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Effects of a prescribed fire on water use and photosynthetic capacity of pitch pines

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Abstract Although wildfires are important in many forested ecosystems, increasing suburbanization necessitates management with prescribed fires. The physiological responses of overstory trees to prescribed fire has received little study and may differ from typical wildfires due to the lower intensity and timing of prescribed fire in the dormant season. Trees may be negatively affected by prescribed fires if injury occurs, or positively affected due to reduced competition from understory vegetation and release of nutrients from partially consumed litter. We estimated sap flow and photosynthetic parameters before a late-March prescribed fire and throughout the growing season in burned and unburned pitch pine (*Pinus rigida* L.) sites in the New Jersey Pinelands to determine how water use and photosynthetic capacity were affected. Water use was similar between sites before the fire but 27 % lower in burned trees immediately following the fire. After about a month, water use in the burned site was 11–25 % higher than pines from the unburned site and these differences lasted into the summer. Photosynthetic capacity remained similar between sites but instantaneous intrinsic water use efficiency increased by 22 % and maximum Rubisco carboxylation rate (V_{cmax}) was over three times greater in the summer compared to the pre-fire period in the burned site, whereas the unburned site exhibited similar V_{cmax} and intrinsic water use efficiencies between pre-fire and summer measurements. These differences in physiology suggest that the prescribed fire altered the amount of water and nutrients that pines had access to and led to increased water use and water use efficiency; both of which are important in this water- and nutrient-limited ecosystem.

Keywords Controlled burn · Disturbance · Photosynthesis · Pine-dominated · Sap flow

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Introduction

Fire is a natural part of many forested and grassland ecosystems. Tree species growing in fire-prone areas tend to display specific adaptations to fire, including serotiny, thick bark and basal resprouting (Agee 1998; Keeley 2012). However, with increasing suburban development in and near forests, the occurrence of wildfire has become a concern for both public safety and loss of property. Therefore, in many fire-prone areas, controlled burns are performed to decrease fuel loads in forests, thereby reducing the risk and severity of wildfires. Prescribed fires are generally performed when fuel moisture contents are high and air temperatures are low, resulting in presumably low-intensity fires that consume less fuel, and alter mostly the understory vegetation and forest floor with less damage to overstory trees (Knapp et al. 2007; Schwilk et al. 2006). Long-term prescribed fire programs can be effective in reducing carbon emissions in fire-prone areas (Narayan

et al. 2007), as well as maintaining forest structure so that carbon sequestration rates are maintained. Fire is also increasingly being incorporated into global vegetation models (Murphy et al. 2011). However, prescribed fires and wildfires will have different effects on the forest and our ability to accurately model the effects of each disturbance depends on our knowledge of how these fires affect the functioning of trees.

In order to better understand the effects of prescribed fire on carbon and water dynamics and better incorporate prescribed fire into models, we need to understand the physiological changes that occur in response to prescribed fires. The damage that prescribed fires have on trees is related to the time of year they are performed with Harrington (1993) finding that mortality rates were higher when actively growing trees experienced a prescribed fire vs. fires that occurred when trees were dormant. Depending on the height of trees, intensity of the fire and time since last fire, significant crown scorch can occur (Clinton et al. 2011; Hood et al. 2010). Non-structural carbohydrate stores in coarse roots have been shown to be significantly decreased after prescribed fires (Varner et al. 2009) presumably due to a demand for stored carbohydrates after losses of leaves and possibly fine roots. Fine roots may be at increased risk for damage if early spring burns are performed at a time when soils are generally moist and trees are beginning to become more active (Busse et al. 2000; Smith et al. 2004). Some studies have found significant fine root damage after prescribed burns (Smirnova et al. 2008; Swezy and Agee 1991); however, the moisture of the litter layer tends to prevent significant combustion of the organic horizon (Richter et al. 1982) in early spring prescribed burns. Prescribed fires can also alter soil microbial communities, decreasing biomass and changing species composition (Certini 2005; Tuininga and Dighton 2004). Burning of the litter layer also changes the degree of insolation of soils (Dumas et al. 2007; Yevdokimenko 2011), can create hydrophobic layers of material in the soil (Certini 2005) and change the albedo of the soil through changes in color (Certini 2005). These changes, along with losses of shrubs, can have relatively long-lasting effects on soil heat fluxes and evaporative dynamics. Dumas et al. (2007) found that a prescribed fire in an oak-pine forest increased light penetration to the soil surface causing greater extremes in soil temperatures and lower gravimetric soil water content. These changes to the forest floor following prescribed fires have been found to reduce height and basal area growth in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) trees (Landsberg et al. 1984) and can be as important to the growth of overstory trees as damage to the crowns (Stephens and Finney 2002).

There is also evidence to suggest that overstory trees and the forest in general may benefit from the implementation of prescribed burns. Boerner et al. (1988) found that a prescribed burn increased growth of white oak (*Quercus alba* L.) by 55 % and chestnut oak (*Quercus prinus* Willd.) by 38 %. Specifically for early season burns, heating of soils that are below an optimal temperature may stimulate root growth (Sword Sayer and Haywood 2006). Likewise, pyrolysis of forest floor materials converts organic forms of nitrogen to ones that can be more readily taken up by plants (Certini 2005; Gray and Dighton 2006). Covington and Sackett (1992) found that burning increased ammonium–nitrogen concentrations in the mineral soil. This release of nutrients is especially important in nutrient-limited systems, but is only meaningful if plants are in a position to extract these nutrients when they become available (Gray and Dighton 2009; Richter et al. 1982). For example, influxes of nitrate to the soil will leach away if not taken up by plants and microbes (Certini 2005) especially in the excessively sandy soils of the New Jersey Pinelands and along the Atlantic Coastal Plain. Prescribed fires can also increase the availability of phosphorus to plants by converting it to more labile forms and increasing the pH of the soil (Certini 2005; Gray and Dighton 2009). Another benefit of prescribed fires for overstory trees is the removal of competition for water and nutrients from shrubs and understory trees (Rozas et al. 2011). Skov et al. (2004) found that ponderosa pine stands that were thinned and burned had experienced less drought stress than unthinned, unburned stands.

In this study, we determined the effects of an early spring prescribed fire on water use and photosynthetic capacity of pitch pines (*Pinus rigida* L.) in the New Jersey Pinelands. We investigated both short-term effects as well as effects that were sustained throughout the growing season. We hypothesized that water use would be higher following a fire in the burned stand than an unburned stand because the fire would remove competition for water from understory shrubs. Likewise, we hypothesized that photosynthetic capacity would increase as a result of the fire compared with trees in an unburned stand due to the mineralization of the litter layer. Both water use and photosynthetic capacity are important for the growth and productivity of trees, especially in the Pinelands; a system that is nutrient- and water limited during much of the growing season due to its sandy, well-drained soils (Pan et al. 2006). Understanding tree physiology during prescribed fire cycles will also aid in more accurate modeling of carbon and water dynamics in similar pine forest ecosystems in which prescribed fires are routinely performed. Likewise, because this prescribed fire occurred during the window of increased wildfire danger in this region, these data can also help elucidate how pitch pines will respond to early season wildfires as well.

Materials and methods

Site description

This study was conducted within the Brendan T. Byrne State Forest (39°53′N, 74°30′W), a 14,800-ha tract in the New Jersey Pinelands, USA. This temperate forest has an average summer temperature of 22.7 °C, an average winter temperature of 1.3 °C and receives about 1,200 mm of precipitation per year. Soils in the area are acidic, nutrient poor sands (>95 %) with low cation exchange capacity and low water holding capacity (Schäfer 2011). The site is composed primarily of pitch pine with scattered overstory oak species including white oak, chestnut oak, and black oak (*Quercus velutina* Lam.). The understory consists of scrub oaks (*Q. marilandica* Muench., *Q. ilicifolia* Wangenh.) as well as various shrub species including blueberry (*Vaccinium* spp.) and huckleberry (*Gaylussacia* spp.), and herbaceous species including bracken fern (*Pteridium aquilinum* L. Kuhn), sedges, mosses and lichens. Shrub species possess deep root systems and are adapted to fire by readily resprouting from basal meristems after their aboveground biomass is burned (Forman and Boerner 1981; Matlack et al. 1993).

At the beginning of the experiment in February 2011, two stands (radius of 9.8 m) within the site were selected that were approximately 400 m from one another and contained a similar size distribution of pitch pines. One stand was located within the area to be burned, the other remained unburned. Basal areas of the burned and unburned stands were 27.2 and 26.5 m^2 ha^{-1}, respectively (Table 1). In mid-March 2011 and late September 2011, diameter at breast height (dbh), total height and height to the base of the live crown were measured in all pines within the burned and unburned stands (31 and 27 trees in total, respectively). Projected leaf area index (LAI) of each stand was measured before the fire with an LAI 2000 Plant Canopy Analyzer (LiCor Inc., Lincoln, NE, USA) and did not differ significantly ($p = 0.64$) between the stands (Table 1).

An operational prescribed fire was conducted by the New Jersey Forest Fire Service on 20 March 2011. Minimum temperature the previous night was −3.1 °C and the maximum temperature on this date was 10.0 °C with a minimum relative humidity of 34 % and a maximum vapor pressure deficit of 0.44 kPa. Soil moisture averaged about 10 % and the last rain event (20 mm) occurred 4 days prior (Fig. 1). Pre- and post-burn sampling (36 and 27 samples, respectively, measuring 1 m^2 ground area from various locations within the prescribed fire treatment) indicated that mean consumption of fuels on the forest floor in the O_i horizon was 327 g m^{-2}, representing about 40 % of this layer, and understory stem consumption was 363 g m^{-2}. Residual material on the forest floor after the burn was 521 ± 187 g m^{-2}, and little consumption of the O_a horizon was observed. Pine boles in the burned stand exhibited some charring of their outer, lower bark up to about a meter from ground level. Crowns were, on average, 6 m above ground (i.e., height to the base of the live crown; Table 1); therefore, minimal heat scorch of the leaves occurred in the site and was between 5 and 10 % of the total leaf area of the pines. Most of the aboveground biomass of shrubs was killed, but many shoots resprouted from underground buds about 2 weeks after the leaf out of the shrubs at the unburned stand.

Sap flux measurements

In late-February 2011, ten pines from each stand were fitted with Granier heat dissipation sap flow sensors (Granier 1987). In each stand, pines were selected to cover the size distribution of the site ranging from 11.5 to 42.3 cm dbh. Two-cm long Granier sensors were inserted radially into the sapwood at about 1.3 m above ground on the north side of each measured tree, after removing a portion of the bark. The largest pine (37 and 42 cm dbh) in each stand was also fitted with a sensor located at a depth of 2–4 cm within the sapwood to account for radial patterns in sap flux (Phillips et al. 1996). Sensors consist of both a heated and an unheated probe that continuously measure temperature via thermocouples within the probes. The heated probe is located approximately 10 cm above the unheated probe and, as water is pulled past the probes via transpiration from the leaves, it cools the heated sensor. This heat loss is proportional to sap flux as shown by Granier (1987) (see Eq. 1). Sensors were attached to a datalogger (CR1000 or CR5000 with an AM16/32A multiplexer, Campbell Scientific Inc., Logan, UT, USA) and differences in temperature between the heated and unheated probes were measured every 30 s. and logged every 30 min. Aluminum bread pans placed over the sensors shielded them from temperature differences due to sunflecks. Sensors remained in trees during the prescribed fire, however, the datalogger, battery, solar panel and all cables were removed prior to the fire and reattached immediately afterwards.

Raw temperature differences were converted to sap flux rates (J_s; kg H_20 m^{-2} sapwood area s^{-1}) using Granier's original calibration equation (1987):

$$J_S = 0.119 \times \left(\frac{\Delta T_{Max}}{\Delta T} - 1\right)^{1.23} \quad (1)$$

where ΔT_{max} is the maximum temperature difference between probes when no water is flowing (presumably at night) and ΔT is the temperature difference when sap flux is occurring. We used a Matlab code developed by Oishi

Table 1 Means and standard errors of pre-fire (measured in February 2011) and post-fire (measured in September 2011) site characteristics for the burned and unburned stands

	Pre-fire (Feb.)		Post-fire (Sept.)		
	Burned	Unburned	Burned	Unburned	*p* value
DBH (cm)	18.2 (1.5)	19.1 (1.9)	18.3 (1.5)	19.7 (1.9)	0.64
Height (m)	12.0 (0.6)	12.1 (1.1)	12.8 (0.6)	13.0 (1.2)	0.88
Height to basal crown (m)	6.2 (0.4)	6.1 (0.6)	5.8 (0.5)	7.6 (1.1)	0.09
Leaf area index (LAI)	0.97 (0.02)	1.00 (0.03)			
Stand density (stems ha^{-1})	900	1030			
Basal area (m^2 ha^{-1})	27.2	26.5			

Standard error of dbh, height and height to the basal crown (measured from the ground to the bottom of the canopy) is the deviation around 27 and 31 trees in the burned and unburned stands, respectively, and standard error of LAI is the deviation around 28 and 31 spot measurements at the burned and unburned stands, respectively. *p* values are based on *t* tests of individual seasonal differences of the tree size characteristics between stands (i.e., non-significance means that pre- and post-fire differences were not significant between the two stands)

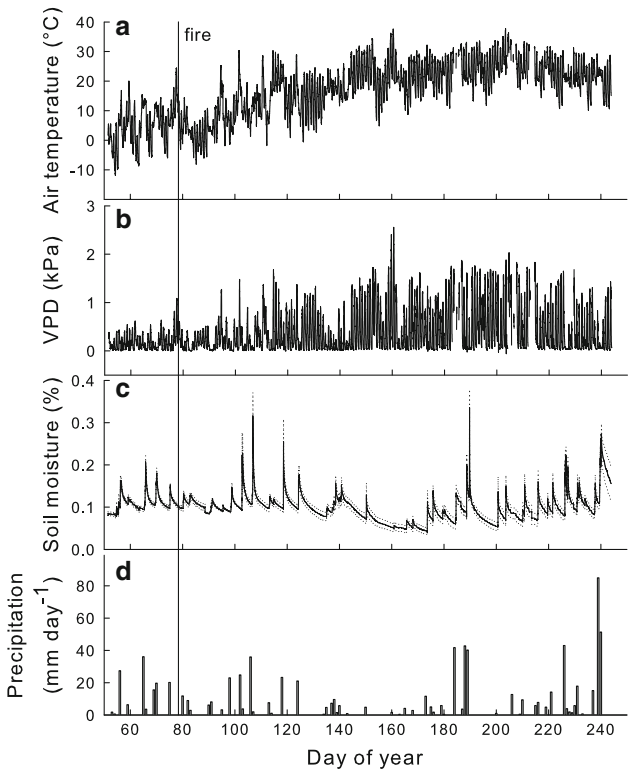

Fig. 1 Meteorological variables measured at the unburned stand throughout the study period including **a** half-hourly averages of temperature (°C), **b** half-hourly averages of vapor pressure deficit (VPD; kPa) calculated from the air temperature and humidity data, **c** half-hourly averages of soil moisture (%) averaged across four sensors where the *solid line* is the mean and the *dotted lines* are ±one standard error around the mean and **d** daily sums of precipitation throughfall (mm day^{-1})

et al. (2008) to convert our raw data to sap flux rates which confirms that ΔT_{max} values were chosen when sap flux was truly zero (i.e., VPD <0.05 kPa and nighttime ΔT values are stable over a 2-h time period). Daily sap flux (kg m^{-2} day^{-1}) was calculated by summing up the half-hourly values and sap flow was scaled to the stand level (mm day^{-1}) by multiplying average sap flux rates by the sapwood area of all trees in a specified area then dividing by that ground area. Sapwood areas were calculated using the following relationship:

$$A_S = 0.3733 \times \text{dbh}^{2.0473} \quad (2)$$

where A_S is sapwood area (cm^2). This relationship ($r^2 = 0.99$) was derived by coring ten pitch pines near the study site across a range of size classes and determining the sapwood to heartwood transition visually via a color change from darker, wet sapwood to lighter, dry heartwood.

Meteorological data were measured continuously throughout the study at the unburned stand and logged every 30 s with 30 min averages stored. These include temperature and relative humidity (Vaisala HMP45C sensor; Campbell Scientific Inc.) which were measured in the mid-canopy (ca. 6 m high), soil moisture (CS616 sensors, Campbell Scientific Inc.) at four locations in each cardinal direction from the plot center at 0–30 cm depth and precipitation throughfall (Texas Electronics TE525M tipping bucket; Campbell Scientific Inc.) (Fig. 1). Temperature and relative humidity were used to calculate vapor pressure deficit of the air (VPD; kPa). Overstory photosynthetically active radiation (PAR) was measured by a LI-200 sensor (LI-COR Biosciences Inc.) located 18 m aboveground on a tower at Silas Little Experimental Forest which is about 5 km from the study site.

Photosynthesis measurements and leaf carbon and nitrogen composition

Photosynthesis measurements were performed three times on the same trees during the course of this experiment with a LiCor 6400 photosynthesis system with a red/blue LED light source attached (LiCor Inc., Lincoln, NE, USA).

Measurements were made on the 1st and 2nd March 2011 ('pre-fire') which experienced average ambient temperatures during the measurement period of 7.1 and 12.0 °C, respectively. 'Post-fire' measurements were then made on the 20th and 21st April 2011 with ambient temperatures averaging 26.2 and 16.0 °C, respectively, during the measurement period. One final round of measurements was made on the 1st and 2nd August 2011 ('summer') with ambient temperatures averaging 32.6 and 30.8 °C, respectively, during the measurement period. Pre-fire and post-fire measurements were made on the 2010 needle cohort and summer measurements were made on the newly produced, 2011 cohort. Both light response curves and photosynthesis to internal CO_2 concentration (A/C_i) curves were made on leaves from a single branch that was located in the lower canopy and collected from each of three trees within each stand during each measurement period. Since branches could not be accessed directly, they were cut first with a pole pruner, recut underwater to remove any embolisms from the stem, and then kept in a container of water throughout the measurement period. Light response curves were made by maintaining the CO_2 concentration in the chamber at 400 ppm and varying the light levels. The A/C_i curves were made by maintaining light levels in the chamber at 1,200 μmol m^{-2} s^{-1} and varying the CO_2 concentration. After measurements were made, the leaves in the chamber were collected so that their area could be determined and the photosynthesis measurements properly scaled. Leaves were kept in sealed, plastic bags and returned to the lab where they were placed on a flatbed scanner (Epson V30, Long Beach, CA) with a known scaling factor. Their area was determined using Image J (Scion Image, Frederick, MD, USA). These samples were then ground finely using a ball mill and sealed in aluminum capsules so that their carbon isotopic ratios ($\delta^{13}C$) and carbon and nitrogen concentrations could be determined (Duke University Stable Isotope facility DEVIL, Durham, NC).

Data analysis and statistics

Since this study was unreplicated in terms of the prescribed fire, we cannot say specifically that post-fire differences were a result of the burn treatment. However, if the burned and unburned stands were not different before the fire and only differed after the burn treatment that lends support to the perceived effects of the fire on tree physiology (Oksanen 2001). Analysis of variance (ANOVA) was performed using R version 2.5.1 (The R Foundation for Statistical Computing, http://www.R-project.org) for the estimated gas exchange, photosynthetic parameters and leaf composition across site (categorical) and time (continuous) and the interaction between the two which would suggest a fire effect (Tables 2, 3). The error terms in these ANOVAs were adjusted to account for the repeated measurements made on individual trees.

To estimate parameters from light response curves, data was plotted and equations fitted to the data using Sigmaplot (SPSS Inc. Chicago, IL, USA). Maximum assimilation values at saturating light and ambient CO_2 (A_{max}) and light compensation points were obtained from the fitted exponential equations for each light response curve. Data from the initial linear portion of the light response curves were used to fit linear regressions to estimate quantum yield (slope of linear fit) and dark respiration rates (y-intercept of linear fit). To obtain estimates for CO_2 compensation point (Γ), maximum Rubisco carboxylation rate (V_{cmax}), electron transport rate (J), and triose phosphate utilization (TPU) from the A/Ci curves, data were uploaded to the Oak Ridge National Laboratory (ORNL) LeafWeb program (www.leafweb.ornl.gov) which uses exhaustive dual optimization to parameterize A/Ci curves based on the Farquhar-von Caemmerer-Berry model (Gu et al. 2010). For each curve, four parameters were estimated based on different sets of constraints for the model and we chose the parameter with the best fit based on the first and second partial derivatives of the cost function of each parameter.

Stomatal conductance (g_s; mol H_2O m^{-2} s^{-1}) and instantaneous intrinsic water use efficiency ($IWUE_{instant.}$; photosynthetic assimilation/stomatal conductance; μmol CO_2 mol^{-1} H_2O) were estimated from measurements where light levels were saturating (1,200 μmol m^{-2} s^{-1}) and CO_2 concentrations were approximately ambient (400 ppm). Likewise, intrinsic water use efficiency was also estimated from the $\delta^{13}C$ needle samples ($IWUE_{isotope}$) as follows (Farquhar et al. 1989):

$$IWUE_{isotope} = \frac{C_a}{1.6} \times \left(\frac{27 - \Delta}{27 - 4.4}\right) \quad (3)$$

where C_a is the ambient CO_2 concentration (390 ppm), and Δ (‰) is the carbon isotopic discrimination calculated as follows:

$$\Delta = \left(\frac{\delta^{13}a - \delta^{13}C}{1,000 + \delta^{13}C}\right) \times 1,000 \quad (4)$$

where $\delta^{13}a$ is the isotopic concentration of the source air measured at around −12.9 ‰ near the study area in January 2010. The value of −12.9 ‰ likely changes seasonally, however, this number was used for all calculations and should not change the relative differences seen between stands.

In order to determine the differences in water use between the two stands across the study period, daily sap flux rates (kg m^{-2} day^{-1}) were averaged across all

Table 2 Means (standard errors; $n = 3$) for stomatal conductance (g_s) and instantaneous intrinsic water use efficiency ($IWUE_{instant.}$) calculated from photosynthetic measurements as well as isotopic concentrations, estimates of intrinsic water use efficiency from isotopes and leaf nutrients from pre-fire (1st and 2nd March 2011), post-fire (20th and 21st April 2011) and during the summer (1st and 2nd August 2011)

	Burned	Unburned	*p* value	
g_s (mol H_2O m^{-2} s^{-1})				
Pre-fire (Mar)	0.18 (0.05)	0.14 (0.02)	0.70	Time
Post-fire (Apr)	0.20 (0.006)	0.15 (0.01)	0.92	Stand
Summer (Aug)	0.13 (0.03)	0.22 (0.03)	**0.04**	Time*stand
$IWUE_{instant.}$ (μmol CO_2 mol^{-1} H_2O)				
Pre-fire (Mar)	63.9 (11.6)	71.8 (12.5)	0.51	Time
Post-fire (Apr)	81.5 (8.2)	76.8 (5.2)	0.41	Stand
Summer (Aug)	94.6 (10.6)	65.0 (5.7)	**0.01**	Time*stand
$\delta^{13}C$ (‰)				
Pre-fire (Mar)	−31.2 (0.20)	−31.7 (0.21)	**<0.001**	Time
Post-fire (Apr)	−30.9 (0.25)	−31.1 (0.20)	**0.006**	Stand
Summer (Aug)	−30.3 (0.26)	−30.7 (0.16)	0.96	Time*stand
$IWUE_{isotope}$ (μmol CO_2 mol^{-1} H_2O)				
Pre-fire (Mar)	87.3 (2.2)	81.9 (2.4)	**<0.001**	Time
Post-fire (Apr)	90.9 (2.7)	88.3 (2.3)	**0.009**	Stand
Summer (Aug)	97.6 (2.9)	92.8 (1.9)	0.98	Time*stand
Leaf N concentration (%)				
Pre-fire (Mar)	1.11 (0.09)	1.09 (0.05)	**0.004**	Time
Post-fire (Apr)	1.23 (0.05)	1.12 (0.09)	0.58	Stand
Summer (Aug)	1.10 (0.04)	0.82 (0.04)	**0.04**	Time*stand
Leaf C concentration (%)				
Pre-fire (Mar)	49.9 (3.5)	54.4 (0.4)	0.34	Time
Post-fire (Apr)	51.5 (1.7)	54.2 (0.4)	0.52	Stand
Summer (Aug)	52.2 (0.8)	49.4 (2.4)	**0.04**	Time*stand
C/N ratio				
Pre-fire (Mar)	45.3 (1.6)	50.5 (2.4)	**<0.001**	Time
Post-fire (Apr)	41.8 (0.7)	50.1 (4.1)	0.29	Stand
Summer (Aug)	48.0 (1.6)	60.8 (2.3)	0.09	Time*stand

p values (bold are significant at $\alpha < 0.05$) are derived from ANOVAs with time*stand as explanatory variables

Table 3 Means (standard errors; $n = 3$) for photosynthetic parameters estimated from light response and A/C_i curves measured on three separate occasions; pre-fire (1st and 2nd March 2011), post-fire (20th and 21st April 2011) and during the summer (1st and 2nd August 2011)

	Burned	Unburned	*p* value	
Dark resp. rate (μmol CO_2 m^{-2} s^{-1})				
Summer (Aug)	1.1 (0.2)	1.8 (0.2)	0.24	Stand
Light compensation pt. (μmol photon m^{-2} s^{-1})				
Summer (Aug)	23.1 (4.3)	33.9 (3.7)	0.29	Stand
A_{max} (μmol CO_2 m^{-2} s^{-1})				
Pre-fire (Feb)	11.9 (2.0)	10.6 (0.34)	0.46	Time
Post-fire (Apr)	15.3 (1.2)	10.1 (1.2)	0.24	Stand
Summer (Aug)	12.0 (2.4)	14.1 (0.66)	0.09	Time*stand
Quantum yield (μmol CO_2 μmol^{-1} photon)				
Pre-fire (Feb)	0.02 (0.007)	0.02 (0.002)	**0.0003**	Time
Post-fire (Apr)	0.03 (0.003)	0.02 (0.004)	0.54	Stand
Summer (Aug)	0.04 (0.003)	0.05 (0.002)	0.16	Time*stand
CO_2 compensation pt. (Γ; ppm)				
Pre-fire (Feb)	21 (7.6)	74 (34)	0.86	Time
Post-fire (Apr)	25 (6.7)	27 (8.5)	0.15	Stand
Summer (Aug)	36 (16)	45 (2.5)	0.31	Time*stand
Max. Rubisco carboxylation rate ($V_{cmax;}$ μmol m^{-2} s^{-1})				
Pre-fire (Feb)	53 (31)	26 (6.8)	**0.02**	Time
Post-fire (Apr)	65 (4.7)	80 (18)	**0.03**	Stand
Summer (Aug)	198 (56)	34 (5.4)	**0.02**	Time*stand
Electron transport rate (J; μmol m^{-2} s^{-1})				
Pre-fire (Feb)	50 (8.4)	50	0.15	Time
Post-fire (Apr)	133 (11)	130 (4.0)	0.88	Stand
Summer (Aug)	100 (12)	95 (11)	0.9	Time*stand
Triose phosphate utilization (TPU; μmol CO_2 m^{-2} s^{-1})				
Pre-fire (Feb)	3.0 (1.0)	5.5 (2.0)	0.94	Time
Post-fire (Apr)	7.1 (0.6)	8.6 (0.1)	0.18	Stand
Summer (Aug)	4.7 (1.1)	5.5 (0.3)	0.56	Time*stand

p values (bold are significant at $\alpha < 0.05$) are derived from ANOVAs with time*stand as explanatory variables

individuals within each site. These sap flux rates were shown to be uncorrelated with dbh of the trees in both sites ($p = 0.37$, $r^2 = 0.05$; data not shown). Therefore, averaging across the size distribution of trees in each site was deemed appropriate. Daily sap flux averages across individuals from each site were then split into specific time periods including 'pre-fire' (27 February 2011 to 20 March 2011), 'post-fire' (21 March 2011 to 15 April 2011), and 30-day time periods until the end of the summer (30 August 2011). A repeated measures ANOVA showed significantly different sap flux between the burned and unburned stand ($p = 0.02$) over the entire measurement period. Therefore, within each time interval, paired *t* tests were performed between daily sap flux averages from the burned and unburned sites where individual days were paired with one another to determine if one site had consistently higher sap flux rates than the other during that specific time interval.

Daily sap flux rates were also plotted vs. average daytime VPD and total daily overstory PAR and equations fitted to the data using Sigmaplot. Linear model comparisons between the burned and unburned stands were performed using R version 2.5.1. In order to linearize the relationship between daily sap flux and average daytime

VPD, VPD values were log transformed prior to linear model comparison.

Results

Stand data

Pines from the burned and unburned stands did not differ in diameter growth increment ($p = 0.64$) or height growth ($p = 0.88$) during the growing season immediately following the fire (Table 1). However, pines that experienced the fire exhibited decreases ($p = 0.09$) in lower crown height compared to pines in the unburned site (Table 1). There was no apparent tree mortality in the first 5 months following the prescribed fire within the burned stand; therefore, tree densities did not change.

Water use

Maximum sap flux rates ranged from about 10 g m^{-2} s^{-1} to about 40 g m^{-2} s^{-1} during the study period (Fig. 2). Integrated over the day and averaged across the ten measured individuals at each stand, daily sap flux ranged from about 50 kg m^{-2} day^{-1} to about 1,400 kg m^{-2} day^{-1} across the measurement period (Fig. 3a) or about 0.1 mm day^{-1} to about 2.0 mm day^{-1} when values were scaled to the stand level (Fig. 3b). Before the prescribed fire, daily sap flux rates (kg m^{-2} day^{-1}) were not significantly different ($p = 0.26$) between the two stands (Fig. 4). In the month following the fire, daily sap flux rates in the burned stand were 27 % lower ($p < 0.001$) than in the unburned stand (Fig. 4). After this initial period, pines in the burned stand had between 11 and 25 % higher daily sap flux rates that differed significantly ($p < 0.04$) from pines in the unburned stand except for the 'late summer' period when rates were not significantly different ($p = 0.54$) from one another (Fig. 4).

Daily sap flux rates from the burned and unburned stands also differed significantly in their relationship with average daytime VPD and total daily PAR following the prescribed fire (Fig. 5). Prior to the prescribed fire, the relationship between daily sap flux and either the log of average daytime VPD or total daily PAR was statistically similar between the two sites with slopes and intercepts not differing significantly. Following the prescribed fire, the burned stand had a statistically greater slope in the relationship between daily sap flux and total daily PAR than the unburned stand ($p = 0.03$). Likewise, the burned stand had statistically higher slope and intercept term in the relationship between daily sap flux and the log of average daytime VPD than the unburned stand ($p = 0.02$ and 0.01, respectively).

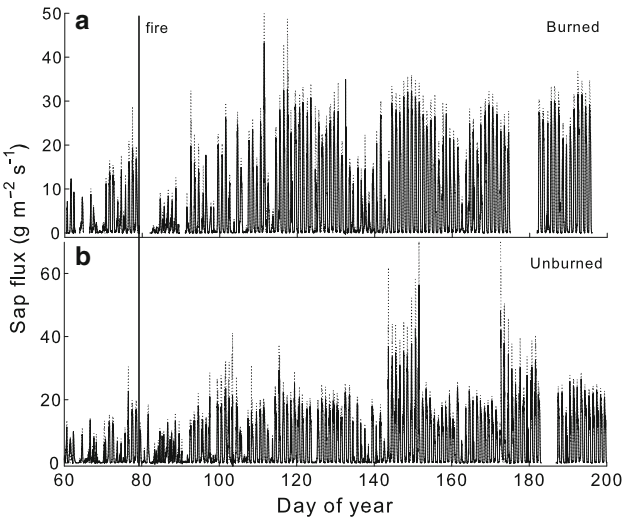

Fig. 2 Half-hourly average sap flux rates (g m^{-2} s^{-1}) from trees in **a** the stand receiving the prescribed fire and **b** the unburned stand throughout the study period. *Solid lines* are the mean sap flux of the ten measured trees from each stand and dotted lines are the mean ± one standard error. The *vertical line* at day of year 79 signifies the date of the prescribed fire

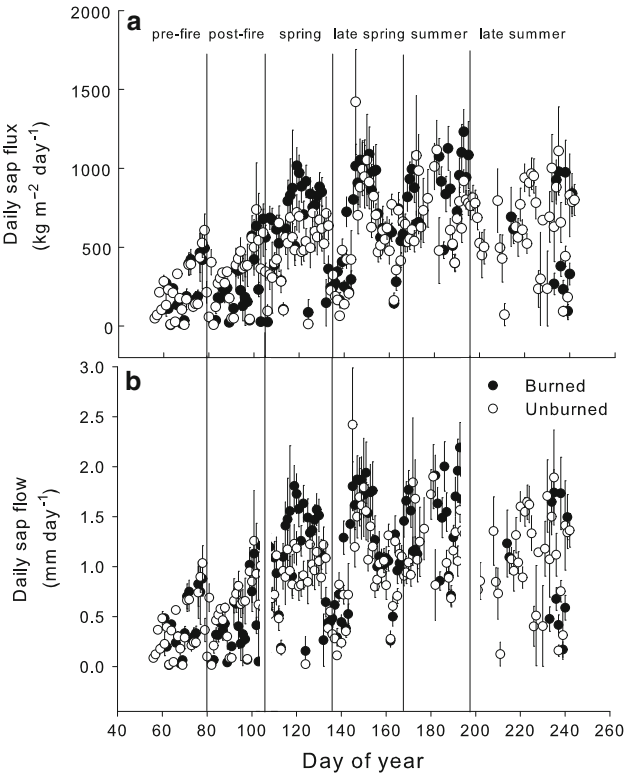

Fig. 3 **a** Daily sap flux rates (kg m^{-2} day^{-1}) and **b** daily stand-level sap flow (mm day^{-1}). *Filled circles* signify values from the stand receiving the prescribed fire and *open circles* signify values from the unburned stand. *Error bars* represent the standard error around the mean of the ten measured trees from each stand. Designated time periods correspond to the comparisons made in Fig. 4

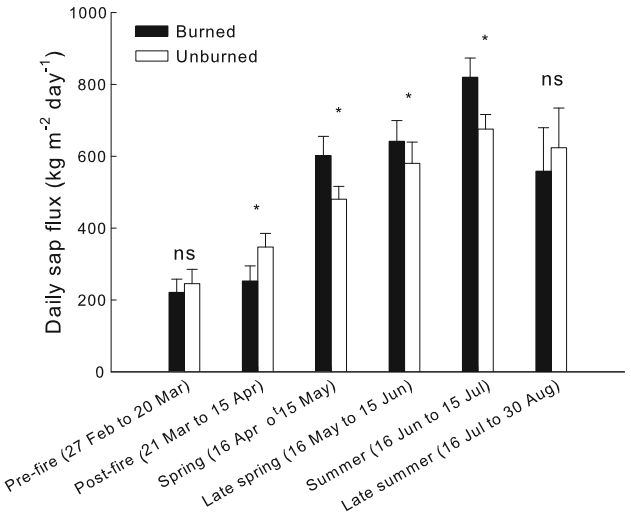

Fig. 4 Mean and standard errors of daily sap flux averages (Fig. 3) in each measurement period for trees at the stand receiving the prescribed fire (*black bars*) and the unburned stand (*white bars*). *Asterisks* signify means that are significantly different at $\alpha = 0.05$ based on paired *t* tests between the burned and unburned stands where daily mean sap flux rates (for the ten individuals) from the same day were compared between the two stands

Pines from the burned and unburned stands also exhibited different leaf-level changes in stomatal conductance (g_s) and instantaneous intrinsic water use efficiency ($IWUE_{instant.}$) throughout the course of the study (Table 2). Leaf-level stomatal conductance increased by about 50 % in the unburned stand, but decreased by about 30 % in the burned stand over the study period ($p_{time*stand} = 0.04$; Table 2). Likewise, $IWUE_{instant}$ increased by about 22 % in the burned stand but decreased by about 12 % in the unburned stand throughout the study ($p_{time*stand} = 0.01$; Table 2). However, in both the burned and unburned stands intrinsic water use efficiency calculated from the carbon isotope data ($IWUE_{isotope}$) increased throughout the study period by about 12 % (Table 2).

Leaf nutrient composition and photosynthetic parameters

The concentration of nitrogen in needles (%N) remained constant in pines in the burned stand across seasons at around 1.1 %, but was about 25 % lower in the unburned stand during the summer than during either of the earlier time periods ($p_{time*stand} = 0.04$; Table 2). The concentration of carbon in needles also followed different trajectories throughout the study period, increasing in the burned stand but decreasing in the unburned stand ($p_{time*stand} = 0.04$; Table 2). C/N ratios were consistently lower in the burned stand than the unburned stand throughout the study period (Table 2).

For the most part, photosynthetic parameters estimated from the light response (Fig. 6) and A/C_i (Fig. 7) curves were similar between stands and across the study period. Maximum photosynthetic assimilation values at saturating light levels (A_{max}) averaged about 12.3 (SE = 0.67) μmol (CO_2) m^{-2} s^{-1}, dark respiration rates averaged 1.27 (SE = 0.2) μmol (CO_2) m^{-2} s^{-1} and light compensation points averaged 33.4 (SE = 5.0) μmol (photon) m^{-2} s^{-1} (Table 3). Quantum yield increased significantly ($p < 0.001$) in both stands throughout the study period from around 0.025 (SE = 0.002) μmol (CO_2) $mmol^{-1}$ (photon) during the pre-fire and initial post-fire period to around 0.047 (SE = 0.002) μmol (CO_2) μmol^{-1} (photon) during the summer (Table 3). CO_2 compensation points were similar between stands and across the study period and averaged around 38 (SE = 8) ppm. Electron transport rates and triose phosphate utilization were also similar between stands and measurement periods at around 93 (SE = 15) and 5.7 (SE = 0.8) μmol m^{-2} s^{-1}, respectively. On the other hand, maximum carboxylation rates differed between the two stands across the measurement period increasing by over three times in the burned stand between the pre-fire and the summer time period but remaining relatively constant in the unburned stand ($p_{time*stand} = 0.02$).

Discussion

One of the main findings of this study is that pitch pines exposed to an early spring prescribed fire had significantly higher water use during the subsequent growing season than trees located in the unburned stand. We also saw no decreases in photosynthetic capacity in trees in the burned stand. Daily sap flux rates prior to the fire were similar between the two stands suggesting that the fire was the primary agent leading to the subsequent differences in water use between the two stands. However, in the approximately 1-month period immediately following the fire, pitch pine sap flux rates in the burned stand were significantly lower than in the unburned stand by about 27 %. This decrease was likely the result of loss of leaf area due to heat scorch of needles on lower branches and possibly damage to surface roots. In 2008, a spring prescribed fire conducted in a pitch pine-dominated stand at the Cedar Bridge Ameriflux site in the Pinelands reduced overstory leaf area and evapotranspiration by about 25 %, with most of this leaf area being recovered the following year (Clark et al. 2012). Surface roots may be at increased risk for damage if early spring burns are performed at a time when soils are generally moist and trees are beginning to become more active (Busse et al. 2000; Smith et al. 2004). Some studies have found significant fine root

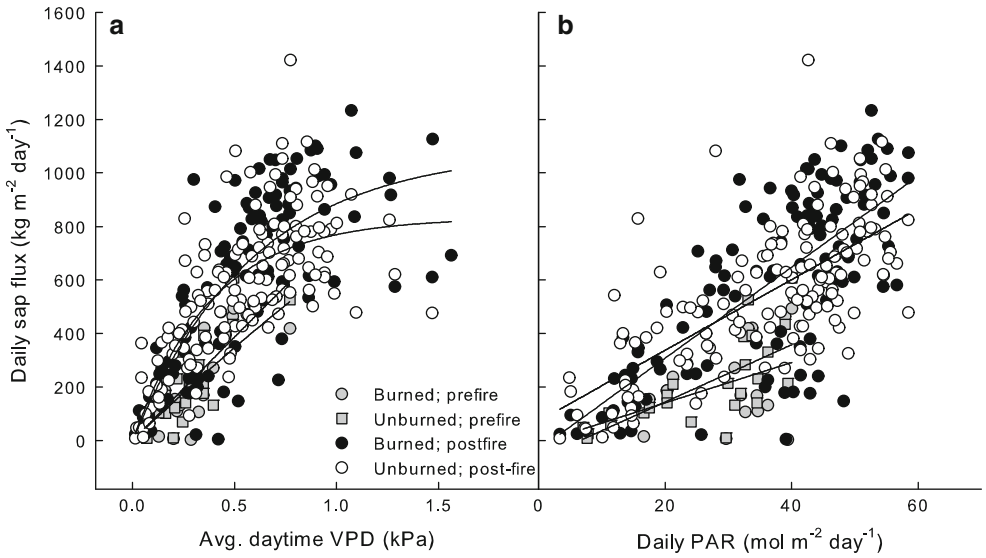

Fig. 5 Relationship between daily sap flux rates (kg m^{-2} day^{-1}) and **a** average daytime VPD (kPa) and **b** total daily PAR (mol m^{-2} day^{-1}) measured throughout the study. Values measured before the prescribed fire are in *gray* (*circles* values from the stand to be burned, *squares* values from the unburned stand), post-fire values at the burned stand are in *black* and post-fire values at the unburned stand are in white. Exponential relationships were fitted to the VPD vs. daily sap flux data for the pre-fire, burned stand ($y = 3{,}140*(1-e^{-0.23x})$; $r^2 = 0.58$), the pre-fire, unburned stand ($y = 18{,}300*(1-e^{-0.04x})$; $r^2 = 0.69$), the post-fire, burned stand ($y = 1{,}090*(1-e^{-1.69x})$; $r^2 = 0.63$) and the post-fire, unburned stand ($y = 832*(1-e^{-2.59x})$; $r^2 = 0.57$). Linear relationships were fitted to the PAR vs. daily sap flux data for the pre-fire, burned stand ($y = 7.54x-9.52$; $r^2 = 0.18$), the pre-fire, unburned stand ($y = 10.7x-69.6$; $r^2 = 0.51$), the post-fire, burned stand ($y = 17.0x-32.2$; $r^2 = 0.54$) and the post-fire, unburned stand ($y = 13.2x-73.5$; $r^2 = 0.49$)

damage after prescribed fires (Smirnova et al. 2008; Swezy and Agee 1991), however, Zeleznik and Dickmann (2004) found that temperatures lethal to roots were only reached on the mineral soil surface and thus fine root dynamics of red pine (*Pinus resinosa* Ait.) were not affected. We found that approximately 40 % of the O_i horizon was consumed in the burn, but the O_a horizon (and presumably fine roots) remained intact which is consistent with measurements made during 25 other prescribed fires conducted in the Pinelands from 2004 to 2010 (Clark et al. 2011). Heat damage to the cambial and phloem tissues may also have caused the observed initial decline in daily sap flux rates in our burned pitch pines given that most trees had some charring of the lower bark. However, Ducrey et al. (1996) found no differences between gas exchange of Aleppo pines (*Pinus halepensis* Mill.) that received partial (70 % circumference) controlled heating to the boles and control trees. Only trees that received controlled heating around 90 % of the bole exhibited significantly lower gas exchange rates. These pines, along with pitch pines, have very thick bark tissues and are adapted to withstand the heat from a fire (Little 1998).

Following this initial decline, daily sap flux rates in trees that received the prescribed fire treatment were 11–25 % higher than in the unburned stand during the growing season. Likewise, daily sap flux in the burned stand was significantly higher for a given increase in either total daily PAR or average daytime VPD than at the unburned stand. However, since leaf-level stomatal conductance decreased throughout the season in the burned stand but increased in the unburned stand, this suggests that increases in total leaf area in pines in the burned stand explain the increased water use compared to the unburned trees. Pitch pines contain numerous epicormic buds and can replace lost leaf area rapidly after a disturbance (Landis et al. 2005). Indeed, we found a lowering of the crowns in pines after the fire suggesting growth from dormant, epicormic buds. Reich et al. (1990) also found that a low-intensity fire increased transpiration rates and mean leaf conductances in northern hardwood species. Likewise, after a wildfire in Scots pine (*Pinus sylvestris* L.) forests, Beghin et al. (2011) found that carbon isotope ratios were more negative than pre-fire conditions indicating that trees were less water-stressed following fire. We found less negative carbon isotope ratios following the fire in the burned and unburned stands and similar increases in $IWUE_{isotope}$ in both stands throughout the study period. However, the isotopic estimation of IWUE integrates the signal of all the carbon in the leaf tissue and carbon in new needles produced following the fire may be largely from the previous growing season and therefore, may not show the effects of the fire. Our leaf-level measurements of instantaneous IWUE suggested that leaves became more water use efficient as a result of the fire, whereas $IWUE_{instant}$ in trees from the unburned stand remained more or less constant throughout the study period.

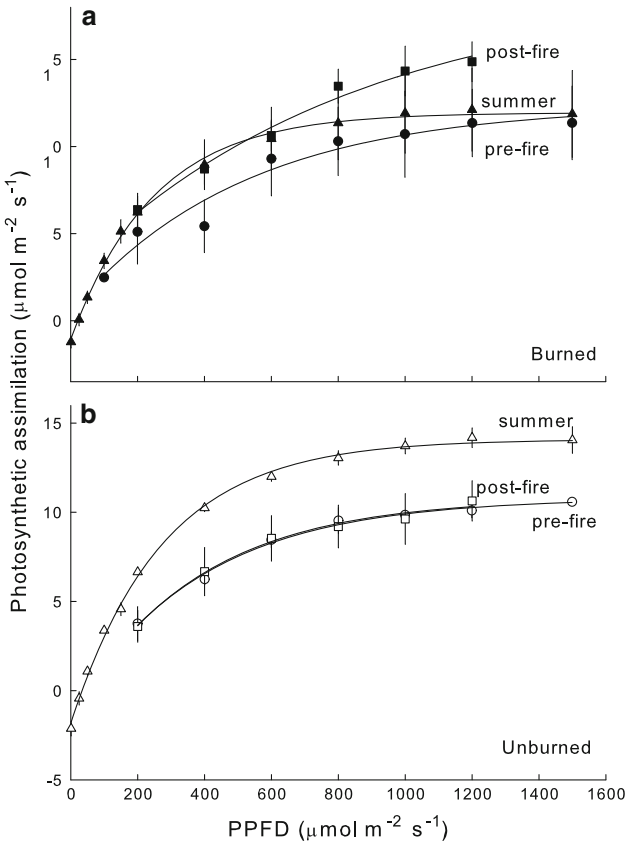

Fig. 6 Light response curves of photosynthetic assimilation (μmol CO_2 m^{-2} s^{-1}) vs. photosynthetic photon flux density (PPFD; μmol photons m^{-2} s^{-1}) for **a** the stand receiving the prescribed fire (*closed symbols*) and **b** the unburned stand (*open symbols*). Each point represents the average value of three measured trees and the *error bars* are the standard error around the mean. *Circles* represent pre-fire (1st and 2nd March 2011) measurements for the burned [$y = -0.26 + 12.3(1-e^{-0.0022x})$] and the unburned [$y = -1.2 + 12.0\ (1-e^{-0.0026x})$] stand. Squares represent post-fire (20th and 21st April 2011) measurements for the burned [$y = -1.3 + 17.1(1-e^{-0.0023x})$] and the unburned [$-1.5 + 12.3(1-e^{-0.0027x})$] stand. *Triangles* represent summer (1st and 2nd August 2011) measurements for the burned [$y = -1.1 + 13.0(1-e^{-0.004x})$] and the unburned [$y = -1.8 + 15.9(1-e^{-0.0036x})$] stand

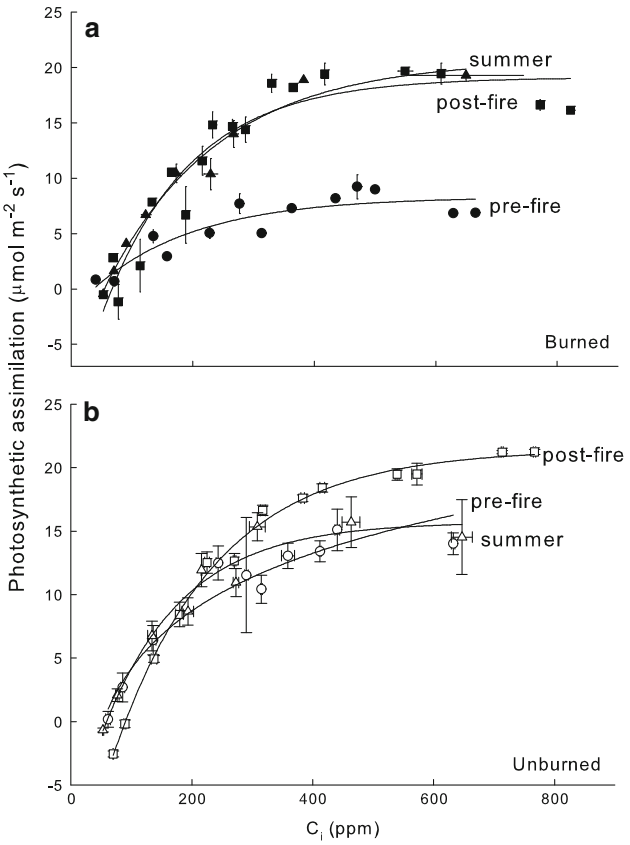

Fig. 7 A/C_i curves of photosynthetic assimilation (μmol CO_2 m^{-2} s^{-1}) vs. concentration of CO_2 inside the leaf (C_i; ppm) for **a** the stand receiving the prescribed fire (*closed symbols*) and **b** the unburned stand (*open symbols*). Each point represents the average value of three measured trees and the *error bars* are the standard error around the mean. *Circles* represent pre-fire (1st and 2nd March 2011) measurements for the burned [$y = -2.0 + 10.3\ (1-e^{-0.0059x})$] and the unburned [$y = -4.2 + 20.9\ (1-e^{-0.0043x})$] stand. *Squares* represent post-fire (20th and 21st April 2011) measurements for the burned [$y = -11.3 + 30.4(1-e^{-0.0069x})$] and the unburned [$y = -14.7 + 36.2\ (1-e^{-0.0058x})$] stand. *Triangles* represent summer (1st and 2nd August 2011) measurements for the burned [$y = -7.0 + 27.7\ (1-e^{-0.0075x})$] and the unburned [$y = -8.8 + 24.5(1-e^{-0.0075x})$] stand

Our results may also differ from other studies on post-fire physiology of trees because of differing intensities of the studied fires. For example, O'Brien et al. (2010) found much reduced rates of sap flux in longleaf pines (*Pinus palustris* Mill.) that were exposed to fire after a long period of fire exclusion in this system. This exclusion caused organic material to build on the forest floor as well as ingrowth of fine roots into this organic horizon. Consumption of the forest floor removed much of these roots which O'Brien et al. (2010) attribute to the lower sap flux rates and eventual death of more than one-third of the study trees. We found little consumption of the O_a horizon which is the likely location of surface roots in the organic horizon. Other studies differ due to the occurrence of more extensive crown scorch and loss of leaf area following fire. Clinton et al. (2011) found similar sap flow rates in fire-scorched and control longleaf pines but significant increases in transpiration per unit leaf area in the remaining needles of fire-scorched trees that lost 77 % of their needles to heat scorch. Likewise, Cernusak et al. (2006) saw slight but significantly higher stomatal conductances in leaves from Australian eucalypts (*Eucalyptus* sp.) in a burned plot relative to unburned trees which they attributed to increased soil moisture due to decreased overall crown conductance resulting from crown scorch. We observed relatively little crown scorch, lower leaf-level stomatal conductance but higher overall transpiration rates suggesting increased leaf area during the growing season after the prescribed fire.

Trees in our burned stand likely experienced decreased competition from the surrounding shrubs and understory trees following the fire which resulted in their increased uptake of water. Water usage was most divergent between the two stands in late spring (about 20 %) and this period corresponds with the timing of leaf-out of the understory shrubs (pers. obs.). Shrubs in the burned stand resprouted from basal meristems approximately 2 weeks after leaf-out in the unburned stand. Even then, shrubs that were burned by the fire likely failed to replace all of their previous aboveground leaf area. It is also interesting to note that in late spring (15 May 2011 to 15 June 2011) sap flux rates between the two stands were only 10 % different and in late summer (15 July 2011 to 30 August 2011) they were not significantly different. These two time periods correspond with times of relatively abundant soil moisture that possibly alleviated water stress in the unburned stand. In a study of northern hardwoods receiving a surface fire, Reich et al. (1990) reported no discernable effect of the fire on tree water status compared to an unburned stand, which they attributed to relatively high rainfall throughout the growing season. The period from 15 June 2011 to 15 July 2011 (summer) was relatively dry with soil moistures dropping to around 5 % volumetric soil moisture content and this time period corresponds to the second largest divergence in sap flux rates between the two sites of around 18 %. This suggests that water use of the pitch pines in the unburned stand was more affected by these drought conditions than trees at the burned stand which experienced less competition for water.

In terms of photosynthetic capacity, pines in the burned and unburned stands displayed similar parameters estimated from the light response and A/C_i curves throughout the study period. Therefore, the prescribed fire did little, if any, damage to needles and they were able to function similarly to the unburned stand. However, because both water use efficiency and total water use increased in the burned stand, the prescribed fire can be associated with increased carbon uptake and assimilation. Cernusak et al. (2006) also did not find differences in light-saturated photosynthetic rates in Australian savanna trees that were burned vs. unburned, but Reich et al. (1990) found that maximum photosynthetic rates were between 30 and 50 % higher in trees from a burned stand vs. an unburned stand. They attribute this increase to increases in N, P, and K that were found in trees from the burned stand relative to the unburned stand. Wallin et al. (2003) also found that net photosynthetic rates were higher in undamaged foliage from ponderosa pine trees that had moderate levels of crown scorch compared with unburned trees, but they attribute this result to improved water relations of remaining needles and not increased photosynthetic capacity. We did find that maximum carboxylation rates increased significantly between the pre-fire and the summer measurement period in trees from the burned stand but remained relatively constant in trees from the unburned stand over the same time period. This may be related to more nitrogen made available following the prescribed fire.

We found that N concentrations as well as C/N ratios were maintained at a constant level in needles from the burned stand throughout the year, despite higher leaf area as opposed to the unburned stand where N concentrations decreased throughout the season. Therefore, nitrogen was apparently more limiting in the unburned stand, presumably because of increased competition from shrubs for nitrogen. The release of previously unavailable nitrogen that resulted from the prescribed fire may have kept the nitrogen constant in the burned stand. Beghin et al. (2011) showed that % N was higher in surviving Scots pine trees after a wildfire suggesting changes in the soil nitrogen supply after the fire. Rodríguez et al. (2009) found that the spatial distribution of nitrogen in the soil can be altered after a fire with more nutrients accumulating around large trees due to ash and litter deposition there. Boerner and Lord (1984) calculated mineralization rates of about 25 kg ha^{-1} for nitrogen and about 2 kg ha^{-1} for phosphorus after a prescribed fire in the New Jersey Pinelands, although this influx of nutrients was not evident a few months later. This may mean that these nutrients had leached from the root available zone due to the sandy soils (Boerner and Lord 1984; Boerner et al. 1988), or that nutrients released were quickly taken up by biological activity (Gray and Dighton 2009; Richter et al. 1982). Studies have also found increased phosphorus concentrations in plant tissues after a fire which, in conjunction with increased plant growth, suggest that phosphorus is limiting in the Pinelands (Boerner et al. 1988; Gray and Dighton 2009). Our preliminary data also suggest that phosphorus, potassium, and magnesium concentrations increased in leaf tissues after the fire, although more work is needed to confirm this.

Prescribed fires are often used as a fire suppression management strategy for reducing fuel loads in wildfire-prone areas, but relatively little was known about the ecophysiological response of overstory trees to this treatment. We found that pitch pines that experienced a prescribed fire used more water during the growing season but had higher intrinsic water use efficiency presumably because of increased maximum carboxylation rates than trees from the unburned stand. These results suggest that pitch pines that receive low intensity, early season, prescribed fires will most likely experience more favorable growing conditions through higher water availability and presumably higher N availability, at least in the short term. This is especially important in fire-prone areas where drought and water stress are prevalent during the growing

season and could mean that early spring prescribed fires would be particularly beneficial if a subsequent summer drought is predicted. Overstory stems are likely making use of water made available by the decrease in shrub leaf area resulting from the prescribed fire. Therefore, overall ecosystem water use may not significantly change following prescribed fire, but the proportion transpired by individual components (i.e., shrubs, overstory stems, etc.) may be different. Likewise, the increased carbon uptake of the overstory pines following prescribed fire may offset the carbon consumed by the fire. This extra carbon does not appear to be going to increased stem growth according to our data, but could be added to non-structural stored carbon reserves. Greater amounts of stored carbon should make trees more resilient in terms of drought, insect disturbances and storm damage (Galiano et al. 2011, 2012; Wiley and Helliker 2012) that can be prevalent in the New Jersey Pinelands. Finally, these data are important in helping elucidate the responses of trees to prescribed fires in the Northeast as well as modeling carbon sequestration and hydrologic dynamics in these ecosystems that routinely experience prescribed fire as a management strategy as well as low-intensity wildfires which will create similar conditions.

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References

Agee JK (1998) Fire and pine ecosystems. In: Richardson DM (ed) Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, pp 193–218

Beghin R, Cherubini P, Battipaglia G, Siegwolf R, Saurer M, Bovio G (2011) Tree-ring growth and stable isotopes (^{13}C and ^{15}N) detect effects of wildfires on tree physiological processes in *Pinus sylvestris* L. Trees 25:627–636

Boerner RE, Lord TR (1984) First year loss of mass and nutrients from leaf litter in the New Jersey Pine Barrens. Bartonia 50:12–20

Boerner RE, 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

Busse MD, Simon SA, Riegel GM (2000) Tree-growth and understory responses to low-severity prescribed burning in thinning *Pinus ponderosa* forests of Central Oregon. For Sci 46:258–268

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, Heilman W, Hom J (2011) Fuel consumption and particulate emissions during fires in the New Jersey Pinelands. 3rd Fire Behavior and Fuels Conference, Spokane

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. Agric For Meteorol 166–167:50–61

Clinton BD, Maier CA, Ford CR, Mitchell RJ (2011) Transient changes in transpiration, and stem and soil CO_2 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 Manage 54:175–191

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

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, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40:503–537

Forman RTT, Boerner RE (1981) Fire frequency and the Pine Barrens of New Jersey. Bull Torrey Bot Club 108:34–50

Galiano L, Martínez-Vilalta J, Lloret F (2011) Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. New Phytol 190:750–759

Galiano L, Martínez-Vilalta J, Sebaté S, Lloret F (2012) Determinants of drought effects on crown condition and their relationship with depletion of carbon reserves in a Mediterranean holm oak forest. Tree Physiol 32:478–489

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol 3:309–320

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

Gu L, Pallardy SG, Tu K, Law BE, Wullschleger SD (2010) Reliable estimation of biochemical parameters from C_3 leaf photosynthesis-intercellular carbon dioxide response curves. Plant Cell Environ 32:1852–1874

Harrington M (1993) Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. Int J Wildland Fire 3:65–72

Hood SM, Smith SL, Cluck DR (2010) Predicting mortality for five California conifers following wildfire. For Ecol Manage 260:750–762

Keeley JE (2012) Ecology and evolution of pine life histories. Ann For Sci 69:445–453

Knapp EE, Schwilk DW, Kane JM, Keeley JE (2007) Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. Can J For Res 37:11–22

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

Landsberg JD, Cochran PH, Finck MM, Martin RE (1984) Foliar nitrogen content and tree growth after prescribed fire in ponderosa pine. USDA Pacific Northwest Forest and Range Experiment Station, Portland

Little S (1998) Fire and plant succession in the New Jersey Pine Barrens. In: Forman RTT (ed) Pine Barrens: Ecosystem and Landscape. Rutgers University Press, New Brunswick, pp 297–314

Matlack GR, Gibson DJ, Good RE (1993) Regeneration of the shrub *Gaylussacia baccata* and associated species after low-intensity fire in an Atlantic coastal plain forest. Am J Bot 80:119–126

Murphy B, Williamson G, Bowman D (2011) Fire regimes: moving from a fuzzy concept to geographic entity. New Phytol 192:316–318

Narayan C, Fernandes P, van Brusselen J, Schuck A (2007) Potential for CO_2 emissions mitigation in Europe through prescribed burning in the context of the Kyoto Protocol. For Ecol Manage 251:164–173

O'Brien JJ, Hiers JK, Mitchell RJ, Varner JM III, Mordecai K (2010) Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. Fire Ecol 6:1–12. doi: 4996/fireecology.0602001

Oishi AC, Oren R, Stoy PC (2008) Estimating components of forest evapotranspiration: a footprint approach for scaling sap flux measurements. Agric For Meteorol 148:1719–1732

Oksanen L (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94:27–38

Pan Y, Birdsey R, Hom J, McCullough K, Clark K (2006) Improved estimates of net primary productivity from MODIS satellite data at regional and local scales. Ecol Appl 16:125–132

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

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

Richter DD, Ralston CW, Harms WR (1982) Prescribed fire: effects on water quality and forest nutrient cycling. Science 215:661–663

Rodríquez A, Durán J, Fernández-Palacios JM, Gallardo A (2009) Short-term wildfire effects on the spatial pattern and scale of labile organic-N and inorganic-N and P pools. For Ecol Manage 257:739–746

Rozas V, Pérez-de-Lis G, García-González I, Ramón 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

Schäfer KVR (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: doi: 10.3389/fpls.2011.00015

Schwilk DW, Knapp EE, Ferrenberg SM, Keeley JE, Caprio AC (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For Ecol Manage 232:36–45

Skov KR, Kolb TE, Wallin KF (2004) Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. For Sci 50:1–11

Smirnova E, Bergeron Y, Brais S, Granström A (2008) Postfire root distribution of Scots pine in relation to fire behaviour. Can J For Res 38:353–362

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

Stephens SL, Finney MA (2002) Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For Ecol Manage 162:261–271

Swezy DM, Agee JK (1991) Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can J For Res 21:626–634

Sword Sayer MA, Haywood JD (2006) Fine root production and carbohydrate concentrations of mature longleaf pine (*Pinus palustris* P. Mill.) as affected by season of prescribed fire and drought. Trees 20:165–175

Tuininga AR, Dighton J (2004) Changes in ectomycorrhizal communities and nutrient availability following prescribed burns in two upland pine-oak forests in the New Jersey pine barrens. Can J For Res 34:1755–1765

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 Manage 258:2467–2474

Wallin KF, Kolb TE, Skov KR, Wagner MR (2003) Effects of crown scorch on ponderosa pine resistance to bark beetles in Northern Arizona. Environ Entomol 32:652–661

Wiley E, Helliker B (2012) A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. New Phytol 195:285–289

Yevdokimenko MD (2011) Forest-ecological consequences of fires in light conifer forests of Transbaikalia. Russian J Ecol 42:205–210

Zeleznik JD, Dickmann DJ (2004) Effects of high temperatures on fine roots of mature red pine (*Pinus resinosa*) trees. For Ecol Manage 199:395–409