson et al. 1974).

Canopy stomatal conductance (G_{si}) was calculated as follows:

$$G_{\text{si}} (\text{mmol m}^{-2} \text{s}^{-1}) = \frac{n \times E_L \times G_v \times T_A}{\text{VPD} \times R} \quad (2)$$

where n is the molar weight of water ($0.018 \text{ kg mol}^{-1}$), E_L is canopy transpiration per unit leaf area, G_v is the universal gas constant scaled for water vapor ($0.461 \text{ m}^3 \text{ kPa kg}^{-1} \text{ K}^{-1}$), T_A is air temperature in Kelvin, VPD is vapor pressure deficit ($\text{VPD} > 0.6 \text{ kPa}$) and R is the molar volume of an ideal gas ($0.0224 \text{ m}^3 \text{ mol}^{-1}$). This equation assumes that the canopy is well coupled to the atmosphere and that water storage in the trunk of the tree was negligible to overall sap-flux, or VPD was time lagged appropriately (Köstner et al. 1992, Granier and Loustau 1994, Phillips et al. 1997). For the oak/pine forest (SL), the canopy is assumed to be well coupled as a study had shown that the middle of the canopy was only 3% different in VPD than the top of the canopy (Renninger et al. 2014). The pine-dominated forests (CB and BTB) were assumed to be like most coniferous forests, which have been shown to be well coupled in past studies (Phillips et al. 1996).

Once G_{si} for the pines was calculated, the response of G_{si} was plotted against the natural logarithm of VPD, by separating the

data into bins of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (Schäfer et al. 2000). Then, after applying boundary line analysis to select the optimal data, the justification and benefits of which are outlined in Vanderklein et al. (2012), the relationship between the intercept and slope for G_{si} at saturated PPFD levels (G_{sisat}) (mean of light levels $>1600 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) was selected to compare the burned plots with control (burned) plots, as this is an adequate indicator of how G_{si} responds to VPD under optimum environmental conditions (Oren et al. 1999, Schäfer et al. 2000).

Statistical analysis

For analyzing the photosynthetic parameters, we used generalized linear mixed regression models in Matlab version R2014b (fitglme procedure, The Mathworks Inc.), accounting for the repeated measurements before, immediately after the fire and the summer after the fire as a fixed effect (time) to account for pre-fire conditions (Blackwell et al. 2006) with the sites (CB, SL and BTB) as grouping (nesting) variables and the burned and control plot as random effects in the model (Blackwell et al. 2006). Furthermore, forest type (pine or oak/pine) and its interaction with a fire effect were included as potential explaining variables (fixed effects) in the model. This analysis accounts for the spatial and the temporal heterogeneity as each burned site is compared with its pre-fire condition and with a control site. The three groups (sites) can then be evaluated in their tendencies (increase, decrease or no change) that by elimination can only be due to the fire. A P -value of <0.05 was assumed to be significant. Furthermore, to quantify whether the individual fires had an effect on sap-flux rates for their respective stands, a generalized linear mixed regression model was employed as above, grouping daily sap-flux rates for each corresponding burned and control (unburned) plots, in order to test for effects of the fires, forest type and interaction thereof. This statistical analysis was chosen as it is not based on the assumptions inherent in the analysis of variance such as having equal variance and a balanced design, due to missing data (Blackwell et al. 2006, Bolker et al. 2009).

Results

Understory and forest floor consumption

All prescribed fires were primarily surface fires that affected the forest floor and understory shrubs, but had little to no effect on overstory trees. Consumption data differed in quality and quantity for each fire, reflecting initial fuel loading and fire behavior (Figure 2).

At BTB, the fire consumed similar quantities of shrub biomass and forest floor litter in 2011. While this fire did have the least amount of forest floor consumption (256 g m^{-2}), total consumption (both forest floor and shrubs) was intermediate (690 g m^{-2}) to all three sites. In 2012, the SL fire consumed only a small amount of shrub stems ($\sim 43 \text{ g m}^{-2}$) and a comparable amount

of forest floor (465 g m^{-2}) to the BTB site. In the 2013 CB fire, the highest biomass was consumed, with nearly $1400 \text{ g biomass m}^{-2}$, $\sim 80\%$ of which was fine litter and wood on the forest floor, and had a consumption of nearly 300 g of shrub biomass (Figure 2).

While similar quantities of forest floor were consumed at BTB and SL, at CB far more litter than in BTB and SL was consumed resulting in a significant difference pre- and post-fire in forest floor mass ($P < 0.0001$) with a significant effect of forest type ($P = 0.02$), but no interaction effect. While CB had the highest total consumption (95% higher than the BTB fire and 160% higher than the SL fire), it actually had 22% less shrub consumption than the BTB fire. Finally, SL had the least amount of shrub consumption, as it only had 12% of the shrub biomass that was consumed in the BTB fire and 15% of the CB fire, still resulting in a significant effect of shrub consumption ($P < 0.0001$), with an effect of forest type ($P = 0.001$) and a significant interaction across sites of fire and forest type ($P = 0.001$).

Photosynthetic parameters

The physiological responses of the overstory pines in all stands were analyzed using a linear mixed effects model and it was found that for almost all of the estimated parameters, there was no difference ($P > 0.05$, Tables 3 and 4, see Tables S1 and S2 available as Supplementary Data at *Tree Physiology* Online) between the burned and control (unburned) plots due to the fire except for the light compensation point, dark respiration and maximum assimilation of the $A-C_i$ curve (Table 3). Furthermore, a closer look into the data revealed that the effect of forest type in which the pines grew (either pure pine stand or oak/pine stand) was significant (Tables 3 and 4) for some parameters.

Light response curves Light response curves for the burned and control (unburned) plots did not differ in maximum assimilation rate or quantum yield, both before and after the fire, but did differ due to the forest type (Table 3). While light compensation point was significantly higher at the control plot at all sites both before and after the fire, forest type did not affect the light compensation point (Table 3). Pre-fire, the light compensation point was nearly five times greater for the burned plot compared with the control (unburned) plot (Table 3, see Table S1 available as Supplementary Data at *Tree Physiology* Online), while following the fire, it was only $\sim 50\%$ greater in the control plot, indicating more of an increase in the burned plot post-fire, but there was no effect due to forest type and no interaction between forest type and fire (Table 3).

Net assimilation to leaf internal CO_2 concentration curves The J_{max} and TPU of the overstory pines in all of the stands did not differ following the fire, but did differ due to forest type (Table 3). However, V_{Cmax} exhibited no effect due to fire, forest type or an

Table 3. Results of photosynthetic parameters derived from light response and A–C_i curves. The table displays average values and standard errors (in parentheses) grouped for all control (unburned) and burned plots pre-fire and all post-fire values. The *P*-values show the results from the generalized linear mixed effects model with time as fixed effect to account for pre-burn differences. The effect of fire, forest type (oak/pine or pine forest) and interaction were tested, with burn and control (unburned) nested within sites. Significances are marked by bold lettering ($\alpha = 0.05$).

	Pre-fire		Post-fire		Fire effect	Forest type	Fire x forest type
	Control (unburned)	Burned	Control (unburned)	Burned			
Light curve parameter							
Maximum assimilation (μmol CO ₂ m ⁻² s ⁻¹)	8.7 (1.72)	11.2 (1.72)	15.4 (1.09)	13.6 (0.96)	0.56	0.0001	0.51
Quantum yield (μmol CO ₂ μmol ⁻¹ photon)	0.025 (0.0018)	0.029 (0.0037)	0.040 (0.0030)	0.039 (0.0021)	0.58	0.003	0.07
Light compensation point (μmol photon m ⁻² s ⁻¹)	67.0 (14.02)	12.6 (2.58)	38.8 (5.34)	26.8 (3.81)	0.017	0.58	0.77
Dark respiration rate (μmol CO ₂ m ⁻² s ⁻¹)	2.11 (0.66)	0.43 (0.127)	1.59 (0.237)	1.11 (0.203)	0.03	0.08	0.94
A–C _i curve parameter							
Maximum assimilation (μmol CO ₂ m ⁻² s ⁻¹)	11.6 (1.34)	12.2 (2.53)	21.1 (1.69)	19.6 (1.83)	0.02	0.03	0.10
Carboxylation efficiency (μmol CO ₂ m ⁻² s ⁻¹ pp.m. ⁻¹)	0.077 (0.013)	0.042 (0.004)	0.100 (0.007)	0.130 (0.032)	0.77	0.17	0.03
CO ₂ compensation point (ppm)	68.9 (21.39)	34.2 (5.77)	59.6 (7.05)	57.6 (6.58)	0.88	0.0005	0.84
V _{Cmax} (μmol CO ₂ m ⁻² s ⁻¹)	41.9 (8.36)	49.9 (7.85)	60.2 (4.83)	70.3 (7.26)	0.64	0.12	0.12
J _{max} (μmol CO ₂ m ⁻² s ⁻¹)	81.1 (25.95)	72.4 (10.62)	120.4 (13.95)	105.7 (14.55)	0.76	0.0014	0.99
Tri-phosphate utilization (μmol CO ₂ m ⁻² s ⁻¹)	3.7 (1.08)	3.3 (0.3)	7.6 (0.75)	7.1 (0.88)	0.91	<0.0001	0.72

Table 4. Results of instantaneous photosynthetic parameters derived from saturated light (PPFD 1500 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ and greater) and ambient CO₂ (400 pp.m.) and isotopic analysis. The table displays average values and standard errors (in parenthesis) grouped for all control (unburned) and burned plots pre-fire and all post-fire values. Same analysis as Table 3.

	Pre-fire		Post-fire		Fire effect	Forest type	Forest type × fire
	Control (unburned)	Burned	Control (unburned)	Burned			
<i>C_i/C_a</i> instantaneous	0.64 (0.051)	0.63 (0.062)	0.64 (0.014)	0.57 (0.021)	0.19	0.63	0.28
<i>G_{si}</i> (mol H ₂ O m ⁻¹ s ⁻¹)	0.13 (0.02)	0.13 (0.03)	0.20 (0.016)	0.15 (0.013)	0.32	0.20	0.56
Water-use efficiency ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$)	3.9 (0.54)	4.1 (0.68)	3.2 (0.19)	3.6 (0.35)	0.40	0.46	0.055
Intrinsic water-use efficiency ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$)	80.1 (12.45)	83.5 (14.07)	76.5 (3.44)	95.9 (5.15)	0.27	0.65	0.20
$\delta^{13}\text{C}$ (‰)	–30.6 (0.39)	–30.1 (0.39)	–30.5 (0.16)	–30.4 (0.17)	0.89	0.053	0.44
$\delta^{15}\text{N}$ (‰)	–4.3 (0.35)	–3.9 (0.17)	–3.8 (0.17)	–4.1 (0.16)	0.95	0.52	0.09
<i>C</i> (‰)	51.1 (0.87)	48.6 (1.26)	48.3 (0.76)	50.0 (1.17)	0.03	0.37	0.33
<i>N</i> (‰)	1.1 (0.07)	1.1 (0.07)	1.1 (0.03)	1.1 (0.03)	0.001	0.0001	0.016
<i>C/N</i>	46.7 (2.72)	46.6 (2.72)	47.0 (1.4)	44.8 (1.04)	0.03	<0.0001	0.08
Isotopic water-use efficiency ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$)	93.2 (4.3)	99.0 (4.3)	94.3 (1.79)	95.1 (1.99)	0.89	0.053	0.44
Δ (‰)	18.5 (0.37)	18.0 (0.37)	18.4 (0.16)	18.3 (0.18)	0.89	0.053	0.44
<i>C_i/C_a</i>	0.62 (0.017)	0.61 (0.017)	0.62 (0.007)	0.62 (0.008)	0.89	0.053	0.44

interaction thereof (Table 3). Furthermore, carboxylation efficiency was not different due to fire or due to forest type, but showed a significant interaction of forest type and fire effects (Table 3). Upon further investigation, it was found that only the pine-dominated stands were different pre-fire, but similar post-fire, while the oak/pine stands were similar in the pre-fire period and different post-fire (see Table S1 available as Supplementary Data at [Tree Physiology](#) Online). The carboxylation efficiency in the control plot was nearly double the burned plot in the pine stands pre-fire, while post-fire, they were not different. The oak/pine stand showed no difference between burned and control plots pre-fire, but was higher in the burned plot (over twofold) post-fire; thus, fire had no effect overall, but the responses depended on forest type (Table 3, see Table S1 available as Supplementary Data at [Tree Physiology](#) Online).

Instantaneous gas exchange parameters In terms of instantaneous leaf-level gas exchange parameters derived from photosynthetic measurements at saturated light and ambient CO₂ levels, none exhibited any significant effect due to fire, forest type or any interactions (Table 4). Pre-fire and post-fire conditions for all of the instantaneous leaf-level parameters were not significantly different, although instantaneous C_i/C_a was roughly 11% higher in the control (unburned) plot post-fire compared with the burned plots, while instantaneous water-use efficiency was ~12% higher in the burned plot post-fire compared with the control (unburned) plot (Table 4). Intrinsic water-use efficiency was similar between burned and control (unburned) pre-fire, and 25% greater in the burned plot post-fire when compared with the control plot; however, none of them exhibited any statistical significance due to fire, forest type or an interaction thereof (Table 4, see Table S2 available as Supplementary Data at [Tree Physiology](#) Online).

Isotope analysis

Across forest types, there were no significant differences between burned and control (unburned) plots either before or after the fire for any isotopically derived parameters (Table 4). However, when considering forest type as a contributing factor, $\delta^{13}C$, isotopic water-use efficiency and C_i/C_a were slightly different in the oak/pine stand but similar in the pine-dominated stands (see Table S2 available as Supplementary Data at [Tree Physiology](#) Online); thus, there was no overall significant effect of forest type or interactions on these variables (Table 4). In

contrast, the N and C concentrations were significantly different due to the fire, as well as the C to N ratio (see Table S2 available as Supplementary Data at [Tree Physiology](#) Online), with a significant interaction of N concentration with forest type and fire (Table 4, see also Table S2 available as Supplementary Data at [Tree Physiology](#) Online). The C to N ratio was different due to forest type as well (see Table 4, Table S2 available as Supplementary Data at [Tree Physiology](#) Online).

Needle nutrient analysis

Following the fire at the CB stand, only potassium (K⁺) concentration significantly increased in pine needles in the burned plot (from 0.31 ± 0.01 to $0.35 \pm 0.05\%$), being ~30% higher compared with the control (unburned) plot post-fire ($0.27 \pm 0.02\%$, $P = 0.06$). All other nutrients analyzed either marginally increased in the control (unburned) plot, such as Mg²⁺ and Zn²⁺, or had no significant change. By the first summer growing season following fire, there were no longer signs of higher concentrations of K⁺ in the needles collected from the burned plot at CB ($0.30 \pm 0.03\%$, averaged across all sites, $P = 0.31$). At the BTB stand, the first summer after the fire K⁺ was also not different between the burned and control (unburned) plots ($0.50 \pm 0.11\%$ for both, $P = 0.59$). At SL, the opposite effect was observed with regards to K⁺, with no differences observed immediately prior to or right after the fire, but in the first summer growing season after the fire with the burned plot having 10% lower K⁺ ($0.50 \pm 0.11\%$) than the control (unburned) plot ($0.55 \pm 0.10\%$), but that was, however, not significant ($P = 0.72$).

The nutrient analysis of the senesced needles and leaves provided insight into the effects of overstory species composition nutrient loading on the forest floor and, thus, litter quality for the three sites (Table 5). Almost all nutrients analyzed had higher concentration by % weight in the oak leaves when compared with pine needles (Table 5). Nitrogen, phosphorus, calcium, manganese and boron were all ~70% higher, while potassium, copper and iron were ~50% higher in oak leaves (Table 5); thus, combustion of a similar quantity of oak leaves on the forest floor returns more cations to the soil than the combustion of needles.

Sap-flux

Due to similar meteorological and edaphic conditions between the burned and control (unburned) plots that were compared, the differences and changes in sap-flux can be attributed to the fire (Figure 3). Temperature range (approximately -10 to

Table 5. Leaf nutrient analysis results of recent dead leaves at the SL and CB sites. Values are concentrations by percent for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na), and in p.p.m. for zinc (Zn), copper (Cu), manganese (Mn), iron (Fe) and boron (B). Asterisks indicate a significant difference between oak and pine leaves ($\alpha = 0.05$). Standard errors are shown in parentheses.

Leaf type	N*	P*	K*	Ca*	Mg*	Na	Zn*	Cu*	Mn*	Fe*	B*
Oak	1.1 (0.07)	0.05 (0.00)	0.12 (0.08)	0.68 (0.04)	0.12 (0.00)	0.008 (0.00)	26 (2.2)	7.6 (0.29)	1398 (97.9)	46 (3.2)	26 (1.8)
Pine	0.6 (0.05)	0.02 (0.00)	0.08 (0.01)	0.35 (0.02)	0.06 (0.00)	0.010 (0.00)	49 (1.7)	5.2 (0.22)	610 (139.8)	33 (3.3)	13 (1.3)

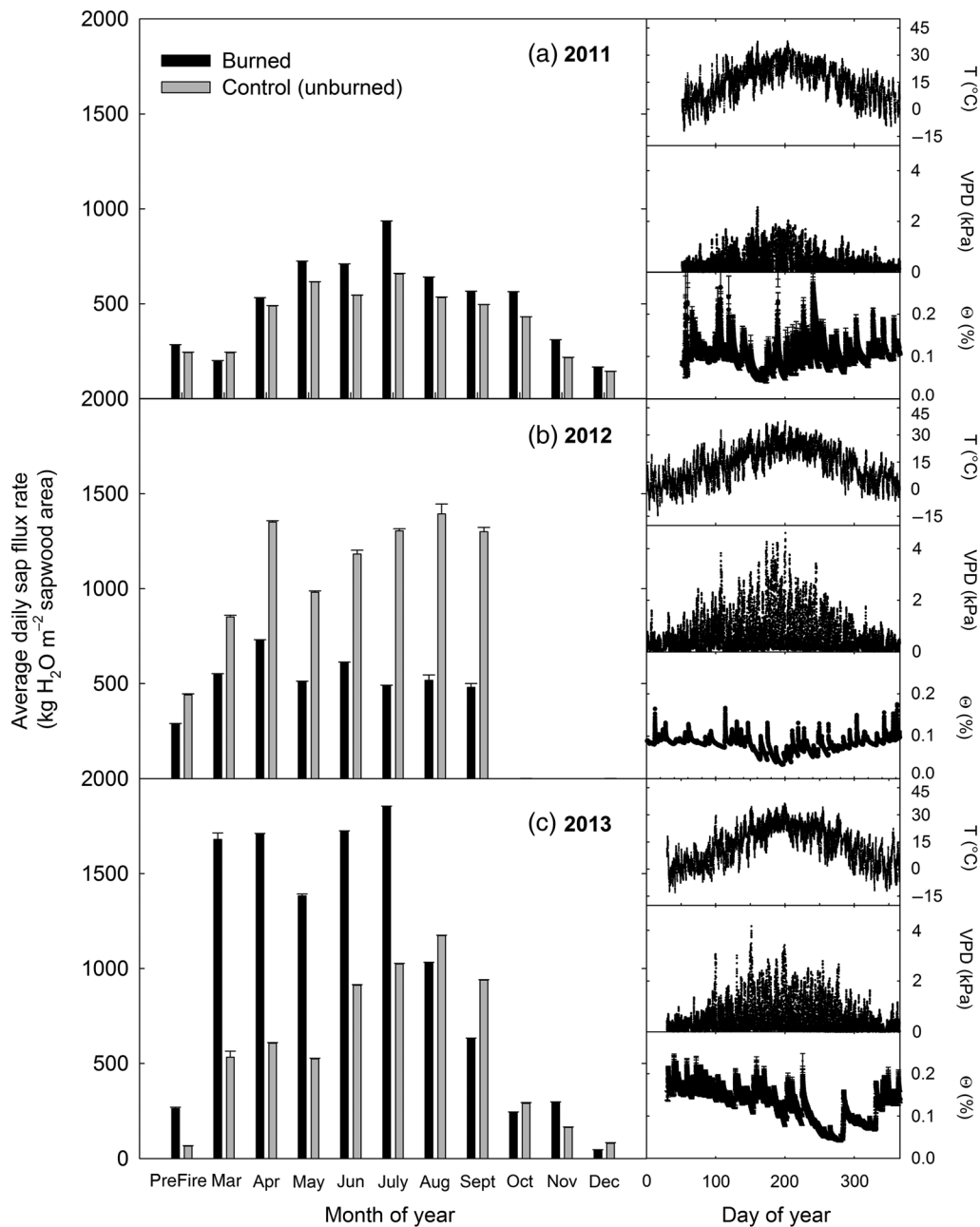


Figure 3. Daily sap-flux in kg H₂O m⁻² sapwood area averaged by month for all plots. BTB (a), burned in 2011; SL (b), burned in 2012; and CB (c), burned in 2013. Only days where both burned and control (unburned) plots had sufficient data were analyzed. Beside each graph are the corresponding meteorological data for that year with air temperature (°C) at the top, VPD (kPa) in the middle and volumetric water content (% soil moisture) at the bottom for each year, recorded at the control (unburned) plot for each site.

30 °C) and seasonality matched throughout all study sites and years, while VPD was between 0 and 4 kPa, and soil moisture content was generally between 5 and 20%. Comparing the meteorological conditions in the 3 years of study, mean daily VPD rarely exceeded 2 kPa in 2011, whereas in 2012, it even exceeded 4 kPa, significantly increasing evaporative demand. Likewise, soil moisture varied between the years, whereby average soil moisture was higher in 2011 than in 2012 or 2013. In 2013 in particular, a long drying period occurred at the end of the growing season (Figure 3).

The BTB fire of 2011 had no statistically significant influence on the amount of water being transpired per unit sapwood area, as evidenced by a lack of change in daily sap-flux totals for the burned plot compared with the control (unburned) plot (Figure 3a). However, steady increases in transpiration were shown in the burned plot when compared with the control plot for the first few months after the fire (Figure 3a).

The fire in the SL oak/pine forest of 2012 (Figure 3b) showed a more complex pattern, as the burned and control (unburned) plots were different in their transpiration rates pre-fire and

post-fire, persisting until August, while due to power outages and equipment failure, there were no sufficient data for the last few months (Figure 3b). However, it was found that, pre-fire, the pines in the burned plot were only transporting water at roughly two-thirds the rate of the control (unburned) plot per unit sapwood area. For the few months after the fire (April, May and June), the burned plot pines were transpiring water at only half the rate as the control (unburned) plot (Figure 3b). Finally, in the 3 months following June, the burned plot was only moving a little more than one-third the volume of water when compared with the control (unburned) plot (Figure 3b). Thus, as the growing season progressed, the pines in the burned plot were moving increasingly less water when compared with the control (unburned) plot.

In contrast, for the fire at CB in 2013, a clear increase of sap-flow rates at the fire site when compared with the control (unburned) site was demonstrated post-fire (Figure 3c). Initially, pre-fire and a few days following the fire in March, sap-flux rates between the burned and control (unburned) plots were comparable (Figure 3c). However, in the 4 months following the fire, the sap-flux rates at the burned plot were higher than the pines in the control (unburned) plot by 280, 260, 190 and 180%, respectively (Figure 3c).

Applying a linear mixed effects model for all three fires combined with fire and forest type plus interaction as fixed effects accounting for repeated measurements pre- and post-fire showed a significant effect of the fire ($P < 0.0001$) and forest type ($P = 0.01$) on daily sap-flow rates, as well as a significant interaction term ($P = 0.02$). Thus, the pines in each forest type responded to the fire, but in opposite directions, therefore signifying the importance of forest type in the analysis of effects of fires on transpiration.

Canopy stomatal conductance response to environmental parameters

By evaluating the response of G_{si} in pitch pine to the natural logarithm of VPD by separate PPFD levels, the slope and intercepts from the linear regressions of the higher PPFD values were used to infer the sensitivity of stomata to VPD, which is an indicator of how efficiently the stomata can act to prevent cavitation, with a ratio of 0.60 being the optimal range (Oren et al. 1999). This method allows for assessment of differences in G_{si} under similar VPD and light under the most optimal conditions. Thus, by comparing all burned and control (unburned) plots, the degree of deviation from the optimal line could be observed to assess what level of impact these fires were having on canopy-level stomatal conductance (Figure 4). Furthermore, since the optimal meteorological conditions for the 3 years were chosen and standardized to 1 kPa VPD, a comparison of the data was further justified (Figures 3 and 4). At CB, the fire of 2013 resulted in the burned plot being closer to the optimal range of 0.6, with a mean ratio of 0.49, while the control (unburned) plot

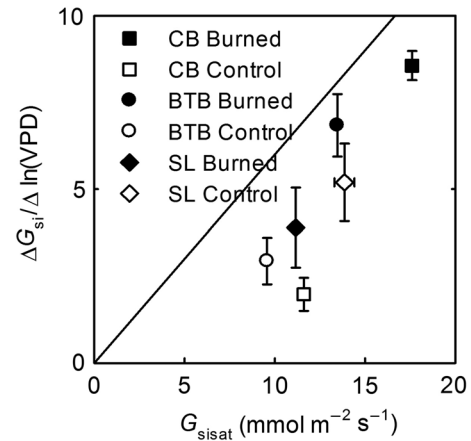


Figure 4. Average ratio of the response of G_{si} to VPD: slope ($\Delta G_{si}/\Delta \ln(\text{VPD})$) vs intercept at the three highest PPFD bins (mean $\sim 1600 \mu\text{mol m}^{-2} \text{s}^{-1}$) for all three sites, burned plots and control (unburned) plots, the year of their respective fires. Cedar Bridge (2013) is denoted by squares, SL (2012) is denoted by diamonds and BTB (2011) is denoted by circles. Filled symbols are burned plots and open symbols are unburned plots. Bidirectional error bars denote deviations from the mean for the slope and intercept for the three highest PPFD bins. The solid line denotes a 0.60 ratio, which is the optimal ratio to prevent uncontrollable embolism.

only had a mean ratio of 0.17 (Figure 4). The other pine-dominated site (BTB 2011) showed similar results, where the mean ratio was 0.51 at the burned plot, and only 0.30 at the control (unburned) plot (Figure 4). In contrast, the ratios were similar in the year of the fire for the oak/pine site (SL 2012), which had a mean ratio of 0.35 at the burned and 0.37 at the control (unburned) plot (Figure 4). Overall, there was a significant fire effect on the ratio ($P = 0.0005$), but not for the forest type ($P = 0.08$); however, there was a significant interaction (forest type $\times$ fire $P = 0.014$). Finally, it was shown that throughout the year of the fire, the CB burned plot had lower soil volumetric water content than the CB control (unburned) plot (data not shown). At the SL site, the opposite trend occurred, where the control (unburned) plot's soil had higher soil water content throughout the year of the fire compared with the burned plot (data not shown).

Discussion

The genus *Pinus* has a long ecological history of adapting to fire (Givnish 1981, Schwikl and Ackerly 2001, He et al. 2012) and, thus, is prone to rebound from fire quickly. However, due to management practices in forest stands, it is unclear whether prescribed fires that occur in the dormant season and are less intense (Keeley 2009) confer any significant advantage on overstory pine trees (Boerner 1981, Ryan et al. 2013). The goal of this study was to quantify the effects of prescribed fire on gas exchange and sap-flux rates in overstory pines, as this built upon a previous study by Renninger et al. (2013). By analyzing the

data using additionally two other fires in different stands, we could test whether the results of this study held true across multiple forest stand types and fire events in this region. Our measurements of the same physiological parameters pre- and post-fire at three different forest sites indicate that relatively low-intensity prescribed fires can cause moderate changes in some parameters, and that these changes are partially dependent on forest composition of each stand. Furthermore, not only did the forest type affect the response of pitch pine to prescribed fire, but the inherent differences between the consumption of each fire could have potentially affected the response as well (Boerner 1983, Reich et al. 2001). Thus, by assessing the biomass consumed by the fire, a possible explanation for the different responses in each site can be conjectured.

Effects of prescribed fire on gas exchange

Previous studies focusing on single fire events have found responses that both support and contradict the findings in this study. In an Australian savanna, Cernusak et al. (2006) demonstrated an increase in stomatal conductance and C_i/C_a in burned plots, but no change in photosynthetic assimilation rates. When the results from all three fires were pooled in our study, we observed no change in photosynthetic assimilation rates, in instantaneous C_i/C_a or in stomatal conductance (Table 4). In contrast, a study in a Wisconsin mixed oak forest showed an increase in photosynthetic rates following one fire instance across four different species of trees, primarily due to increased foliar N due to post-fire mineralization (Reich et al. 1990). Also, an increase in photosynthetic capabilities was found post-fire in maple and oak seedlings due to higher foliar nutrient content, but this effect diminished over time (Gilbert et al. 2003). Furthermore, in a ponderosa pine stand, transient responses of photosynthetic rate and stomatal conductance to prescribed fire treatment were observed with no difference in foliar N (Sala et al. 2005).

Across all three fires, pre-fire burned and control (unburned) and post-fire control (unburned) $V_{C_{max}}$ values were consistently within the range of 40–60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (see Table S1 available as Supplementary Data at *Tree Physiology* Online), which is consistent with what has been found in maritime pine (*Pinus pinaster*) (Porté and Loustau 1998) and ponderosa pine (*Pinus ponderosa*) (Misson et al. 2006). Only burned plots post-fire exceeded these values, where $V_{C_{max}}$ averaged 70 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which was higher than the control (unburned) plots post-fire (Table 3, see Table S1 available as Supplementary Data at *Tree Physiology* Online). A possible explanation for this increase could be an increase of available nutrients post-fire (Boerner 1983, Gray and Dighton 2009). However, in the needle nutrient results, in which concentrations were analyzed pre- and post-fire and not the total amount of nutrients due to lack of needle biomass estimates, no differences were found in any significant nutrient concentrations except an increase in needle N at the CB

site (Busse et al. 2000, Pellegrini et al. 2015). In addition, no needle scorch was observed within the experimental plots and, thus, no observable difference in needle leaf area between control (unburned) and burned plots (Clark et al. 2015). These results could be partially due to the differences in the quality or quantity of fuel combusted, as oak leaves were found to have many more nutrients than pine needles (Figure 2, Table 5); however, the stand that had increased leaf N concentration had few oaks, but had the highest forest litter combustion, which could have made more N available (CB, see Table S2 available as Supplementary Data at *Tree Physiology* Online, Figure 2; Boerner 1983, Gray and Dighton 2009).

Effects on sap-flux

Higher photosynthetic rates may either lead to increased water savings or higher C uptake with similar water use (Katul et al. 2010). The long-term isotopic data, however, indicated a decrease in isotopic water-use efficiency over time, although it is a long-term average and may not have been indicative of the fire's short-term effects but reflective of the long-term growth condition. For example, a previous prescribed fire in 2008 in the same pine-dominated CB stand as in this study, showed a 25% reduction in overall evapotranspiration due to loss of both understory and overstory leaf area in the flux footprint area (Clark et al. 2012, 2014a) and as was also shown in other pine stands (Dore et al. 2010). Thus, it is not surprising that the clearest effect in terms of temporary increase of water use of the overstory pines was observed in this stand (Figure 3), as the burned plot had higher sap-flux rates in the few months following the fire, before it became equivalent with its control (unburned) plot again (Clark et al. 2015). The increase found in this study could either largely be due to cavitation or damage to the understory shrubs (Kavanagh et al. 2010), and/or an increase in N concentration from the burned litter (Boerner 1983, Reich et al. 2001, Certini 2005, Gray and Dighton 2009). The transient increase in sap-flux rates could also be attributed to delayed shrub growth in the understory following a resurgence of greater growth later in the growing season (Lavoie et al. 2010, Clinton et al. 2011). The fire did effectively reduce shrub growth early in the season, but the stimulated growth, which is common after a fire (Ahlgren and Ahlgren 1960), could have been responsible for the loss of increased transpiration rates, explaining why water use equaled the control (unburned) plot by August of the same year (Figure 3).

In contrast, at the pine-dominated BTB stand, there was no difference in average daily transpiration per m^2 A_{SW} between the control (unburned) and the burned plot following the fire, which is consistent with results found in previous studies on pines (Lavoie et al. 2010, Clinton et al. 2011). With a relatively moderate burning of the aboveground understory biomass, it is possible that reduction in competition in the understory could still have occurred (Dumas et al. 2007).

Finally, the most intricate results of the three stands were associated with the oak/pine SL stand, because pre-fire transpiration rates of the overstory pines were different pre-fire, with the control (unburned) plot having higher sap-flow rates (Figure 3). However, a decline in rates post-fire was noted at the burned plot, as it gradually moved less water when compared with the control (unburned) plot. Due to a lack of shrubs consumed, and despite the moderate amount of forest floor litter consumed, which could make the needles more productive, sap-flux rates did not increase, but decreased as signified by the forest type–fire interaction term. This could be a result of very little competition being removed via understory shrub consumption, coupled with an increase in growth of the surrounding oaks and some possible root damage (Busse et al. 2000, Smith et al. 2004, Varner et al. 2009). Previous studies have shown oaks and other hardwoods to increase photosynthetic capacity (Boerner et al. 1988) and transpiration (Reich et al. 1990) post-fire, indicating that the overstory and understory oaks may have been capitalizing on the extra resources, outcompeting the overstory pines (Boerner 1981). This could have resulted in decreased rates in the burned plot post-fire, as no needle scorch was observed. Alternatively, in the burned plot at SL, the removal of some understory and litter with black charred forest floor may have increased radiation load and thus soil evaporation during the dormant season, thus reducing soil moisture availability in this site (Whelan et al. 2015); however, this was not found at this site as soil moisture was actually higher in the burned plot. Although the actual rooting depth of the pines and oaks are not known, some evidence seems to suggest that the oaks do have access to groundwater or deeper soil water (Robinson et al. 2012, Song et al. 2014, Renninger et al. 2015).

Effects on canopy stomatal response to environmental parameters

Canopy-level data indicated that both pine-dominated stands were more suited to capitalize on available nutrients as a result of the fire via their stomatal response to VPD than the oak/pine stand. Despite all of the relationships falling below the 0.60 optimization line, which is consistent with a study conducted on dwarf pitch pine in the Long Island Pine Barrens (Vanderklein et al. 2012), the burned plots in the pine-dominated stands were significantly closer to the 0.60 line than pines in the control (unburned) plots. This indicates that the pines in the burned plots in pine-dominated stands were transpiring more per unit leaf area than their corresponding control (unburned) plot on any given day due to their heightened coupling with VPD, which is consistent with the sap-flux rate data (Figure 4). A possible explanation could be a higher availability of water due to lessened competition from the understory, although this it is hard to determine as the CB control (unburned) plot actually had higher soil moisture on average than the CB burned plot the year of the fire. However, this could be a result of the overstory pines in the

CB burned plot using more water. Thus, this would indicate that utilization of nutrients is a limiting factor (Renninger et al. 2015), as the pines in the pine-dominated control (unburned) plot were transpiring less even though they had more available water.

In contrast to the pine-dominated stands, pines in the burned and control (unburned) plots at the oak/pine stand showed no differences of G_{si} response to VPD (significant forest type–fire interaction term). The burned plot had higher soil moisture levels than the control (unburned) plot, but there was no difference in throughfall depths (data not shown). The SL burned plot's similarity to the control (unburned) plot's sensitivity to VPD suggests that they did not alter their canopy stomatal behavior due to the prescribed fire. However, the overstory pines were limited by some other factor, possibly competition from highly productive oaks as a result of the fire.

Conclusion

This study suggests that fire did indeed affect gas exchange and water use in overstory pines, although forest type and quality and quantity of combusted fuels played a role in how they were affected. Certain leaf-level photosynthetic parameters, such as light compensation point, dark respiration and maximum assimilation of the $A-C_i$ curve, decreased as a result of the fire, and particularly in the oak/pine forest, concurrent with the release of nutrients from partially consumed fuels during the fire and reduced understory competition. However, due to growth conditions, it was found that other photosynthetic parameters, such as CO_2 compensation point, J_{max} and quantum yield, were increased in the overstory pines in the oak/pine stand, but not in the pine-dominated stands, differences that reflected forest type and were not a result of the fire per se. Also, it was found that at the pine-dominated stands, sap-flux rates increased as a result of the fire, where the stand with the highest understory combustion showed the clearest trend. However, at the oak/pine stand, a decrease in sap-flux rates was noted, despite some reduction in competition from the understory. This can be potentially attributed to an increase in productivity of codominant oaks in the stand (significant forest type effect) or increased soil evaporation. Furthermore, it was evident that the pines in the pine-dominated stand were more sensitive to changes in VPD on the canopy level and thus optimized water consumption under a given condition more than their control (unburned) plot counterparts, indicating that they were better suited to optimize available resources. Therefore, while relatively low-intensity prescribed fires did have some effect on photosynthetic parameters and water use of overstory pines and effectively made more resources available, the degree to which individual trees were able to capitalize upon newly available resources relied heavily on the composition of the surrounding stand.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Acknowledgments

The authors thank R. Tripathee for laboratory support, Dr D. Vanderklein for reviewing and editing the manuscript, the New Jersey Forest Fire Service for conducting the prescribed fires and the Rutgers Pinelands Field Station crew.

Conflict of interest

None declared.

Funding

This research was supported by United States Department of Agriculture joint venture agreement 10-JV-11242306-136 and by the U.S. Department of Energy, Office of Science (Biological and Environmental research), United States Department of Energy under award number DE-SC0007041 both to K.V.R.S.

References

- Abrahamson WG (1984) Post-fire recovery of Florida Lake Wales ridge vegetation. *Am J Bot* 71:9–21.
- Abrahamson WG, Abrahamson CR (1996) Effects of fire on long-unburned Florida uplands. *J Veg Sci* 7:565–574.
- Ahlgren IF, Ahlgren CE (1960) Ecological effects of forest fires. *Bot Rev* 26:483–533.
- Anderson HE (1982) Aids to determining fuel models for estimating fire behavior. USDA For. Serv. Gen. Tech. Rep. INT-122. Intermt. For. and Range Exp. Stn., Ogden, UT, 22 p.
- Battipaglia G, Strumia S, Esposito A, Giuditta E, Sirignano C, Altieri S, Rutigliano FA (2014) The effects of prescribed burning on *Pinus halepensis* Mill. as revealed by dendrochronological and isotopic analyses. *For Ecol Manag* 334:201–208.
- Bernacchi CJ, Pimentel C, Long SP (2003) *In vivo* temperature response functions of parameters required to model RuBP-limited photosynthesis. *Plant Cell Environ* 26:1419–1430.
- Blackwell E, de Leon CFM, Miller GE (2006) Applying mixed regression models to the analysis of repeated-measures data in psychosomatic medicine. *Psychosom Med* 68:870–878.
- Boerner REJ (1981) Forest structure dynamics following wildfire and prescribed burning in the New Jersey pine barrens. *Am Midl Nat* 105:321–333.
- Boerner REJ (1983) Nutrient dynamics of vegetation and detritus following two intensities of fire in the New Jersey pine barrens. *Oecologia* 59:129–134.
- Boerner REJ, Lord TR, Peterson JC (1988) Prescribed burning in the oak-pine forest of the New Jersey pine barrens: effects on growth and nutrient dynamics of two *Quercus* species. *Am Midl Nat* 120:108–119.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135.
- Boring LR, Hendricks JJ, Wilson CA, Mitchell RJ (2004) Season of burn and nutrient losses in a longleaf pine ecosystem. *Int J Wildland Fire* 13:443–453.
- Bova AS, Dickinson MB (2005) Linking surface-fire behavior, stem heating, and tissue necrosis. *Can J For Res* 35:814–822.
- Brewer NW, Smith AMS, Hatten JA, Higuera PE, Hudak AT, Ottmar RD, Tinkham WT (2013) Fuel moisture influences on fire-altered carbon in masticated fuels: an experimental study. *J Geophys Res Biogeosci* 118:30–40.
- Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *Am J Bot* 82:1024–1030.
- Busse D, Simon A, Riegel GM (2000) Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. *For Sci* 46:258–268.
- Campbell G, Norman JM (1998) An introduction to environmental biophysics, 2nd edn. Springer, New York, 286 p.
- Čermák J, Deml M, Penka M (1973) A new method of sap flow rate determination in trees. *Biol Plant* 15:171–178.
- Cernusak LA, Hutley LB, Beringer J, Tapper NJ (2006) Stem and leaf gas exchange and their responses to fire in a north Australian tropical savanna. *Plant Cell Environ* 29:632–646.
- Certini G (2005) Effects of fire on properties of forest soils: a review. *Oecologia* 143:1–10.
- Clark KL, Skowronski N, Gallagher M, Renninger H, Schäfer K (2012) Effects of invasive insects and fire on forest energy exchange and evapotranspiration in the New Jersey pinelands. *Agr For Meteorol* 166–167:50–61.
- Clark KL, Skowronski NS, Gallagher MR, Renninger H, Schäfer KVR (2014a) Contrasting effects of invasive insects and fire on ecosystem water use efficiency. *Biogeosci Discuss* 11:6509–6523.
- Clark KL, Skowronski N, Gallagher M (2014b) The fire research program at the Silas Little Experimental Forest, New Lisbon, New Jersey. In: Hayes CD, Stout LS, Crawford HR, Hoover PA (eds) *USDA Forest Service experimental forests and ranges: research for the long term*. Springer, New York, pp 515–534.
- Clark KL, Skowronski N, Gallagher M (2015) Fire management and carbon sequestration in pine barren forests. *J Sustain Forest* 34:125–146.
- Clinton BD, Maier CA, Ford CR, Mitchell RJ (2011) Transient changes in transpiration, and stem and soil CO₂ efflux in longleaf pine (*Pinus palustris* Mill.) following fire-induced leaf area reduction. *Trees* 25:997–1007.
- Covington WW, Sackett SS (1992) Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For Ecol Manag* 54:175–191.
- Daniau A-L, Bartlein PJ, Harrison SP et al. (2012) Predictability of biomass burning in response to climate changes. *Global Biogeochem Cycles* 26:GB4007. doi:10.1029/2011GB004249
- DeSouza J, Silka PA, Davis SD (1986) Comparative physiology of burned and unburned *Rhus laurina* after chaparral wildfire. *Oecologia* 71:63–68.
- Dore S, Kolb TE, Montes-Helu M et al. (2010) Carbon and water fluxes from ponderosa pine forests disturbed by wildfire and thinning. *Ecol Appl* 20:663–683.
- Dumas S, Neufeld HS, Fisk MC (2007) Fire in a thermic oak-pine forest in Linville Gorge wilderness area, North Carolina: importance of the shrub layer to ecosystem response. *Castanea* 72:92–104.
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149:78–90.
- Forman RTT, Boerner RE (1981) Fire frequency and the pine barrens of New Jersey. *Bull Torrey Bot Club* 108:34–50.
- Gilbert NL, Johnson SL, Gleeson SK, Blankenship BA, Arthur MA (2003) Effects of prescribed fire on physiology and growth of *Acer rubrum*

- and *Quercus* spp. seedlings in an oak-pine forest on the Cumberland Plateau, KY. *J Torrey Bot Soc* 130:253–264.
- Givnish TJ (1981) Serotiny, geography, and fire in the pine barrens of New Jersey. *Evolution* 35:101–123.
- Goff JA, Gratch S (1946) Low-pressure properties of water from –160 to 212 F. *Trans Am Soc Heat Vent Eng* 52:95–122.
- Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol* 3:309–320.
- Granier A, Loustau D (1994) Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agr For Meteorol* 71:61–81.
- Gray DM, Dighton J (2006) Mineralization of forest litter nutrients by heat and combustion. *Soil Biol Biochem* 38:1469–1477.
- Gray DM, Dighton J (2009) Nutrient utilization by pine seedlings and soil microbes in oligotrophic pine barrens forest soils subjected to prescribed fire treatment. *Soil Biol Biochem* 41:1957–1965.
- Grimm EC (1984) Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. *Ecol Monogr* 54:291–311.
- Harley PC, Sharkey TD (1991) An improved model of C_3 photosynthesis at high CO_2 : reversed O_2 sensitivity explained by lack of glycerate reentry into the chloroplast. *Photosynth Res* 27:169–178.
- Hart SC, Classen AT, Wright RJ (2005a) Long-term interval burning alters fine root and mycorrhizal dynamics in a ponderosa pine forest. *J Appl Ecol* 42:752–761.
- Hart SC, DeLuca TH, Newman GS, MacKenzie MD, Boyle SI (2005b) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *For Ecol Manag* 220:166–184.
- He T, Pausas JG, Belcher CM, Schwillk DW, Lamont BB (2012) Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. *New Phytol* 194:751–759.
- Hiers JK, O'Brien JJ, Mitchell RJ, Grego JM, Loudermilk EL (2009) The wildland fuel cell concept: an approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. *Int J Wildland Fire* 18:315–325.
- Hobbs NT, Schimel DS, Owensby CE, Ojima DS (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72:1374–1382.
- Katul G, Manzoni S, Palmroth S, Oren R (2010) A stomatal optimization theory to describe the effects of atmospheric CO_2 on leaf photosynthesis and transpiration. *Ann Bot* 105:431–442.
- Kavanagh K, Dickinson MB, Bova AS (2010) A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. *Fire Ecol* 6:80–94.
- Keeley JE (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *Int J Wildland Fire* 18:116–126.
- Keeling EG, Sala A (2012) Changing growth response to wildfire in old-growth ponderosa pine trees in montane forests of north central Idaho. *Glob Change Biol* 18:1117–1126.
- Kinerson RS, Higginbotham KO, Chapman RC (1974) The dynamics of foliage distribution within a forest canopy. *J Appl Ecol* 11:347–353.
- Köstner B, Granier A, Čermák J (1998) Sapflow measurements in forest stands: methods and uncertainties. *Ann Sci For* 55:13–27.
- Köstner BMM, Schulze ED, Kelliher FM, Hollinger DY, Byers JN, Hunt JE, McSeveny TM, Meserth R, Weir PL (1992) Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91:350–359.
- Landis RM, Gurevitch J, Fox GA, Fang W, Taub DR (2005) Variation in recruitment and early demography in *Pinus rigida* following crown fire in the pine barrens of Long Island, New York. *J Ecol* 93:607–617.
- Lavoie M, Starr G, Mack MC, Martin TA, Gholz HL (2010) Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in Florida. *Nat Area J* 30:82–94.
- Little S (1973) Eighteen-year changes in the composition of a stand of *Pinus echinata* and *P. rigida* in southern New Jersey. *Bull Torrey Bot Club* 100:94–102.
- Little S (1998) Fire and plant succession in the New Jersey Pine Barrens. In: Forman R (ed.) *Pine Barrens: ecosystem and landscape*. Rutgers University Press, New Brunswick, NJ, USA, pp 297–314.
- Little S, Moore EB (1945) Controlled burning in South Jersey's oak-pine stands. *J Forest* 43:499–506.
- Little S, Moore EB (1949) The ecological role of prescribed burns in the pine-oak forests of Southern New Jersey. *Ecology* 30:223–233.
- Little S, Allen JP, Moore EB (1948) Controlled burning as a dual-purpose tool of forest management in New Jersey's pine region. *J Forest* 46:810–819.
- Loudermilk EL, O'Brien JJ, Mitchell RJ, Cropper WP Jr, Hiers JK, Grunwald S, Grego J, Fernandez-Diaz JC (2012) Linking complex forest fuel structure and fire behaviour at fine scales. *Int J Wildland Fire* 21:882–893.
- Loudermilk EL, Achtemeier GL, O'Brien JJ, Hiers JK, Hornsby BS (2014) High-resolution observations of combustion in heterogeneous surface fuels. *Int J Wildland Fire* 23:1016–1026.
- Mabuhay JA, Nakagoshi N, Horikoshi T (2003) Microbial biomass and abundance after forest fire in pine forests in Japan. *Ecol Res* 18:431–441.
- Meyn A, Taylor SW, Flannigan MD, Thonicke K, Cramer W (2010) Relationship between fire, climate oscillations, and drought in British Columbia, Canada, 1920–2000. *Glob Change Biol* 16:977–989.
- Mikita-Barbato RA, Kelly JJ, Tate RL III (2015) Wildfire effects on the properties and microbial community structure of organic horizon soils in the New Jersey Pinelands. *Soil Biol Biochem* 86:67–76.
- Misson L, Tu KP, Boniello RA, Goldstein AH (2006) Seasonality of photosynthetic parameters in a multi-specific and vertically complex forest ecosystem in the Sierra Nevada of California. *Tree Physiol* 26:729–741.
- Mkhabela MS, Amiro BD, Barr AG et al. (2009) Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests. *Agr Forest Meteorol* 149:783–794.
- Moritz MA, Moody TJ, Krawchuk MA, Hughes M, Hall A (2010) Spatial variation in extreme winds predicts large wildfire locations in chaparral ecosystems. *Geophys Res Lett* 37:L04801. doi:10.1029/2009GL041735
- Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. *For Ecol Manag* 122:51–71.
- O'Brien JJ, Hiers JK, Mitchell RJ, Morgan Varner J III, Mordecai K (2010) Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. *J Assoc Fire Ecol* 6:1–12.
- Oishi AC, Oren R, Stoy PC (2008) Estimating components of forest evapotranspiration: a footprint approach for scaling sap flux measurements. *Agr For Meteorol* 148:1719–1732.
- Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schafer KVR (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ* 22:1515–1526.
- Pellegrini AFA, Hedin LO, Staver AC, Govender N (2015) Fire alters ecosystem carbon and nutrients but not plant nutrient stoichiometry. *Bull Ecol Soc Am* 96:340–343.
- Peterson DL, Ryan KC (1986) Modeling postfire conifer mortality for long-range planning. *Environ Manag* 10:797–808.
- Phillips N, Oren R, Zimmermann R (1996) Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant Cell Environ* 19:983–990.
- Phillips N, Nagchaudhuri A, Oren R, Katul G (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees Struct Funct* 11:412–419.
- Porté A, Loustau D (1998) Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. *Tree Physiol* 18:223–232.

- Reich PB, Abrams MD, Ellsworth DS, Kruger EL, Tabone TJ (1990) Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology* 71:2179–2190.
- Reich PB, Peterson DW, Wedin DA, Wragg K (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest–grassland continuum. *Ecology* 82:1703–1719.
- Renninger HJ, Schäfer KVR (2012) Comparison of tissue heat balance and thermal dissipation-derived sap flow measurements in ring-porous oaks and a pine. *Front Plant Sci* 3:103.
- Renninger HJ, Clark KL, Skowronski N, Schäfer KVR (2013) Effects of a prescribed fire on water use and photosynthetic capacity of pitch pines. *Trees* 27:1115–1127.
- Renninger HJ, Carlo N, Clark KL, Schäfer KVR (2014) Physiological strategies of co-occurring oaks in a water- and nutrient-limited ecosystem. *Tree Physiol* 34:159–173.
- Renninger HJ, Carlo NJ, Clark KL, Schäfer KVR (2015) Resource use and efficiency, and stomatal responses to environmental drivers of oak and pine species in an Atlantic Coastal Plain forest. *Front Plant Sci* 6:297. doi:10.3389/fpls.2015.00297
- Richter DD, Ralston CW, Harms WR (1982) Prescribed fire: effects on water quality and forest nutrient cycling. *Science* 215:661–663.
- Robinson JL, Slater LD, Schäfer KVR (2012) Evidence for spatial variability in hydraulic redistribution within an oak–pine forest from resistivity imaging. *J Hydrol* 430–431:69–79.
- Rozas V, Pérez-de-Lis G, García-González I, Arévalo J (2011) Contrasting effects of wildfire and climate on radial growth of *Pinus canariensis* on windward and leeward slopes on Tenerife, Canary Islands. *Trees* 25:895–905.
- Ryan KC, Reinhardt ED (1988) Predicting postfire mortality of seven western conifers. *Can J For Res* 18:1291–1297.
- Ryan KC, Knapp EE, Varner JM (2013) Prescribed fire in North American forests and woodlands: history, current practice, and challenges. *Front Ecol Environ* 11:e15–e24.
- Sala A, Peters GD, McIntyre LR, Harrington MG (2005) Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. *Tree Physiol* 25:339–348.
- Schäfer KV (2011) Canopy stomatal conductance following drought, disturbance, and death in an upland oak/pine forest of the New Jersey Pine Barrens, USA. *Front Plant Sci* 2:15. doi:10.3389/fpls.2011.00015
- Schäfer KVR, Oren R, Tenhunen JD (2000) The effect of tree height on crown level stomatal conductance. *Plant Cell Environ* 23:365–375.
- Schäfer KVR, Renninger HJ, Carlo NJ, Vanderklein DW (2014a) Forest response and recovery following disturbance in upland forests of the Atlantic Coastal Plain. *Front Plant Sci* 5:294. doi:10.3389/fpls.2014.00294
- Schäfer KVR, Renninger HJ, Clark KL, Medvigy D (2014b) Hydrological responses to defoliation and drought of an upland oak/pine forest. *Hydrol Process* 28:6113–6123.
- Scheller RM, Van Tuyl S, Clark KL, Hom J, La Puma I (2011) Carbon sequestration in the New Jersey pine barrens under different scenarios of fire management. *Ecosystems* 14:987–1004. doi:10.1007/s10021-011-9462-6
- Schwilke DW, Ackerly DD (2001) Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94:326–336.
- Sharkey TD (1985) Photosynthesis in intact leaves of C_3 plants: physics, physiology and rate limitations. *Bot Rev* 51:53–105.
- Sharkey TD, Bernacchi CJ, Farquhar GD, Singaas EL (2007) Fitting photosynthetic carbon dioxide response curves for C_3 leaves. *Plant Cell Environ* 30:1035–1040.
- Skowronski N, Clark K, Nelson R, Hom J, Patterson M (2007) Remotely sensed measurements of forest structure and fuel loads in the Pine-lands of New Jersey. *Remote Sens Environ* 108:123–129.
- Skowronski NS, Clark KL, Gallagher M, Birdsey RA, Hom JL (2014) Airborne laser scanner-assisted estimation of aboveground biomass change in a temperate oak–pine forest. *Remote Sens Environ* 151:166–174.
- Smith JE, McKay D, Niwa CG, Thies WG, Brenner G, Spatafora JW (2004) Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. *Can J For Res* 34:2477–2491.
- Song X, Clark KS, Helliker BR (2014) Interpreting species-specific variation in tree-ring oxygen isotope ratios among three temperate forest trees. *Plant Cell Environ* 37:2169–2182.
- Steppe K, De Pauw DJW, Doody TM, Teskey RO (2010) A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agr For Meteorol* 150:1046–1056.
- Thaxton JM, Platt WJ (2006) Small-scale fuel variation alters fire intensity and shrub abundance in a Pine savanna. *Ecology* 87:1331–1337.
- Vanderklein DW, Schäfer KVR, Martinez-Vilalta J (2012) Crown conductance in dwarf, medium, and tall pitch pines in the Long Island Pine Plains. *Trees* 26:1617–1625.
- van Wilgen BW (2013) Fire management in species-rich Cape fynbos shrublands. *Front Ecol Environ* 11:e35–e44.
- van Wilgen BW, Forsyth GG, De Klerk H, Das S, Khuluse S, Schmitz P (2010) Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *J Appl Ecol* 47:631–638.
- Varner JM, Putz FE, O'Brien JJ, Hiers JK, Mitchell RJ, Gordon DR (2009) Post-fire tree stress and growth following smoldering duff fires. *For Ecol Manag* 258:2467–2474.
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- Whelan A, Starr G, Staudhammer CL, Loescher HW, Mitchell RJ (2015) Effects of drought and prescribed fire on energy exchange in longleaf pine ecosystems. *Ecosphere* 6:1–22.
- Whittaker R, Woodwell GM (1968) Dimension and production relations of trees and shrubs in the brookhaven forest, New York. *J Ecol* 56:1–25.