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Fuel loads, fire regimes, and post-fire fuel dynamics in Florida Keys pine forests

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Abstract. In forests, the effects of different life forms on fire behavior may vary depending on their contributions to total fuel loads. We examined the distribution of fuel components before fire, their effects on fire behavior, and the effects of fire on subsequent fuel recovery in pine forests within the National Key Deer Refuge in the Florida Keys. We conducted a burning experiment in six blocks, within each of which we assigned 1-ha plots to three treatments: control, summer, and winter burn. Owing to logistical constraints, we burned only 11 plots, three in winter and eight in summer, over a 4-year period from 1998 to 2001. We used path analysis to model the effects of fuel type and char height, an indicator of fire intensity, on fuel consumption. Fire intensity increased with surface fuel loads, but was negatively related to the quantity of hardwood shrub fuels, probably because these fuels are associated with a moist microenvironment within hardwood patches, and therefore tend to resist fire. Winter fires were milder than summer fires, and were less effective at inhibiting shrub encroachment. A mixed seasonal approach is suggested for fire management, with burns applied opportunistically under a range of winter and summer conditions, but more frequently than that prevalent in the recent past.

Additional keywords: char height; fuel consumption; path analysis; pine rocklands; prescribed fire; slash pine.

Introduction

In a pyrogenic plant community, the amount of fuel available for combustion is an important determinant of fire intensity (Byram 1959). In general, higher fuel loads generate more severe fires (Dodge 1972; Rothermel 1972; Brown and Davis 1973), though this pattern may be overridden by the effects of fuel moisture or prevailing weather conditions (Bessie and Johnson 1995; Hely *et al*. 2001). The quantity of fuels present locally is characterized by strong historical contingency, i.e. the intensity and timing of the most recent fire remain an influence on current conditions. Specifically, the intensity of previous fire affects how much of the antecedent understory survived and how much was consumed or transformed into dead fuels, and the timing defines the period in which newly produced fuels have had the chance to accumulate. In general, a long interval between fires usually facilitates fuel accumulation, resulting in more intense and destructive wildfires (Rothermel 1972; Van Wilgen 1982; Hobbs and Gimingham 1984; Reggan *et al*. 1988), whereas a short fire interval can drastically reduce fuel biomass (Van Wilgen and Kruger 1981). Fuel reduction is one rationale for employing prescribed fire in different ecosystems, including South Florida pine forests, which in the absence of fire develop progressively into hardwood forests, known locally as hammocks (Alexander and Dickson 1972; Myers 2000). A corollary implication of this successional sequence is that the contribution of broadleaf species to pine forest fuel loads usually increases with time since last fire.

Fire history also affects the relative proportions of live and dead fuels, which vary in moisture content and therefore are important in controlling fire behavior. Dead fuels, which have relatively low moisture content (Pyne *et al*. 1996), usually increase in total load asymptotically over time (Rothermel and Philpot 1973; Schimmel and Granstrom 1997). Likewise, Baeza *et al*. (2002) showed that moisture content in live shrubs decreased with maturity, resulting in more intensive fire in a Spanish Mediterranean shrubland. In forests, however, the relationship between fuels and fire behavior is more complex, as fuels derived from various species differ in flammability (Behm *et al*. 2004), and various life forms

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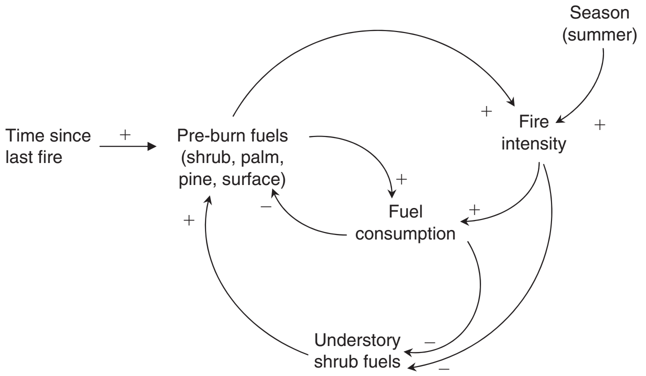

Fig. 1. A conceptual model showing hypothetical relationships among fuel loads, fire behavior, and post-fire fuel accumulation in Florida Keys pine forests.

have different intrinsic fuel properties (DeBano *et al.* 1998). The relative effects of different life forms in determining fire behavior may vary depending on their contribution to the total fuel loads, growth stage, and moisture content (Scott and Burgan 2005). For instance, many shrubs and palms that grow in the understory of south-eastern pine forests contain a high concentration of volatile compounds, and therefore are very flammable (Myers 2000). Moreover, these growth forms accentuate vertical fuel continuity, potentially contributing to fire intensity (Ryan 2002). However, shrubs may also burn less intensely than the surrounding herbaceous vegetation, because they create a humid understory microenvironment (Wade *et al.* 1980; Slocum *et al.* 2003). Information regarding the nature and distribution of fuels is important in prescribed burning programs, particularly in projecting how rapidly fires will spread, their intensity, and ultimately their ecological effects (Rothermel 1972; Paatalo 1998; Baeza *et al.* 2002). In the present paper, we examine the quantity of various fuel components, their role in fire behavior, and the effects of fire on subsequent fuel dynamics in a South Florida slash pine forest.

Figure 1 depicts a hypothetical model of the relationships among fuel characteristics, fire intensity, and post-fire fuel dynamics in pine forests of the Florida Keys. Long-term exclusion of fire from limestone-based pine rockland ecosystems throughout South Florida has resulted in a dense understory vegetation of broadleaved hardwood species (Robertson 1953; Myers 2000). The standing biomass of hardwoods includes both a component of understory fuel and a contributor of litter to the surface fuels. In general, the higher the fuel loads in both forest floor and understory, the higher the fire intensity. However, where hardwood shrubs become well established, forming dense local patches in the understory, shrub components in the total fuel may burn less intensively (Wade *et al.* 1980), resulting in lower fuel consumption. Moreover, fire intensity may also vary depending on season and prevailing weather conditions. In south-eastern forests, fire is more intense and fuel consumption is higher in summer than winter (Robbins and Myers 1992; Waldrop *et al.* 1992). Intense fire also kills hardwood species (Taylor and Herndon 1981), a desirable objective of prescribed burns, but one that may also increase pine mortality (Menges and Deyrup 2001) and slow plant community recovery (Spier and Snyder 1998), thereby constraining the development of understory fuels in the post-burn period. In contrast, when fire intensity is low to moderate, much of the hardwood vegetation resprouts quickly, creating an even greater density of hardwoods (Hofstetter 1974; Wade *et al.* 1980; Taylor and Herndon 1981), and resulting in increased understory fuel accumulation.

As suggested by the studies cited above, most fire research in south Florida has been done in mainland pine forests. In the lower Florida Keys, where encroachment of broadleaved species into the pine forest canopy in the absence of fire is estimated to take twice as much time as on the mainland (Alexander and Dickson 1972), fuel dynamics and fire behavior have not been well studied. Nevertheless, pine forests at the wildland–urban interface in the Keys have been periodically burned since 1957 to reduce the fuel loads and avoid catastrophic fire, and to suppress the growth of hardwood species. The development of effective strategies to manipulate the fire cycle in these forests requires a comprehensive understanding of fuel dynamics and the effect of fuels on fire behavior. Our objectives in the present study were therefore: (1) to estimate total aboveground biomass in Florida Keys pine rocklands; (2) to examine the direct and indirect effects of pre-burn fuels and season on fire intensity and fuel consumption; and (3) to examine the dynamics of understory fuel accumulation after fire. More generally, our goal was to provide fire managers with information useful in deciding when and where to burn to perpetuate these unique pine forests. The results of this study should assist not only in maintaining the Keys pine rocklands but also in the management of other low-productivity pine forests growing directly on limestone substrate in the Caribbean basin.

Materials and methods

Study area

The study area is located in the National Key Deer Refuge (NKDR) in the lower Florida Keys. Pine forests within NKDR are species-rich communities that include much of the plant species diversity in the Refuge, and are considered to be critical habitat for the federally endangered Key Deer (*Odocoileus virginianus clavium*). Pine forests once covered much of the lower Florida Keys, but the combined effects of sea level rise (Ross *et al.* 1994) and residential development over the last century have reduced them to less than 1000 ha scattered over seven islands. Our study focused on the pine forests of Big Pine Key, the largest of these islands.

Florida Keys pine forests are characterized by a canopy of south Florida slash pine (*Pinus elliottii* var. *densa*), a very diverse shrub layer dominated by West Indian tropical hardwoods and several palm species, and a diverse herb layer. Many of the herbs are endemic to the rocklands of south Florida, where skeletal soils are discontinuously distributed on a karstic, limestone substrate. South Florida slash pine forests are adapted to frequent burning. In its absence, the pine overstory is replaced by a dense hardwood 'hammock' – a southern Florida forest type dominated by West Indian, broadleaved tree species – resulting in a loss of the characteristic pineland herb flora (Robertson 1953). Hence, fire has been the primary tool available for maintaining forest structure and composition in South Florida pine rocklands, including those in the lower Florida Keys (Alexander and Dickson 1972; Wade *et al*. 1980; Taylor and Herndon 1981; Snyder *et al*. 1990; Myers 2000; Slocum *et al*. 2003).

Since the creation of NKDR in 1957, fuel reduction has been an important consideration in pine forest management due to the proximity of residences to Refuge boundaries. Prescribed fire was applied opportunistically through 1992 (Bergh and Wisby 1996), but during the next 5–6 years, the US Fish and Wildlife Service prescribed fire program was inactive. Lightning fires were actively suppressed throughout the period. This intermittent fire history has allowed a relatively heavy shrub understory to develop in many NKDR forests.

Experimental design

In 1998, we initiated a burning experiment in a randomized complete block design: during 3 consecutive years, three treatments were to be carried out in a single well-defined block in two characteristic understory types. The two understory types were: (1) a relatively sparse shrub layer and well-developed herb layer ('open'); and (2) a dense shrub layer and poorly developed herb layer ('shrubby'), and the three burn treatments were: (1) summer burn; (2) winter burn; and (3) no burn, or control. We delineated six relatively homogeneous blocks, three open and three shrubby, which represented the geographic and structural range of forests present on Big Pine Key. In each block, we established three 1-ha plots, separated by buffer strips $\geq$20 m, and randomly assigned them to the three treatments (Fig. 2). The 18 plots thereby established were identified by year of intended treatment (1998, 1999, 2000), block, or characteristic understory (open, shrubby), and treatment (summer burn, winter burn, control). For instance, the open plot intended to be burned in the summer of 1999 was designated as 1999-O-S, and winter-burned plot in the same block was 1999-O-W. Prior to our study, all areas within five blocks had been burned most recently between 1985 and 1991, whereas the 2000-S block was unburned since at least 1970 (Table 1).

Weather and logistical constraints did not allow the experiment to be completed as planned. In 1998, the summer and winter burns in both blocks were completed on schedule. In 1999, both summer burns were completed, but the winter burn in the 1999-O block was deferred till 2000, and the 1999-S-W burn was not completed during the study. The summer and winter burns planned for 2000 were not completed in that year, and all four plots were burned in the summer of 2001. Thus, 11 prescribed burns were completed during the study. Eight summer burns were carried out during June to August, the early part of the south Florida wet season, when lightning-caused fires are most likely to occur (Robertson 1953; Wade *et al*. 1980; Snyder 1991). Three winter burns were completed during December, when plants are most dormant and burning conditions are relatively mild (Table 1).

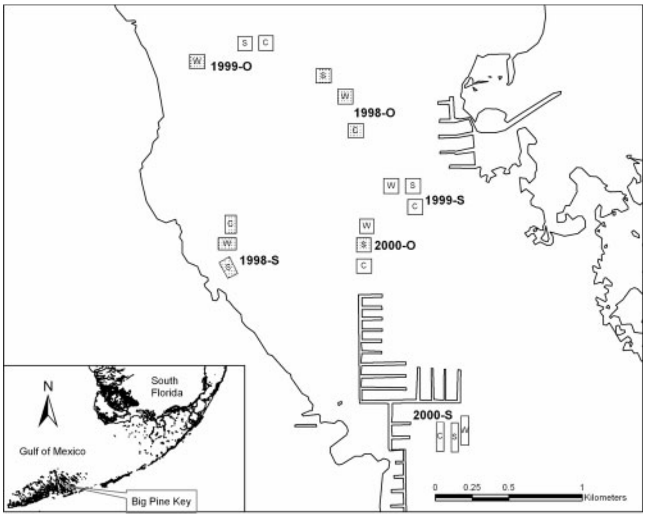

Fig. 2. Study area map showing the layout of experimental plots. Note that the winter burn in the 1999-O block was delayed until winter 2000, and that summer and winter plots in both the 2000-O and 2000-S blocks were burned in the summer of 2001. The summer plot in the 1999-W block was not burned. Plots with tree locations mapped are indicated by dotted pattern.

Because of the configuration of available parcels of pine rockland, the 1-ha vegetation plots were of three shapes: 100×100 m (12 plots), 80×125 m (three plots), and 50×200 m (three plots). All trees >5 cm diameter at breast height (DBH) within the borders of the plot were measured, and the location of each tree was determined to the nearest meter in eight plots (all 1998 plots, 1999-O-W, and 2000-O-S). Other fuel categories were sampled in subplots centered on 20 points selected through a stratified random method that ensured adequate representation of all regions of the plot.

Fuel and biomass estimation

We estimated fuel and biomass within the following broad structural categories: (1) ground layer; (2) shrubs; (3) palms; (4) pines; and (5) hardwood trees. Each component was estimated at least once in each of the 18 plots, and several

Table 1. Experimental plots within six blocks with the burn dates, weather conditions at the time of burning, and flame lengths

Each block had one of two characteristic understory types: open (O), and shrubby (S). The three treatments were: control (C), summer (S), and winter (W). KBDI, Keetch–Byram drought index; NB, not burned; ND, not determined

Burning treatment	Plot ID	Year when plots were last burned	Date of experimental burn	Wind speed ($km\,h^{-1}$)	Temperature (°C)	Relative humidity (%)	Total rainfall in 7 days (mm)	KBDI	Flame length (m)	
									Backing fire	Flanking fire
1998-O										
C	1998-O-C	1990	NB							
S	1998-O-S	1990	16 August 1998	8–16	31–33	62–70	39	574	ND	ND
W	1998-O-W	1990	15 December 1998	13–19	19–21	56–65	19	260	0.3–1.0	ND
1998-S										
C	1998-S-C	1986	NB							
S	1998-S-S	1986	17 August 1998	10–14	31–33	63–69	41	580	2.5–4.5	ND
W	1998-S-W	1986	15 December 1998	13–19	19–21	56–65	19	260	0.3–1.0	ND
1999-O										
C	1999-O-C	1991	NB							
S	1999-O-S	1991	18 July 1999	14–19	31–32	71–73	33	221	0.3–1.0	2.0–3.0
W	1999-O-W	1985	12 December 2000	8–11	26–28	78–89	23	307	0.3–2.5	2.5–4.5
1999-S										
C	1999-S-C	1988	NB							
S	1999-S-S	1988	22 June 1999	8–10	29–32	69–81	70	133	0.3–1.0	0.6–2.0
W	1999-S-W[A]	1988	NB							
2000-O										
C	2000-O-C	1986	NB							
S	2000-O-S[B]	1986	19 July 2001	10–14	29–31	65–81	67	126	0.6–2.0	1.5–3.0
W	2000-O-W[B]	1986	19 July 2001	10–14	29–31	65–81	67	126	0.6–2.0	1.5–3.0
2000-S										
C	2000-S-C	Before 1970	NB							
S	2000-S-S[B]	Before 1970	18 July 2001	8–11	28–30	68–77	67	119	0.3–1.2	1.0–3.0
W	2000-S-W[B]	Before 1970	18 July 2001	8–11	28–30	68–77	67	119	0.3–1.2	1.0–3.0

[A]Never burned; [B]burned in summer 2001.

were estimated in multiple years in some stands. Methods of estimation are described below.

Ground layer

Ground layer fuel (live vegetation <1 m height, litter, and coarse woody debris on the forest floor), hereafter termed 'surface fuels', was measured in all plots, including the controls, before the burns in each block. Surface fuel quadrats were centered on the 20 randomly selected points described above. Two 1-m^2 quadrats were arranged 4.5 m from the shrub subplot center, in opposite cardinal directions. Three 0.25-m^2 sub-quadrats were established within each quadrat, and assigned for pre-burn, post-burn, or final harvest. Pre-burn sub-quadrats were harvested in all 18 stands, post-burn sub-quadrats were harvested within 1 month of fire in 10 of the 11 burned stands, and a final harvest was completed in 17 of 18 stands at the conclusion of the project.

Surface fuel harvest was accomplished by (1) clipping live vegetation at ground level and collecting all standing plant material less than 1 m in total height, including palms; and (2) collecting all undecomposed litter and woody debris <2.54 cm in diameter (1-h and 10-h fuels). Samples were separated into live and dead fuels. Live fuels were further separated into forbs, ferns, graminoids (including grasses, sedges, and grass-like forbs), woody plants, and palms, and dead fuels were separated into fine litter or 1-h fuels (<0.64 cm), and coarse litter or 10-h fuels (≥0.64 cm but <2.54 cm in diameter). Separated samples were oven-dried for 48 h at 70°C and weighed.

Shrubs

Shrub biomass was estimated by applying regression models to plant dimensional data. Circular 4-m radius subplots were centered on the 20 random points in each plot, and all woody stems >1 m height and <5 cm diameter rooted within the subplot borders were measured. Measurements differed for shrub-like and tree-like species. For shrub-like species, we treated clumping stems as a single individual, and measured height and two crown widths, i.e. the longest axis and its perpendicular. For tree-like plants, we measured total height and DBH if >1.4 m tall. Regression models based on these measurements were developed from a sample of 8–19 stems of each of the major shrub species, collected outside the study plots on Big Pine Key, and used to estimate total biomass and biomass of leaves and stems <0.64 cm diameter (Sah *et al*. 2004). Mixed-species equations were used to calculate biomass of less common species for which individual regressions were not developed (Sah *et al*. 2004).

Palms

Total palm biomass was calculated as the summation of trunk and leaf biomass estimates, which were derived separately from palm dimensional data. Because height is often a good predictor of palm biomass (e.g. Frangi and Lugo 1985), we measured total height and apical height (height to the apical meristem) of each individual belonging to four palm species (*Coccothrinax argentata*, *Sabal palmetto*, *Serenoa repens*, and *Thrinax morrisii*) within the shrub subplots described above, regardless of stem diameter. For biomass estimation purposes, we categorised palm individuals into 10 size-classes based on apical height (Table 2).

Table 2. Palm apical height size classes

Size class	Apical meristem height (m)	Mean ± s.d.
1	<0.5	0.31 ± 0.11
2	0.51–1.0	0.74 ± 0.14
3	1.01–1.5	1.25 ± 0.14
4	1.51–2.0	1.76 ± 0.15
5	2.01–2.5	2.23 ± 0.14
6	2.51–3.0	2.75 ± 0.13
7	3.01–3.5	3.30 ± 0.11
8	3.51–4.0	3.82 ± 0.17

To estimate the biomass of palm trunks, it was necessary to estimate the bole volume and stem specific density for each tree sampled. Assuming a cylindrical form for a palm trunk, we calculated the volume ($v = \pi(d/2)^2 h$) of each individual tree, where h was the measured apical height, and d was the mean basal diameter (measured at 10 cm above palm-butt) obtained from 3 to 5 randomly selected individuals in each of the 10 height classes listed in Table 2. Stem specific density (SD) was calculated for a pie-slice or cylinder excised from the trunk of six trees, three each of *Coccothrinax argentata* and *Thrinax morrisii*. Following the oven-dry method described by Barajas-Morales (1987), stem sections were dried to a constant weight at 70°C, and their volumes were determined by the mass of water displaced when the sample was completely submerged in a beaker of water placed on a digital balance of 2000 g capacity. The increase in the beaker's weight in grams was equivalent to the volume of the palm slice in cubic centimeters. Specific density was calculated as the ratio of the oven-dry mass divided by the volume of the stem samples. Trunk biomass was then calculated for each tree as the product of stem specific density and bole volume.

Palm leaf (blade + petiole) biomass was estimated according to methods described in Cooley (2004). She found that height was a poor predictor of palm leaf biomass, and developed equations based on crown area and leaf number, which are parameters not included in the shrub sampling protocols. Therefore, in order to obtain estimates of live and dead leaf biomass for *C. argentata* and *T. morrisii*, we multiplied the number of censused individuals in each palm size class by the mean live and dead standing leaf biomass of an average individual within the class. We determined the mean leaf biomass in each size class by applying best regression equations to 10 randomly chosen individuals per class in six blocks (Cooley 2004).

Table 3. Best fit regression equations to calculate biomass of slash pine (*Pinus eliottii* var. *densa*) saplings
DBH, diameter at breast height; HT, height; SEE, standard errors of estimate

Regression equations	a	b	c	R^2	*P*-value	SEE
Total biomass = a + b(DBH^{2}HT)	0.458	0.35	–	0.966	<0.001	0.320
Fine fuel = a + b(DBH^2) + c(HT)	0.263	36.58	–0.98	0.630	0.019	0.184

Pines

Pine sapling (height > 1 m and DBH < 5 cm) biomass was estimated by using regression equations developed locally for *Pinus elliottii* var. *densa* stems of this size. Independent variables tested were height and DBH. Thirteen individuals from an area of old growth pineland in Big Cypress National Preserve were measured, collected, and weighed. The best regression model (Table 3) was applied to dimensional data collected from the shrub subplots.

Pine tree (DBH ≥ 5 cm) biomass was estimated using equations developed for various tree components in a north Florida slash pine plantation (Gholz and Fisher 1982). The regression models were applied to tree DBH data collected from all 18 1-ha plots before the experimental burns. Using DBH as a predictor, we calculated the dry weight of stem bark and wood, live and dead branches, and total foliage, and summed them to derive a total aboveground biomass of pine trees.

Hardwood trees

Biomass of hardwood trees (DBH > 5 cm) was estimated using a generalized equation developed by Brown *et al.* (1989) for dry tropical forests. The regression equation was applied to the hardwood tree DBH data, as described above for pines.

We defined potential fuel or fuel loads to include: (1) total ground layer biomass (surface fuels); (2) shrub leaves and twigs (<0.64 cm in diameter); (3) palm leaves and petioles; and (4) pine sapling needles and twigs (<0.64 cm in diameter). We used the term 'understory fuels' for broadleaved shrubs, palms, and pine saplings as a group.

Conditions during experimental burns

Weather conditions at the time of ignition differed among experimental burns (Table 1). Temperatures varied from 19 to 28°C and from 28 to 33°C in the winter and summer burns, respectively. Relative humidity ranged between 56 and 89%. The Keetch–Byram drought index (KBDI), a measure of wildland fire potential, was calculated using the mathematical model of Keetch and Byram (1968). To calculate the KBDI, we used meteorological data from Key West, 30 miles from the study area, because long-term continuous data for Big Pine Key were not available. As the calculation of KBDI should be initialised when soil is near saturation (Keetch and Byram 1968), we initialized the calculation from 6 October 1996, when 156 mm of cumulative precipitation fell in 1 week. Setting the KBDI value at 0 on that day, we calculated a drought factor and then KBDI for subsequent days following Janis *et al*. (2002). KBDI values were lower than 350 on all burning days except those in summer 1998 (Table 1). All burns were carried out under relatively low wind speeds, within a few days of a significant rain event. In general, the precipitation ranged from 19 to 70 mm within 7 days, and from 1 to 34 mm within the 36 h before burning. At one site, 55 mm of rain fell 4 days before a 1999 summer burn. Because of these rain events, the duff layer was moist at the time of ignition in almost all plots. During the active burns, wind speeds ranged from 8 to 19 km h^{-1}. The firing patterns used in the prescribed burns resulted in both backing and flanking fires within the plots, with flame lengths up to 2.5 m and 4.5 m, respectively. In most cases, flame lengths were 0.5–1.5 m in backing fires and 1–3 m in flanking fires, resulting in low to medium frontline fire intensity. Duff consumption varied from 50 to 80%. However, in many cases, relatively high moisture in the duff layer protected the pine roots from burning. Fire never reached the crowns of pine trees in the overstory, and in some cases, even the top portion of palms in the mid-story (1–2 m) was not consumed.

Fire intensity and burn severity

In the present study, fire-line intensity – which is the rate of energy release per unit of length of fire front, and is commonly expressed as heat yield of fuel × fuel load × rate of fire spread (Byram 1959) – could not be determined, as the rate of fire spread was not measured. However, in seven out of 11 burned plots, fire temperature was estimated from the response of temperature-sensitive paints (Tempilaq; Big Three Industries, South Plainfield, NJ, USA), with melting temperatures spaced at 50°F intervals between 200° and 650°F (27.8°C intervals between 93.3 and 343.3°C). The paints were dabbed on 7.5 cm × 7.5 cm × 3 mm steel plates hung vertically from a rebar at ground level. Crown scorch percentage and char height were assessed in all burned plots. Crown scorch percentage, a measure of the amount of live needles killed by the fire (percentage crown scorch volume; Fowler and Sieg 2004), was estimated visually. Crown scorch percentage represents the post-fire environment and is considered a measure of burn severity (Jain 2004). Char height, a commonly used indicator of fire intensity (Waldrop and Brose

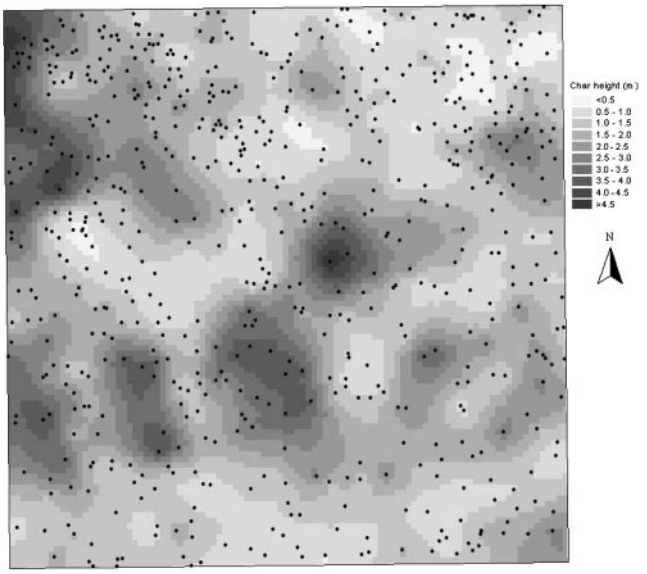

Fig. 3. An experimental plot (1998-O-W), showing the distribution of trees and the char height grids produced by spatial interpolation of point measurements.

1999; Menges and Deyrup 2001), was measured directly on all individual tree trunks within the burned plots. Following the method described in USDI-NPS (2001), we measured char height as the maximum height of charring on the bole, irrespective of direction. In the six burned plots in which the trees were mapped, the spatial pattern of fire intensity was determined by interpolation of the point measurements via a kriging algorithm (Maclean and Cleland 2003; Taylor *et al.* 2004). In these plots, the mean tree density was 559 ± 101 trees ha^{-1}. Trees ranged broadly in size, and were well distributed throughout the plots (Fig. 3). Using the Geostatistical function in ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, USA), ordinary kriging was performed in two steps: semivariogram analysis (Isaaks and Srivastava 1989), and gridding. A spherical model was applied to fit semivariograms for char height, and a search distance of 15 m was used in the gridding process. The performance of models was evaluated based on root mean square error (RMSE). RMSE of the best fit models for the six plots ranged between 9.4 and 14.4% of mean char height. The output was a map of 1×1 m grid cells with an estimated scorch percentage and char height in each cell. Within each burned plot, we then overlaid polygons associated with 20 circular, 4-m radius subplots, which served as understory sampling units (see below), and we calculated a mean crown scorch percentage and char height for the grid cells within each subplot.

Statistical analysis

We used one-way analysis of variance (one-way ANOVA) to assess pre-burn differences among blocks in total biomass and potential fuels. Using the same pre-burn data, we applied a space-for-time substitution at the plot level to assess the correlation (Pearson's *r*) between several biomass components and time since fire. One-way ANOVA was also used to determine differences among burned plots in surface fuel consumption. Relationships of surface fuel consumption with pre-burn surface fuel and time since last fire were examined by fitting a linear regression equation to the plot-level data using standard least-squares techniques. Only two blocks, 1998-O and 1998-S, were burned in two different seasons during the same year. Two-way analysis of variance (two-way ANOVA) was used to examine the effects of block and season on surface fuel consumption calculated for each of the 20 shrub subplots per plot.

We used path analysis to model direct and indirect effects of fuel types and char height on fuel consumption. Path analysis involves integration of multiple linear models linked in a path diagram that relates independent, intermediary, and dependent variables in a network of causal relationships (Sokal and Rohlf 1981). Because the correlations among predictor variables may affect the regression models by inflating the standard errors of estimate and destabilizing the regression coefficients, the independent variables were tested for colinearity. We modeled the causal effects across the network and used path coefficients (standardized partial regression coefficients) to assess the relative strength of direct and indirect causal paths on the dependent variable. We calculated indirect effects of an independent variable as a sum of products of path coefficients along all paths leading to a target dependent variable (Sokal and Rohlf 1981; see also Wootton 1994; Smith *et al.* 1997). Both direct and indirect effects were summed to calculate the total effects of each variable in the model on the surface fuel consumption.

In south-eastern pine forest, fuel loading increases rapidly following fire, followed by a slowing rate of increase until equilibrium is achieved (McNab *et al.* 1978). In the present study, to determine the trend of fuel accumulation and to estimate the approximate time after fire when fuel loads reach equilibrium, the following non-linear regression model was applied:

$$X_{\mathrm{t}} = X_{\mathrm{ss}}(1 - e^{-kt}),$$

where X_{t} is fuel load at stand age t, X_{ss} is the weight of fuel under steady-state conditions, and k is the decomposition constant (McCaw *et al.* 2002). Statistical analyses were carried out using STATISTICA version 6.0 (Statsoft 2001).

Results

Pre-burn total biomass and fuel loads

Mean total aboveground biomass in Big Pine Key pine forests averaged 60.6 Mg ha^{-1} (Fig. 4). Among-block variation was significant ($F_{5,12} = 14.9$, $P < 0.001$), with pine forests in the 1998-S block exceeding other local forests in biomass (84.1 Mg ha^{-1}). Pine trees constituted two thirds (66.0%) of

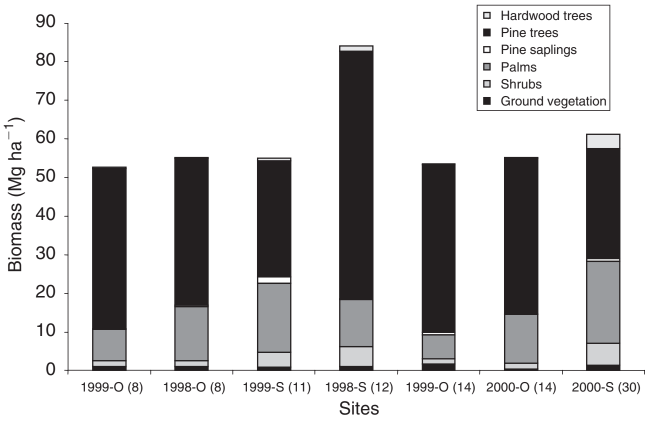

Fig. 4. Total aboveground biomass in six blocks of Big Pine Key pine forests sampled before experimental fire. The numbers in the parentheses represent time (years) since last fire. Pine forests in the 1999-O block consist of two zones: one was burned 8 years and the other 14 years before recent sampling.

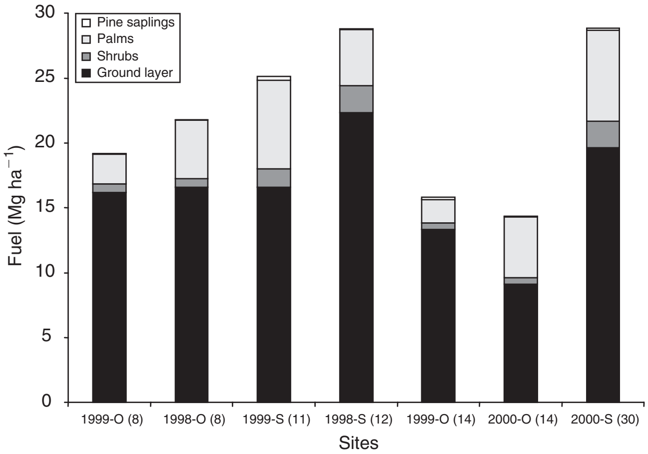

Fig. 5. Potential fuels in six blocks of Big Pine Key pine forests sampled before experimental fire. The numbers in the parentheses represent time (years) since last fire. Pine forests in the 1999-O block consist of two zones: one was burned 8 years and the other 14 years before recent sampling.

the biomass, and palms, the dominant understory contributor, accounted for 23.5%. Broadleaved shrubs and ground layer vegetation constituted 5.2 and 1.7% of total biomass. Hardwood trees, though well distributed throughout the forests, comprised a relatively small percentage (1.7%) of stand biomass. When the Pearson correlation coefficient (r) was calculated using data from all 18 plots, total biomass was found to be uncorrelated with time since fire ($r = +0.08$, $P > 0.05$), but the biomass of palms, broadleaved shrubs, and hardwood trees increased with fire-free period ($r = +0.62$, $+0.59$, and $+0.75$, respectively; $P < 0.05$ for all three).

Potential fuels in lower Florida Keys pine forests averaged 22.8 Mg ha^{-1} (SD = 5.9) (Fig. 5). On Big Pine Key, approximately three-fourths of fine fuels were surface fuels.

Table 4. Pearson's correlation coefficients (*r*) and *P*-values for the relationships between total surface fuel and other biomass components, such as hardwood shrubs and palms in the understory, and pine and hardwood trees in the overstory

Biomass component	*r*	*P*-value
Hardwood shrubs	0.78	<0.001
Palms	0.26	0.319
Pine trees	0.42	0.094
Hardwood trees	0.58	0.015

Table 5. Fire temperature and indirect measures of fire intensity (char height) and burn severity (crown scorch percentage) for the 11 experimental burns

Plot	Years since last burn	Fire temperature (°C)	Scorch (%)	Char height (m)
1998-O-S	8	–	62	2.5
1998-O-W	8	–	46	1.7
1998-S-S	12	–	66	3.0
1998-S-W	12	–	22	1.3
1999-O-S	8	229	55	2.1
1999-O-W	14	188	39	1.3
1999-S-S	11	254	84	2.8
2000-O-S	14	266	58	2.0
2000-O-W[A]	14	281	84	3.4
2000-S-S	>30	251	86	2.6
2000-S-W[A]	>30	273	74	2.7

[A]Plots were burned in summer 2001.

Palm leaves were 21.5% of potential fuels, and broadleaved shrubs comprised another 5.3%. Pine saplings contributed very little to the total fuel loads (<1%). One fine fuel category not included in Fig. 5 is attached pine needles in the forest canopy, because little is directly consumed in most prescribed fires in South Florida pine forests (Snyder 1986). Pine crown fuels comprise a relatively minor component in comparison with potential fuels as defined here (among-stand range: 1.4–2.5 Mg ha^{-1}).

Among-block differences in fuel loads were significant ($F_{5,12} = 18.0$, $P < 0.001$), with 2000-O (14.3 Mg ha^{-1}) containing only approximately half the fuel loads present in the 1998-S and 2000-S blocks (28.8 Mg ha^{-1} each) (Fig. 5). Whereas fuel loads generally increased from the most recently burned plot (1999-O) to the block unburned for the longest time (2000-S), the correlation of potential fuel loading with time since fire was non-significant ($r = 0.20$). Surface fuel, the major constituent of total fuel loads, was positively correlated with the total biomass of broadleaved shrubs and trees, but uncorrelated with total palm, and pine tree biomass (Table 4).

Fire intensity and burn severity

Values of both fire intensity and burn severity indicators are shown in Table 5. For the three blocks in which both summer and winter burns were accomplished (1998-O, 1998-S, and 1999-O), char height and crown scorch

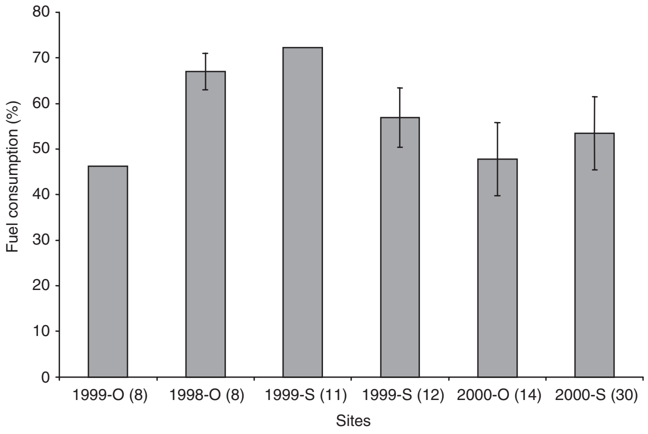

Fig. 6. Mean percentage of surface fuel consumption during experimental burnings in six blocks of Big Pine Key pine forests. The numbers in parentheses are time (years) since last fire.

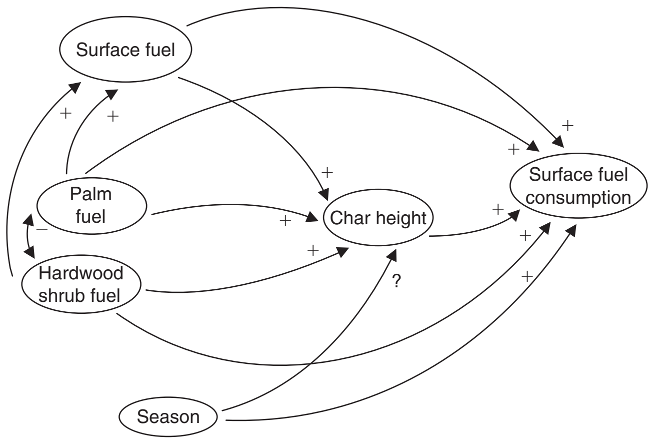

Fig. 7. Variables and arrows showing conceptual causal relationships in the path analysis.

percentage were greater for the summer burns. In fact, the three burns carried out in winter were the least intense of the 11 fires by all three indicators, including fire temperature. Another notable feature of Table 5 is the high degree of variability in fire temperature, char height, and crown scorch percentage among burns in the 2000-O and 2000-S, all carried out in the same week of July 2001.

Surface fuel consumption and recovery

Based on post-fire and pre-fire sample weights available for 10 burned plots, prescribed fire consumed an average of 56.8% of the surface fuel across all plots (Fig. 6). Among-plot differences in the surface fuel consumption were significant, but were not related to time since last fire ($n = 10$, $R^2 = 0.066$, $P = 0.475$). Percentage surface fuel consumption tended to be higher in plots where pre-burn surface fuels were most abundant, but the relationship was not significant at this scale of resolution ($n = 10$, $R^2 = 0.175$, $P = 0.228$). Likewise, percentage consumption of surface fuels was unrelated to crown scorch percentage or char height at the plot level.

In the plot level analysis, patterns evident at a smaller scale may be averaged out, potentially obscuring important relationships. To examine surface fuel consumption at a finer scale, we used path analysis to assess how surface fuel consumption calculated individually for each of the 20 subplots per plot was affected by: (1) the initial, pre-burn quantities of surface fuel present in each subplot; (2) subplot estimates of various components of understory fuels; (3) subplot estimates for char height; and (4) burn season. As complete subplot level data were available only for both summer and winter burn plots in the 1998-O and 1998-S blocks, the combined data from these four burned plots were used in the path analysis. Figure 7 illustrates the possible hypothetical causal relationships among variables measured in this study. Because pine saplings constituted <1% of total biomass, only two shrub fuel types were assumed to be

Table 6. Effect coefficients for variables affecting surface fuel consumption in path analysis for summer and winter burn plots in 1998-O and 1998-S blocks

Variable	Direct effects	Indirect effects	Total effects
Pre-burn surface fuel	0.32	0.05	0.38
Palm fuel	0.11	0.15	0.26
Hardwood shrub fuel	−0.29	0.02	−0.27
Char height	0.27	Not modeled	0.27
Season	0.05	0.14	0.19

the primary contributors to surface fuels. Though both fuel types in the shrub layer were negatively correlated with each other, Pearson correlation coefficients between them were not significant ($P = 0.1$), suggesting that the stability of partial regression coefficients in the path model did not suffer from the colinearity among independent variables. In the path analysis, palm and hardwood shrub fuels, which are exogenous variables in the path analysis, were both positively related to pre-burn surface fuel and char height, whereas only hardwood shrub biomass was a significant predictor of surface fuel consumption. Char height was also found to be a significant predictor of surface fuel consumption. Season was entered as a categorical variable with two levels in the model, and as such was significantly related to char height. Summer burns produced greater char height than winter burns.

The results of the path analysis revealed that surface fuel consumption was strongly influenced by pre-burn surface fuels and fire intensity, as indicated by char height (Table 6). Their positive path coefficients show that percentage consumption increased with both surface fuel mass and char height. Among the understory components, palm fuel had a positive effect on fuel consumption, though most of the effects were indirect, through char height. The significant positive effect (path coefficient $= 0.18$) of palm fuel on char height was probably due to its role as a vertical fuel. However, the same was not true for hardwood shrub fuel, which had a negative effect on surface fuel consumption in our experimental burns (Table 6). Both char height and surface fuel consumption decreased with an increase in hardwood shrub biomass in the subplots (Fig. 8).

The direct effect of season on fuel consumption was low in comparison with its indirect effect (Table 6), as most of its effect was through char height, an indicator of fire intensity (Fig. 8). In the model, the path coefficient for the effect of season on char height was the highest (+0.49) among all paths. Like char height, surface fuel consumption percentage was higher in summer than winter fires (Fig. 9).

Post-fire recovery of fuels

Final harvests in 2001 allowed us to estimate the build-up of surface fuels in seven plots that ranged in time of accumulation from 1 to 3 years (Fig. 10). On average, estimated accumulation rate for surface fuels at these sites was 0.53 Mg ha^{-1} year^{-1} (SD = 0.54). These estimates, which range from 1.20 Mg ha^{-1} year^{-1} in the 3-year-old 1998-S-S plot to −0.26 Mg ha^{-1} year^{-1} in 2-year-old 1999-O-S, indicate very high levels of site variation. Though the live component was only a small fraction of surface fuel, its rate of recovery was much faster than that of the dead fuel mass, owing to the vigorous growth of ground vegetation after fire. In two winter burn plots, the amount of live fuel 3 years after burning was 2-fold higher than before the fire. The recovery rate of live vegetation also differed among growth forms. Forbs, graminoids, and ferns recovered faster than palms and woody plants, though palms also returned to their pre-burn level within 2 years.

Our sampling protocols did not allow us to estimate the consumption of shrub fuels directly, because shrub sampling was not re-initiated until 1 year had passed following fire. However, for the seven plots burned early in the project, it was possible to estimate shrub fuel accumulation during year 2 and in some cases year 3 after fire. The fine fuels associated with palms and broadleaved shrubs declined from the pre-fire condition to year 1 post fire, and then recovered through year 3 across all available plots (Fig. 11). The initial decline in palm fuels was less steep than in broadleaved shrubs (70 and 88%, respectively). After year 1, both groups recovered rapidly. In two blocks, 1998-O and 1998-S, palms and hardwood shrubs reached 64 and 34%, respectively, of their pre-fire fine fuel biomass by year 3. In these two blocks, two-way analysis of variance indicated that hardwood shrub fine fuel recovery through year 1 post fire was significantly affected by both block ($F_{1,75} = 4.4$, $P = 0.04$) and season ($F_{1,75} = 5.6$, $P = 0.02$), but the interaction between block and season was not significant. The initial recovery of hardwood shrub fine fuel was faster in 1998-S-W than in 1998-S-S, 1998-O-S, or

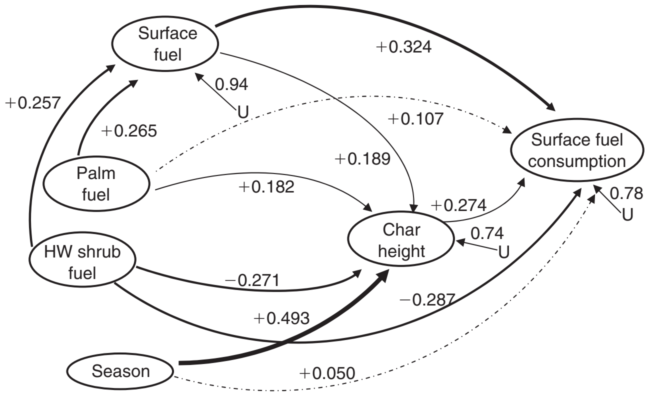

Fig. 8. Path diagram showing the relationships among fuel types, fire intensity, and fuel consumption. Solid and dash paths represent significant and insignificant path coefficients (standardised partial regression coefficients), respectively. The thickness of lines indicates relative strength of significant correlations. U ($\sqrt{1 - R^2}$) is unexplained variation of the regression model. HW, hardwood.

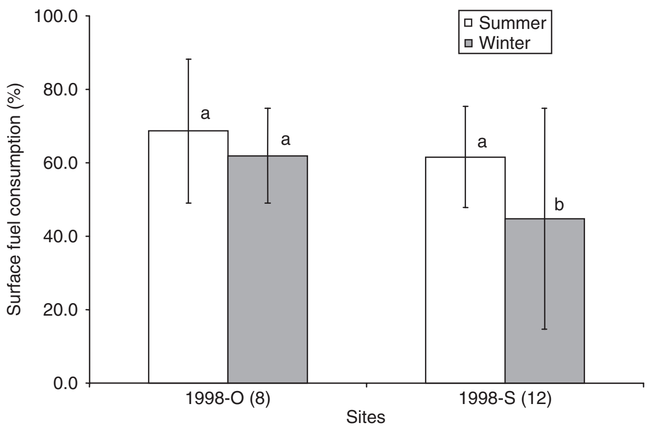

Fig. 9. Mean percentage of surface fuel consumption in the pine forests of 1998-O and 1998-S blocks, burned in two different seasons, summer and winter. The numbers in parentheses are time (years) since last fire. Different letters above the bar indicate a significant seasonal difference within the block (Bonferroni test).

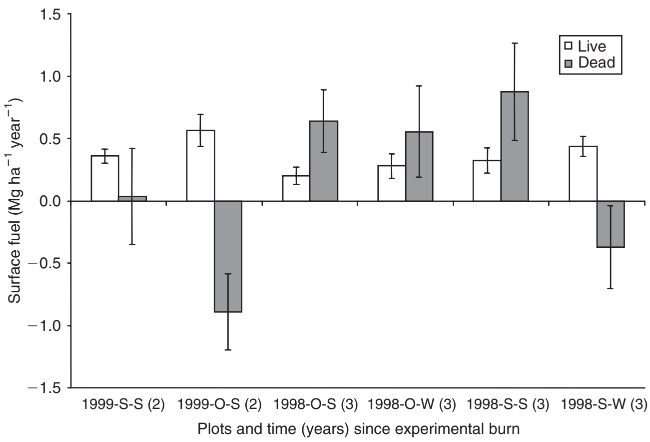

Fig. 10. Mean (±s.e.) surface fuel change after experimental burn in the pine forests of Big Pine Key. Numbers in parentheses are the time since experimental burn.

1998-O-W (Bonferroni test; Table 7); furthermore, hardwood shrub recovery through year 2 was negatively correlated with surface fuel consumption, an indicator of fire severity. In contrast, palm fuel recovery was unaffected by burn season, but was affected by block in both year 1 and year 2 ($F_{1,76} = 21.2$, $P < 0.001$, and $F_{1,76} = 16.2$, $P < 0.001$, respectively); palms recovered more slowly in the 1998-S than the 1998-O block (Bonferroni test; Table 7). In contrast to hardwood shrub fuels, there was no relationship between palm recovery and fire severity, as indicated by percentage fuel consumption.

Long-term fuel accumulation following fire

By combining fuel loads from 18 stands of known fire history with data from a subset of the same stands 1–3 years after fire, Fig. 12 provides a picture of the long-term pattern of fuel accumulation in Florida Keys pine forests. Total fuel loads accumulate rapidly during the early post-fire period, but approach an asymptote at 20–30 Mg ha^{-1} within a decade or so. Although the saturation model provides a reasonable fit to the data ($R^2 = 0.46$), considerable local variation in the shape of the function may be expected, owing to site characteristics or past disturbance history.

Discussion

Biomass estimates

In a fire-adapted pine forest, fire behavior and post-fire fuel build-up are affected by fuel loads that vary with time since last fire and its major co-variants, including a dynamic forest understory of woody plants and/or herbs. Models predicting fire behavior based on fuel loads normally assume that increased fuel loads lead to higher fire intensity (Rothermel 1972). In Florida Key pine forests, however, surface fuels and various components of understory fuels differed in their effects on fire intensity, and spatial variation in their effects were scale dependent. Within-stand variation in both surface and understory fuel distribution, together with season of experimental burns, influenced fine scale fire behavior, which in turn affected fuel consumption and post-fire fuel dynamics.

In Florida Keys pine forests, aboveground biomass (mean = 61 Mg ha^{-1}) is very low in comparison with pine forests elsewhere in the south-eastern USA. Within our study area, only one block (1998-S, 84 Mg ha^{-1}) fell within the range reported by Snyder (1986) for pine forests

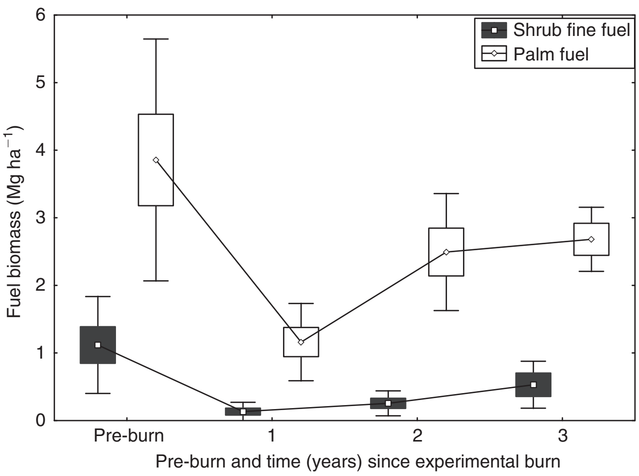

Fig. 11. Shrub fine fuel and palm fuel before and 1–3 years after experimental burns in the pine forests of Big Pine Key.

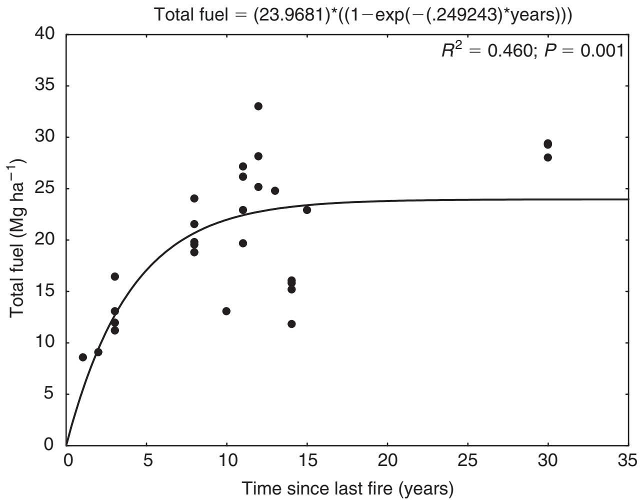

Fig. 12. Total fuel accumulation curve in the Florida Keys Pine forests. Plots ranged from less than 1 year of age to over 30 years since time of last fire.

Table 7. Surface fuel consumption, and palm and shrub fuel recovery in plots burned in 1998
Values within a column followed by different superscripts differed at $P < 0.05$

Plots	Surface fuel consumption (%)	Post-burn understory fuels (% of pre-burn)					
		Shrub fine fuels			Palm fuels		
		Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
1998-O-S	68.7^{a}	3.8^{a}	20.1	31.3	39.7^{a}	72.8^{a}	67.8
1998-O-W	61.9^{a}	5.4^{a}	17.0	26.5	37.2^{a}	72.6^{a}	67.2
1998-S-S	61.6^{a}	4.6^{a}	18.0	39.0	22.7^{b}	51.2^{b}	56.3
1998-S-W	44.8^{b}	16.4^{b}	23.4	37.4	24.5^{b}	50.1^{b}	66.4

on the Florida mainland in Everglades National Park (75–90 Mg ha^{-1}), and all Keys stands were well below values of ~150 Mg ha^{-1} in 25-year-old slash pine plantations in north Florida (Gholz and Fisher 1982). The low stature of Florida Keys forests is attributable to both edaphic and climatic factors. The skeletal organic soils rarely exceed 10 cm in depth over limestone bedrock, providing little capacity to store water or nutrients (Ross *et al*. 2003). Moreover, the highly seasonal climate includes periods of several months' duration in which potential evapotranspiration exceeds precipitation (Ross *et al*. 1992). Applying a function based on climatic factors (mean annual temperature and precipitation) introduced by Brown and Lugo (1982), the total biomass of Florida Keys forests are predicted to be 84% that of forests in Everglades National Park (280 and 334 Mg ha^{-1}, respectively). Estimates based on Brown and Lugo's (1982) function include both aboveground and belowground components, and do not account for seasonality or soil limitation of growth.

Whereas total biomass in Florida Keys pine forests is low, litter mass (9–21 Mg ha^{-1}) is similar to that found in Everglades forests (10–17 Mg ha^{-1}; Snyder 1986). Prior to our study, prescribed burning in NKDR had been sporadic (Table 1), allowing litter to build up to significant depths despite the inherently low site productivity. With approximately three-fourths of pre-fire fine fuels concentrated in the ground layer, and more than 90% of surface fuels composed of litter and standing dead material, litter development is an important component of fuel build-up. Fire history is a strong determinant of fuel loading, but structural variables such as stand density and species composition are also influential (McNab *et al*. 1978). Among-site patterns within our study area indicated no clear relationship between total fuel load and time since fire, but did identify a strong positive association between surface fuel mass and the biomass of broadleaved shrubs and trees. Snyder (1986) also found that in Everglades National Park pine forests unburned for the longest time, hardwood shrubs contributed more to the pool of surface fuels than did the overstory pines. These patterns do suggest an integrated recovery process, but one that is not completely represented by the variable 'time since fire'. Most significantly, this coarse metric fails to account for fire intensity, which Table 5 indicates can vary widely within a relatively homogeneous forest. Hot fires may result in high mortality of broadleaved shrubs, and a slow and patchy accumulation of shrub biomass in the post-burn period, whereas cooler fires leave the shrub layer unchanged. Ultimately, the speed of shrub recovery may drive recovery in surface fuels.

A fundamental tenet of fire management, and a pathway in our initial model (Fig. 1), avers that fire intensity will increase with the quantity of fuel available to be consumed. In Florida Keys pine forests, however, effects of fuel loads on fire intensity were scale-dependent and varied among various components of fine fuels. At the coarser scale, amounts of fuels in various fine fuel categories were unrelated to char height and canopy scorch, whereas the mass of pre-fire surface fuels was positively correlated with surface fuel consumption. We assert that the explanation for these apparent contradictions lies in fine scale variation in the nature of understory and surface fuel components and the environment near ground level in shrubby and open microsites in pine rocklands. Although our experimental design distinguished blocking units characterized by shrubby or open understory structure, a finer-textured path analysis at the subplot level allowed us to recognize the distribution patterns of various fuel components and their direct and indirect effects on fire intensity and fuel consumption. A close association between surface fuel and shrub biomass distributions indicates that Florida Keys pine forests are composed of differently proportioned mosaics of shrub- and herb-dominated patches, and this fine scaled vegetation mosaic is correlated with the patch structure of fuels. Given the linkage between vegetation structure and the character of the ground layer, it seems likely that the composition of litter in shrub- and herb-dominated patches would differ as well, with the broadleaved component more important in the former and pine needles the predominant fuels in the latter. Within a short time, hardwood litter weathers to form a compact, layered structure that retains moisture well (Myers 2000), whereas pine litter remains a loose mixture with little capacity to hold water (Agee 1977). With the shrub canopy above providing shade and thereby reducing evaporative stress, the ground layer beneath shrub patches should be relatively moist and resistant to fire, despite a substantial accumulation of fuels. In fact, the negative coefficient ($\beta = -0.271$) for the direct effects of pre-burn hardwood shrub fuel on the fire intensity in the path analysis suggests that shrubby patches were also resistant to fire (Fig. 8). Other researchers also have reported that shrub patches in south Florida pine rocklands burn less intensively in comparison with surrounding herbaceous vegetation (Wade *et al*. 1980; Slocum *et al*. 2003). Lower flammability of shrubby patches in comparison with graminoid herbaceous vegetation is probably due to higher moisture content in the former (De Castro and Kauffman 1998; see also Bond and van Wilgen 1996; Pyne *et al*. 1996). Indeed, it is this resistance to fire that allows shrub patches to develop, and within a longer time frame has been responsible for the formation and maintenance of hardwood hammocks within the south Florida pine forest matrix. However, when fire does penetrate into the hammocks, especially during periodic droughts, it moves slowly through, sometimes smoldering in the surface litter and interstices of the limestone for weeks or more. Such behavior could explain the positive association we found between pre-burn fuel quantity and the consumption of material at ground level, whereas indicators of broader scale fire intensity associated with the forest canopy, e.g. crown scorch and char height, were uncorrelated with potential surface fuels.

Biomass and seasonal burning effects on fuel consumption and fire intensity

Fuel reduction is one of the major objectives of prescribed fire (Rothermel 1972; Koehler 1993; Outcalt and Wade 2000). During our experimental fires, surface fuel consumption ranged from 40 to 72%. Consumption was thus slightly lower than that observed by Snyder (1986) on Long Pine Key in Everglades National Park, but was within the range observed in other pineland burns (Hough 1978; Sparks *et al.* 2002). In accordance with our initial hypothetical model, season of burn, along with fuel load and fire intensity, was an important determinant of fuel consumption (Table 6). However, the effect of season in the path model was exclusively indirect, through its influence on fire intensity, which was signified by char height in the path model (Fig. 8). In both blocks burned in 1998, surface fuel consumption was higher in summer than in winter, and in all three blocks that experienced both summer and winter fires, scorch percentage and char height were higher in the summer as well (Table 5). Similar results have been reported from other pine forests in the south-eastern USA (Robbins and Myers 1992; Waldrop *et al.* 1992). Such seasonal differences may be attributable to differences in ambient temperature; when temperatures are high, as they were in our summer fires (30–36°C cf. 20–21°C in winter fires), less heat is required to initiate combustion (Van Wagner 1973; Albini 1976; Outcalt and Foltz 2004).

Although surface and understory fuels, char height, and season were good predictors of fuel consumption, causal relationships in the path model did not fully account for all the variation in fuel consumption; the value of error variance (*U*) in Fig. 8 (0.78) indicates that 60% of the variation was unexplained. Like any regression model, path analysis falls short when important predictors are lacking or inadequately represented, or when the causal relationships are imperfectly constructed in the model. For instance, surface fuels in South Florida pine forests include the herbaceous layer and the products of both understory and overstory vegetation. In our study, the input of overstory pine and hardwood trees to surface fuel was not estimated and therefore could not be included among the predictors in the path analysis, certainly resulting in some unexplained variation in fuel consumption in the final model. Moreover, our use of an indicator of fire intensity, i.e. char height, instead of a direct measure of intensity introduced further uncertainty in the set of predictors, and may have limited the performance of the model. Despite its limitations, however, our model did yield significant insights into the fuel consumption process in the Florida Keys, as described above.

Post-fire fuel dynamics

The assessment of post-fire surface fuel dynamics requires a space-for-time substitution, in that a temporal sequence is inferred from surface fuel biomass estimates during a common period, i.e. at the conclusion of the project, among plots burned in different years. Surface fuel loads in seven plots 1–3 years post fire indicate significant fuel build-up during this early stage in recovery (Fig. 10), but also considerable variation (-0.26 to 1.2 Mg ha^{-1} year^{-1}) in surface fuel accumulation among stands. Negative values may result from high decomposition rates (Snyder 1986), or they may simply reflect random microsite variation among adjacent quadrats, a vagary to which the sequential harvest method we used is especially sensitive. In the slash pine plantations studied by Gholz and Fisher (1982), surface fuels accumulated at a constant rate slightly exceeding 1 Mg ha^{-1} year^{-1} through to age 35. The slow rate of surface fuel accumulation in the NKDR pine forests in the immediate post-fire period was probably a result of impacts on understory hardwood shrubs, which were major contributors to the pre-burn surface fuels. Post-fire recovery of ground vegetation and fuels may vary substantially depending on site conditions, fire characteristics, post-fire weather, and most importantly, the nature of the existing vegetation, its susceptibility to fire, and means of subsequent recovery (Miller 2000; Wade *et al.* 2000). One relevant element of vegetation response is the pine canopy itself. Dead fuel accumulation in blocks 1998-O and 1998-S 3 years post fire was higher in summer-burned than winter-burned plots, probably as a result of elevated pine needle input associated with high crown scorch percentages in the former. In loblolly pine (*Pinus taeda*) forests, Waldrop and Van Lear (1984) also found a strong relation between post-burn needle drop and the degree of crown scorch.

Susceptibility of vegetation to fire and the means by which it recovers after fire were important in the recovery of palms and shrubs, which differed greatly in our study. The initial decline in palm fuels was less steep than in broadleaved shrubs (Fig. 11), probably because surviving palms leafed out rapidly from protected apical meristems, which are seldom damaged by fires (Snyder 1986). In contrast, broadleaved shrubs were usually top-killed; when they survived, they generally resprouted from the base of the original shoots, and required more than 1 year to reach 1 m height. Even after year 1, the recovery of palm fuels was faster than that of shrubs. Cooley (2004) demonstrated that attached palm fine fuels tended to reach an asymptote well within a decade after fire in the Keys, whereas fine fuels associated with broadleaved shrubs may take slightly longer to reach a maximum (Sah *et al.* 2004). Snyder (1986) also reported delayed recovery of hardwoods in comparison with herbs and palms on Long Pine Key. In general, recovery of the forest understory after fire is reported to be slow in the Florida Keys compared with mainland pine forests (Alexander and Dickson 1972; Taylor and Herndon 1981; Snyder *et al.* 1990), owing to climate and soil-induced differences in inherent site productivity (Ross *et al.* 1992, 2003).

Shrub biomass recovery by resprouting in the post-fire period also mirrors fire intensity. Burns in summer, when fire intensity is relatively high, usually result in higher mortality and less vigorous resprouting and growth than winter burns (Lotti *et al*. 1960; Lewis and Harshbarger 1976; Langdon 1981). In our study, season of burn also had a significant effect on the recovery of shrub fine fuel in the post-fire period, at least in year 1. In severely burned microsites, sprouting may be delayed or eliminated owing to consumption of the duff layer, which shelters the regenerating parts of perennial shrubs and herbs (Miller 1977). In our study, we did not measure the dynamics of the duff layer, as it was absent in most areas. Nevertheless, we found that shrub recovery through year 2 was negatively correlated with surface fuel consumption. The diminishing effect of fire intensity on shrub biomass recovery by year 3 suggested that, at least at the levels of intensity observed in our study, the effects of individual fires on community function may be relatively short-lived.

Conclusions

Fuel reduction is a major goal of prescribed fire, based on a presumption that total fuel loads and fire intensity are positively related. In Florida Keys pine forests, however, fuel loads and their effects on fire behavior varied depending on site characteristics, time since last fire, fuel types, cover of understory hardwood species, and burn season. The absence of a strong relationship between total fuel loads and time since last fire at the broader scale implies that microscale variation in the distribution of various fuel components causes fires to be heterogeneous in their intensity and effect on post-fire recovery. In our experimental burns, fire intensity increased with surface fuel loads, but tended to be less severe and patchy in forests in which shrubs were an important understory component. It is likely that the surface fuels derived from hardwood shrubs remain associated with moist microenvironments close to the shrub patches and tend to resist fire in comparison with herbaceous fuels and pine needles present in more open surrounding areas, resulting in less intense fire. These observations support the maxim that it is easier to maintain an open pine forest understory than to restore it once shrub encroachment has taken place during a long period without fire.

The use of fire to maintain a relatively open understory in pine rocklands in the Florida Keys serves dual objectives of fire hazard reduction and maintenance of characteristic plant diversity, especially a rich suite of calcicolous herbs. Florida Keys forests differ from most mainland pine forests in the nature of their wildland–urban interface, in which residential development is much more intimately mixed into the remaining natural areas. The structure of the forests differ as well, with woody plants appearing to naturally occupy a more prominent place in the Keys, with its skeletal limestone substrate and seasonal extremes of moisture stress (Ish-Shalom *et al*. 1992). Our data show that winter prescription fires are milder and less risky, but are less effective at inhibiting shrub encroachment. Thus, for the purpose of fire management, a mixed seasonal approach is suggested, with burns applied opportunistically under a range of winter and summer conditions, but with an emphasis on increasing the periodicity of burning above the frequency that prevailed on NKDR before 1998.

Acknowledgements

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