Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species

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Abstract. Long-term fire exclusion has altered ecological function in many forested ecosystems in North America. The invasion of fire-sensitive tree species into formerly pyrogenic upland forests in the southeastern United States has resulted in dramatic shifts in surface fuels that have been hypothesized to cause reductions in plant community flammability. The mechanism for the reduced flammability or "mesophication" has lacked empirical study. Here we evaluate a potential mechanism of reduced flammability by quantifying moisture retention (response time and initial moisture capacity) of foliar litter beds from 17 southeastern tree species spanning a wide range of fire tolerance. A *k*-means cluster analysis resulted in four species groups: a rapidly drying cluster of eight species; a five-species group that absorbed little water but desorbed slowly; a two-species group that absorbed substantial moisture but desorbed rapidly; and a two-species cluster that absorbed substantial moisture and dried slowly. Fire-sensitive species were segregated into the slow moisture loss clusters while fire-tolerant species tended to cluster in the rapid drying groups. Principal-components analysis indicated that several leaf characteristics correlated with absorption capacity and drying rates. Thin-leaved species with high surface area : volume absorbed the greatest moisture content, while those with large, curling leaves had the fastest drying rates. The dramatic shifts in litter fuels as a result of invasion by fire-sensitive species generate a positive feedback that reduce the windows of ignition, thereby facilitating the survival, persistence, and continued invasion of fire-sensitive species in the uplands of the southeastern United States.

Key words: Acer rubrum; *ecological restoration; fire exclusion; fuel moisture; leaf traits; positive feedbacks.*

INTRODUCTION

In fire-prone ecosystems, feedbacks between vegetation (composition and structure) and fire (frequency, intensity, and seasonality) shape and regulate ecosystem processes (Bond and van Wilgen 1996, Platt 1999, Beckage et al. 2009). Fire regimes (frequency, seasonality, and intensity) determine vegetation composition and structure via differential survival across life history stages and regulation of successional pathways (Engber et al. 2011, Trauernicht et al. 2012). Species composition and vegetation structure affect fire regimes through their influence on ignition, spread, and intensity of fire (Kane et al. 2008, Gagnon et al. 2010). A feedback cycle ensues that reinforces both the fire regime and the vegetation that depend on it (Cochrane 1999). When fire regimes are modified via fire exclusion, invasion by fire-sensitive species may lead to fuel dynamics that, in turn, reinforce an alternative fire regime perpetuating an alternative stable ecological state where future fires are less likely to

ignite and spread. This "mesophication" of eastern North American forests is a positive feedback cycle where flammable pyrophytic species (hereafter pyrophytes) are replaced by fire-sensitive mesophytic species (hereafter mesophytes) that presumably reduce community flammability (Abrams 2005, Nowacki and Abrams 2008). In spite of the substantial attention on mesophication across a diversity of fire-prone ecosystems (e.g., Abrams 1992, Kane et al. 2008, Engber et al. 2011, Arthur et al. 2012, Trauernicht et al. 2012), the proximate mechanisms of these fire–vegetation positive feedbacks have yet to be isolated.

Examples of invasion by or increases in fire-sensitive species within historically fire-prone ecosystems are common in eastern North America. Many fire-prone deciduous oak–hickory (*Quercus–Carya*) woodlands and forests have been invaded by the mesophytic red maple (*Acer rubrum*; Abrams 1998, 2005, Nowacki and Abrams 2008). In the southeastern coastal plain, pyrophytic longleaf pine (*Pinus palustris*)–turkey oak (*Quercus laevis*) woodlands (Platt 1999) with interspersed patches of pyrophytic oaks (*Q. falcata, Q. margaretta,* and *Q. incana*) have been invaded by several

TABLE 1. Drying response times and initial moisture content (MC) from moisture desorption experiments of litter beds across tree species of the southeastern United States.

Cluster	Species	Response time, τ (h)	Initial MC (%)	Fire/moisture affinity	Leaf type
1	*Liquidambar styraciflua*	2.7 (1.2)	217 (10)	mesophyte	deciduous
1	*Quercus laevis*	2.7 (0.6)	172 (4)	pyrophyte	deciduous
1	*Quercus stellata*	3.3 (0.5)	281 (28)	pyrophyte	deciduous
1	*Pinus taeda*	3.4 (0.8)	143 (16)	pyrophyte	evergreen
1	*Quercus falcata*	4.1 (1.2)	252 (15)	pyrophyte	deciduous
1	*Quercus alba*	4.3 (1.5)	189 (9)	pyrophyte	deciduous
1	*Pinus palustris*	4.7 (1.4)	105 (9)	pyrophyte	evergreen
1	*Quercus margaretta*	4.8 (1.3)	270 (5)	pyrophyte	deciduous
2	*Magnolia grandiflora*	6.4 (0.3)	227 (19)	mesophyte	evergreen
2	*Quercus hemisphaerica*	6.8 (0.5)	236 (12)	mesophyte	evergreen
2	*Quercus virginiana*	7.2 (1.7)	213 (13)	mesophyte	evergreen
2	*Quercus nigra*	7.3 (0.8)	205 (6)	mesophyte	deciduous
2	*Ilex opaca*	7.3 (0.9)	189 (9)	mesophyte	evergreen
3	*Liriodendron tulipifera*	4.8 (0.9)	387 (12)	mesophyte	deciduous
3	*Fagus grandifolia*	6.9 (0.8)	415 (8)	mesophyte	deciduous
4	*Quercus incana*	11.3 (1.1)	286 (6)	pyrophyte	deciduous
5	*Acer rubrum*	10.4 (2.0)	513 (26)	mesophyte	deciduous

Notes: Values in parentheses are standard deviation. Mean response time and initial MC values for each cluster are given in Fig. 1.

fire-sensitive mesophytic trees including laurel oak (*Q. hemisphaerica*), water oak (*Q. nigra*), sweet gum (*Liquidambar styraciflua*), live oak (*Q. virginiana*), and red maple (Gilliam and Platt 1999, Kush and Meldahl 2000). On xeric sites across much of the region, pyrophytic post oak (*Q. stellata*) savannas and woodlands suffer a similar fate (Frost 2006). These ecosystems were heavily reliant on frequent, low-intensity fires to maintain both structure and composition (Platt 1999). As in many areas, fire exclusion has resulted in invasion and subsequent expansion by this suite of mesophytic species (Table 1) that are replacing fire-tolerant species in woodlands and savannas throughout the eastern United States (Christensen 1977, Abrams and Downs 1990, Abrams 2005, Varner et al. 2005, Nowacki and Abrams 2008). Restoration efforts aimed at reinstating dominance of pyrophytic species through prescribed burning are plagued by the persistence of mesophytes (Green et al. 2010, Arthur et al. 2012) that are capable of resprouting and casting low flammability litter (Provencher et al. 2001, Kane et al. 2008).

Interspecific differences in the flammability of litter are widely acknowledged (Fonda 1998, 2001, Kane et al. 2008, Schwilk and Caprio 2011, Engber and Varner 2012). These differences may be most important in seasonally dry climates (e.g., western North American and Mediterranean landscapes) where fuel moisture tends to remain low during the fire season. In environments with punctuated and somewhat consistent seasonal precipitation, however, as in the eastern United States (Schroeder and Buck 1970), the ability to retain or shed moisture may be a more critical determinant of how and when fires burn. As a result of water's high specific heat, moisture content is the dominant fuel characteristic influencing ignition, heat release, and spread (Rothermel 1972). Above critical fuel moisture thresholds (often referred to as "moisture of extinction") fuels resist ignition and spread; below this threshold, fire behavior increases non-linearly as fuel moisture decreases. As a result, retention of moisture in litter fuels decreases the probability of ignition and retards the rate of fire spread and fuel consumption when ignition does occur.

Both forest structure and fuel bed characteristics may influence moisture regimes of surface fuels (Anderson 1990, Hille and Stephens 2005, Tanskanen et al. 2006, Nelson and Hiers 2008). One hypothesized mechanism for mesophication suggests that alterations to forest structure (i.e., as increased canopy cover) associated with mesophytic invasion cools and dampens surface litter due to both reduced incident solar radiation and restricted airflow (Nowacki and Abrams 2008). If litter input from mesophytic tree species increases the moisture holding capacity of surface litter, this could alter moisture regimes, enhance seedling establishment, reduce flammability, and likely be an important mechanism initiating mesophication in eastern forests.

Fuel moisture dynamics can be evaluated in several ecologically meaningful ways. Two primary considerations are the absorptive capacity of fuels and the subsequent rate of moisture loss during drying. The former indicates potential fuel moisture, while the latter indicates the duration for which fuels retain that moisture. Absorptive capacity may be evaluated simply by quantifying total moisture content following absorption, while drying rates are commonly evaluated using the time lag concept (Byram 1963), where "response time" (Viney and Catchpole 1991) is quantified empirically through experimental drying.

In order to understand how changes in species composition may influence surface fuel moisture regimes through altering litter composition, we evaluated absorptive capacity and drying response time of litter from 17 eastern U.S. tree species that represent two broad ecological groups: (1) pyrophytic species common to

fire-prone ecosystems and (2) mesophytic species that commonly invade these ecosystems when fires are excluded. The objectives of this study were to (1) quantify moisture drying rates of litter beds of these 17 trees, (2) determine whether absorptive capacity and moisture drying rates cluster by species according to the two ecological groups evaluated, and (3) determine to what degree individual leaf morphology controls moisture dynamics of litter beds. By evaluating the potential for mesophytic invaders to dampen fire regimes, ultimately favoring their perpetuation through slowing moisture loss and reducing fire potential, this study will help inform our understanding of a positive feedback "mesophication" common to fire-prone ecosystems of the eastern United States (Abrams 2005, Nowacki and Abrams 2008) and more broadly (Cochrane 1999, Trauernicht et al. 2012).

METHODS

Litter collection

Leaf litter was collected from 17 southeastern tree species in May and June 2010, during typical fire season in the region (Robbins and Myers 1992). Seven pyrophyte species found in frequently burned uplands (*Pinus palustris*, *Quercus laevis*, *Q. falcata*, *Q. incana*, *Q. margaretta*, *Q. stellata*, and *Q. alba*) were collected from Ichauway (Joseph W. Jones Ecological Research Center, Newton, Georgia, USA; 31°13′13″ N, 84°28′44″ W), a frequently burned site in southwestern Georgia. An additional pyrophyte (*Pinus taeda*) and nine mesophyte invaders (*Liquidambar styraciflua*, *Liriodendron tulipifera*, *Q. nigra*, *Q. virginiana*, *Q. hemisphaerica*, *Magnolia grandiflora*, *Ilex opaca*, *Fagus grandifolia*, and *Acer rubrum*) were collected in nearby Torreya State Park, in the panhandle of Florida, USA (30°34′08″ N, 84°56′51″ W). Of the 17 species, six are evergreen (*P. palustris*, *P. taeda*, *M. grandiflora*, *Q. virginiana*, *Q. hemisphaerica*, and *I. opaca*) and 11 are deciduous (*Q. laevis*, *Q. falcata*, *Q. incana*, *Q. margaretta*, *Q. stellata*, *Q alba*, *L. styraciflua*, *L. tulipifera*, *F. grandifolia*, *I. opaca*, and *A. rubrum*). For each species, we collected >20 g (dry mass) of recently fallen litter (uppermost ~2 cm of Oi horizon) beneath each of four replicate trees (~50 m apart), placed them loosely into paper bags, and transported them to the laboratory (<7 days between field collection and lab preparation).

Litter moisture desorption rates

To determine desorption rates we calculated the response time (Viney and Catchpole 1991) of individual litter beds drying under laboratory conditions. Sixty-eight litter beds were created from collected foliar litterfall from 17 southeastern U.S. tree species (*n* = 4 beds per species). All litter was oven dried at 70°C for 24 hours and replicate litter beds were created from 15 g of oven-dried litter (~5 g were reserved for leaf measurements). Litter beds were initially soaked in a water bath for 24 hours, removed, and agitated, then placed into 24

× 24 × 4 cm aluminum pans with 36 holes (5 mm diameter) spaced 25 mm apart to drain. Drying pans were elevated to permit drainage and weighed to establish initial moisture content. Fuel bed heights were allowed to vary naturally to mimic that of natural leaf fall onto the forest floor, i.e., leaves were not packed to specified litter depths. Therefore, fuel bed bulk density varied across species as would likely occur in the field.

Litter beds dried under laboratory conditions (23–24°C, 45–50% relative humidity) for 48 hours to attain equilibrium moisture content. Fuel beds were weighed periodically to determine moisture contents throughout the drying process. Fuel beds were weighed more often during the initial stages of drying and less frequently during later stages, assuming a negative exponential desorption response (Kreye et al. 2012). Fuel moisture content was calculated (Eq. 1) for each time step, for all fuel beds, and subsequently converted to relative moisture content (*E*, Eq. 2) in order to determine desorption response times. Relative moisture content is the remaining proportion of evaporable moisture at a given time (*t*) during desorption from an initial MC to an equilibrium moisture content following an environmental change (Fosberg 1970):

$$m_t = \frac{(\text{litter mass}_t - \text{litter mass}_{od})}{\text{litter mass}_{od}} \quad (1)$$

where m_t is moisture content at time *t*, litter mass$_t$ is fuel mass at time *t*, and litter mass$_{od}$ is oven dry fuel mass. Relative moisture content is then calculated as

$$E = \frac{(m_t - m_f)}{(m_i - m_f)} \quad (2)$$

where *E* is relative moisture content, m_t is moisture content at time *t*, m_f is final moisture content, and m_i is initial moisture content.

To determine drying response times (τ) for each litter bed, we used piece-wise polynomial curve fitting. We separated the natural log of relative moisture content (ln *E*) as a function of time (*t*) into two linear sections: initial and final time lag (Nelson and Hiers 2008), using a linear-linear model with a SIGN(X) "sharp" transition in NCSS (Hintze 2007). For each litter bed, response time was determined from the initial linear portion of the log-transformed curve (Nelson and Hiers 2008, Kreye et al. 2012). Response time was calculated as the negative inverse of the estimated slope of the initial response portion of the curve of the linear-linear model (Kreye et al. 2012).

Leaf characteristics

In order to determine whether species-level differences in litter absorptive capacity or drying response rate were related to leaf morphology, we quantified several leaf characteristics for all 17 species. For each species, seven leaves were randomly removed from the reserved litter and individual leaves measured. For all angiosperms,

leaf curl, length, width, thickness, sinus depth, perimeter, surface area, volume, surface area to volume ratio (SA : V), and oven-dry mass were quantified for each replicate leaf. Leaf curl was quantified as the maximum height of a leaf horizontally oriented on a flat surface in its original curled state as collected from surface litter in the field. All leaves were then flattened to measure maximum length (petioles not included), maximum width, maximum sinus depth, perimeter, and surface area. Leaf perimeter was measured using a mini-pedometer and surface area was measured with a PLANIX planimeter (Tamaya Technics, Tokyo, Japan). To measure leaf thickness, each leaf blade was bisected perpendicular to its main vein axis, halfway between the leaf base and leaf apex, with a razor blade. Using the basal bisected half (nearest the petiole), leaf thickness was measured near the mid-vein and then at the leaf edge, using a caliper to the nearest 0.01 mm. Both thickness values were then averaged for each leaf. Leaf volume was calculated as surface area of one side of the leaf multiplied by leaf thickness. Surface area to volume ratio (SA : V) was calculated as measured surface area divided by leaf volume. Last, leaves were oven dried at 70°C for 24 h and weighed. For all pines, each replicate leaf for measurement was an intact bundle that included three individual needles. Leaf curl was estimated, as with broadleaved species, by measuring the maximum depth of a leaf bundle lying on a flat surface. Needles were straightened to measure maximum length, width, and perimeter, as conducted with broadleaved species. Oven dry leaf mass was that of the leaf bundle. Leaf thickness was measured for each of the three needles within the leaf bundle and then averaged. Leaf volume was calculated for each bundle as leaf length times the leaf cross sectional area ($\pi \times$ radius^2, assuming a circular cross sectional area of a leaf bundle and average needle thickness as its radius). Leaf surface area was estimated using a simplified geometry for needles within leaf bundles. Again, assuming needle thickness as the radius of the leaf bundle cross sectional area, we first calculated circumference for a closed leaf bundle and multiplied it by leaf length to get its "exterior" surface area. We then multiplied needle thickness by leaf length, then multiplied that by six, to estimate total "interior" surface area of all three needles within a bundle. We summed both exterior and interior surface area. Therefore, total leaf surface area was the surface area of all three needles within a leaf bundle. SA : V was then calculated for each leaf bundle by dividing surface area by volume.

Data analysis

Means and standard deviations were calculated for initial moisture content, drying response times, and all leaf measurements, by species. To determine how the 17 tree species grouped according to initial moisture content and drying response time, we used k-means cluster analysis. For analysis, replicate litter beds ($n = 4$ beds) were treated as subsamples, therefore mean response time and mean initial moisture content by species was used for clustering. To determine the number of clusters, the percent variation (PV) (within sum of squares when clustering as a percentage of the within sum of squares without clustering) was used, whereby additional clusters did not significantly reduce PV, they were not used. Little or no reduction in PV means that little or no additional variation in the data is being explained through additional clustering (Sokal and Rohlf 1995).

To determine the role of leaf morphology on litter bed moisture dynamics, we evaluated the relationship between our moisture metrics (initial moisture content and drying response time) and leaf characteristics using regression methods. Litter beds and individual leaves, by species, were treated as subsamples for moisture metrics and leaf measurements, respectively. Therefore, regression analysis was conducted using all species pooled using a single mean value for each species for each moisture metric and each leaf characteristic. Our aim was to determine the role of leaf morphology on moisture dynamics of litter beds through species-level differences in leaf morphology in order to evaluate leaf morphology as a mechanism for observed differences in moisture metrics across species. We first used linear regression to analyze the relationship of each moisture metric (initial moisture content and the natural log of drying response time) with each leaf characteristic. Because leaf characteristics were expected to be correlated, we also used principal-components analysis (PCA) for a multivariate approach to evaluate if combining correlated leaf characteristics influenced moisture holding capacity or drying response time more strongly than individual leaf characteristics alone. PCA was conducted using all leaf characteristics across all species ($n = 7$ for each characteristic by species). Correlated characteristics were then combined through PCA into new factor variables. The Bartlett test was used to examine how well the PCA performed on our data. Factors, combinations of correlated characteristics, with eigenvalues ≥ 1.0 were used for subsequent analyses. For each new variable, factor scores were calculated for each leaf replicate of all species. We then used linear regression to determine the relationship between factor scores and moisture dynamics metrics (initial moisture content and natural log of drying response time) across species. As above, mean factor scores by species were evaluated against mean moisture dynamics metrics (initial moisture content and drying response time) by species.

Results

We found substantial differences in litter moisture retention and drying across the 17 tree species. Following moisture absorption, litter beds ranged from 105% to 513% initial moisture content (Table 1). During the desorption process, drying response time (τ) of litter beds ranged from 2.7 to 11.3 h. The k-means cluster analysis using absorptive capacity and response time generated five distinct clusters explaining 87% (1 − PV)
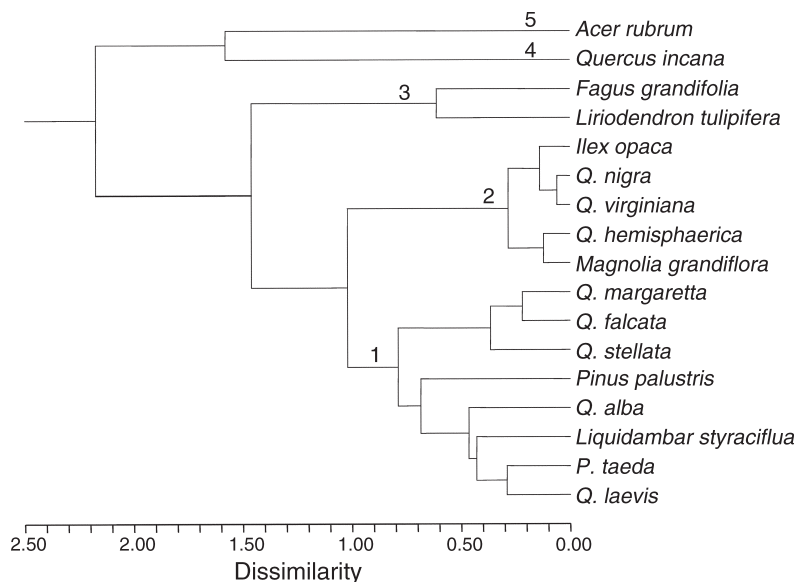
FIG. 1. Dendrogram of 17 southeastern tree species according to their time lag response time and initial moisture content of leaf litter during drying experiments. Five clusters were evident through k-means cluster analysis, as indicated at their respective nodes: cluster 1, rapid response time (3.8 ± 0.9 h [mean ± SD]), low initial moisture content (204% ± 63%); cluster 2, moderate response time (7.0 ± 0.4 h), low initial moisture content (214% ± 18%); cluster 3, moderate response time (5.8 ± 1.5 h), high initial moisture content (401% ± 20%); cluster 4, slow response time (11.3 h), low initial moisture content (286%); cluster 5, slow response time (10.4 h), high initial moisture content (513%).

of the variation in drying response time (τ; $P < 0.001$) and initial moisture content ($P < 0.001$; Table 1, Figs. 1 and 2). Cluster 1 represented species with rapid drying response time (3.8 ± 0.9 h) and low initial moisture content (204% ± 63%). Cluster 1 included seven pyrophytic upland species (*Quercus laevis*, *Q. stellata*, *Q. falcata*, *Q. alba*, *Q. margaretta*, *Pinus palustris*, and *P. taeda*) and one mesophyte (*Liquidambar styraciflua*).
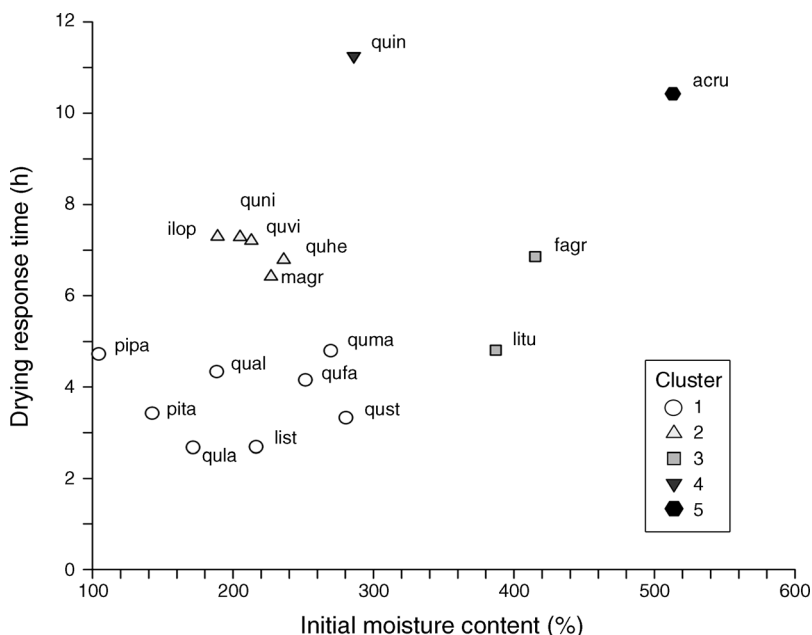

FIG. 2. Bivariate cluster plot of species groupings according to initial moisture content (MC) and drying response time (see Appendix B for species codes): cluster 1, rapid response time (3.8 ± 0.9 h [mean ± SD]), low initial MC (204% ± 63%); cluster 2, moderate response time (7.0 ± 0.4 h), low initial MC (214% ± 18%); cluster 3, moderate response time (5.8 ± 1.5 h), high initial MC (401% ± 20%); cluster 4, slow response time (11.3 h), low initial MC (286%); cluster 5, slow response time (10.4 h), high initial MC (513%).

Cluster 2 represented species with intermediate response times (7.0 ± 0.4 h) and low initial moisture contents ($214\% \pm 18\%$) and included five mesophytes (*Q. hemisphaerica*, *Q. virginiana*, *Q. nigra*, *Magnolia grandiflora*, and *Ilex opaca*). Cluster 3 included two mesophytes (*Liriodendron tulipifera*, *Fagus grandifolia*) and represented moderate response time (5.8 ± 1.5 h), but high initial moisture content ($401\% \pm 20\%$). Cluster 4 included only *Q. incana*, a pyrophyte with slow response time (11.3 h) and low moisture content (286%). *Acer rubrum*, a widespread mesophytic invader, was the only species in cluster 5, having a slow response time (10.4 h) and the highest initial moisture content (513%) of all 17 species.

Physical leaf characteristics of the 17 species span a wide diversity of foliar characteristics. Average leaf measurements are listed by species in Appendix A. Values at the upper and lower extremes include the two pine species (*P. palustris* and *P. taeda*) being the thickest and densest of all the leaves measured and also curling the least. *P. palustris* leaves were longer than all other species, with the greatest perimeter, while *P. taeda* leaves were the lowest in volume and surface area. Of the broadleaved species, *Magnolia grandiflora* leaves were the longest, thickest, had the highest SA, and were the heaviest; however they were also the least dense of all leaves, with the highest volume, lowest SA : V, no leaf sinuses, and curled very little. *Quercus laevis* leaves were the second longest of all species, but with the deepest sinuses and curled the most. *Q. hemisphaerica* curled the least of the broadleaves and *Q. virginiana* leaves were the shortest, with the least SA. *Acer rubrum* leaves were the thinnest and most dense, with the lowest leaf volume and highest SA : V.

Regarding the relationships between leaf characteristics and moisture dynamics metrics, *M. grandiflora* and both pine species (*P. palustris* and *P. taeda*) were outliers in several linear regression analyses, breaking the assumption of linearity, and resulted in performance problems during PCA. Therefore, all three species were excluded from regression analysis and PCA and their values subsequently addressed in *Discussion*. Initial MC was influenced negatively by leaf thickness ($P = 0.002$, $r^2 = 0.57$), but positively by leaf SA : V ($P < 0.001$, $r^2 = 0.74$) and leaf density ($P = 0.008$, $r^2 = 0.46$) (Table 2, Fig. 3). Drying rates, as measured by initial desorption response time (τ), were positively influenced by leaf mass ($P < 0.001$, $r^2 = 0.66$), leaf volume ($P < 0.001$, $r^2 = 0.71$), leaf length ($P < 0.001$, $r^2 = 0.66$), leaf width ($P < 0.001$, $r^2 = 0.66$), leaf surface area ($P = 0.002$, $r^2 = 0.57$), leaf perimeter ($P = 0.002$, $r^2 = 0.57$), sinus depth ($P < 0.001$, $r^2 = 0.70$), and leaf curl ($P < 0.001$, $r^2 = 0.74$; Table 2, Fig. 4). Several leaf characteristics were highly correlated (Table 3), and subsequent PCA resulted in the combining of all measured leaf characteristics into two new factors (Bartlett test = 149.31, $P < 0.001$). Factor 1 was composed of leaf width, mass, volume, surface area, sinus depth, length, curl, and perimeter, according to

TABLE 2. Linear regression results indicating the role of leaf characteristics on two moisture dynamics metrics: initial moisture content following water absorption and the natural logarithm of drying response time during drying.

	Initial moisture content (%)		ln(response time)	
Variable	P	r^2	P	r^2
Leaf characteristics				
Mass (g)	0.50		<0.001	0.66
Curl (cm)	0.84		<0.001	0.74
Length (cm)	0.30		<0.001	0.66
Width (cm)	0.96		<0.001	0.66
Thickness (mm)	0.002	0.57	0.19	
Sinus depth (cm)	0.35		<0.001	0.70
Perimeter (cm)	0.72		0.002	0.57
Surface area, SA (cm^2)	0.69		0.002	0.57
Volume, V (cm^3)	0.27		<0.001	0.71
SA : V	0.001	0.74	0.25	
Density	0.008	0.46	0.30	
PCA factors				
Factor 1†	0.55		<0.001	0.77
Factor 2‡	<0.001	0.62	0.54	

Notes: Leaf characteristics (measured across 14 southeastern U.S. broadleaved tree species) are listed in Appendix A, by species. Response time was measured in hours. Values for r^2 are not given for nonsignificant ($P > 0.05$) effects.

† Factor 1 is a variable created from principal-components analysis (PCA) that incorporated the following correlated leaf characteristics: mass, curl, length, width, sinus depth, surface area, and volume.

‡ Factor 2 is a variable created from PCA that incorporated the following correlated leaf characteristics: thickness, SA : V, and density.

variable correspondence (Table 3), and had an eigenvalue of 6.49. Factor 2 was composed of leaf SA : V, density, and thickness according to correspondence (Table 3), and an eigenvalue of 2.66. Leaf characteristics that loaded into factor 1 were also those that significantly influenced drying response from linear regression analysis with leaf characteristics separately. In addition, those characteristics that loaded into factor 2 were also those that, separately, influenced initial moisture content. Initial moisture content was related to factor 2 (Table 2, Fig. 3; $P < 0.001$, $r^2 = 0.62$), but not factor 1 ($P = 0.55$), while drying response time was related to factor 1 (Table 2, Fig. 4; $P < 0.001$, $r^2 = 0.77$), but not factor 2 ($P = 0.54$). Factor 2 explained 62% of the variation in initial MC, however leaf SA : V alone explained 74%. Factor 1 explained more of the variation in drying response time (77%) than any single leaf characteristics that contributed to factor 1, however, leaf curl explained nearly as much (74%).

Discussion

Absorptive capacity and the ability of fallen litter to retain or shed moisture via drying rates differed among the 17 pyrophyte and mesophyte tree species. The differences among species were linked to physical leaf properties that influence moisture dynamics both directly or indirectly through fuel bed properties (Nelson and Hiers 2008, Kreye et al. 2012). More importantly,
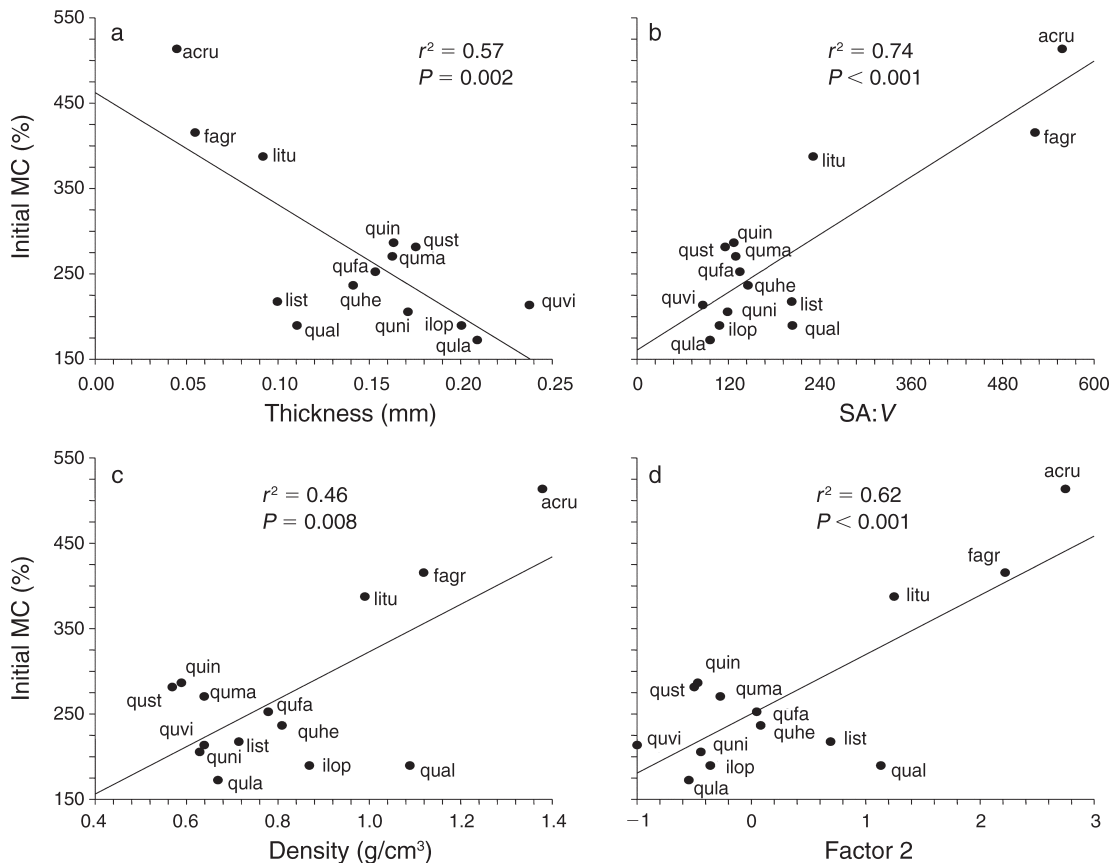
FIG. 3. Relationship of initial moisture content (MC) of litter beds with (a) leaf thickness, (b) leaf surface area (SA) to volume (V) ratio, (c) leaf density, and (d) a composite of these characteristics from principal-components analysis (PCA; factor 3). See Appendix B for species codes.

species-level differences indicate that litter from meso-phyte trees that commonly invade fire-prone ecosystems following fire exclusion absorb more moisture and retain it longer than the fire-facilitating pyrophytes they replace. This phenomenon, in concert with differences observed for fire behavior among facilitating and invader species (Kane et al. 2008), may be an important mechanism in the mesophication of historically fire-prone ecosystems of the eastern USA.

Several leaf characteristics were related to fuel moisture dynamics. Drying rates were best correlated with dry leaf "curl" and leaf size measurements, characteristics likely to influence fuel bed thickness, bulk density, and porosity, presumably the more important factors controlling the drying rates observed in our fuel beds (Anderson 1990, Nelson and Hiers 2008, Kreye et al. 2012). Drying rates were weakly associated with leaf thickness, density, and SA:V. Leaf curl, an important flammability characteristic in other pyro-phytic species (Engber and Varner 2012), explained more variation in drying rates than all other leaf measurements and nearly as much as the combination of correlated leaf size measurements. Larger-leaved

species curled more, an attribute likely to enhance the effects that leaf size has on fuel bed properties. An exception to this generalization was the mesophyte *Magnolia grandiflora* whose large leaves did not curl and had correspondingly slower drying rates. While our results indicate that the size of broadleaved litter, including both deciduous and evergreen species, increases drying rates of litter beds, the slow drying response in magnolia leaves reveals the overarching importance of leaf curling. Both pines were excluded from our leaf characteristics regression analyses because relationships among leaf characteristics were markedly different than those of broadleaves; however, they were the only rapid drying evergreens in this study and fuel bed properties (mass and needle arrangement) have been shown to control moisture drying in pine litter (Nelson and Hiers 2008). Broadleaved evergreens were all moderate in their drying response, while deciduous species spanned the entire range of drying rates. Across all the 14 broad-leaved species evaluated, drying rates were strongly associated with a composite factor of leaf size; leaf curling alone controlled moisture loss almost as
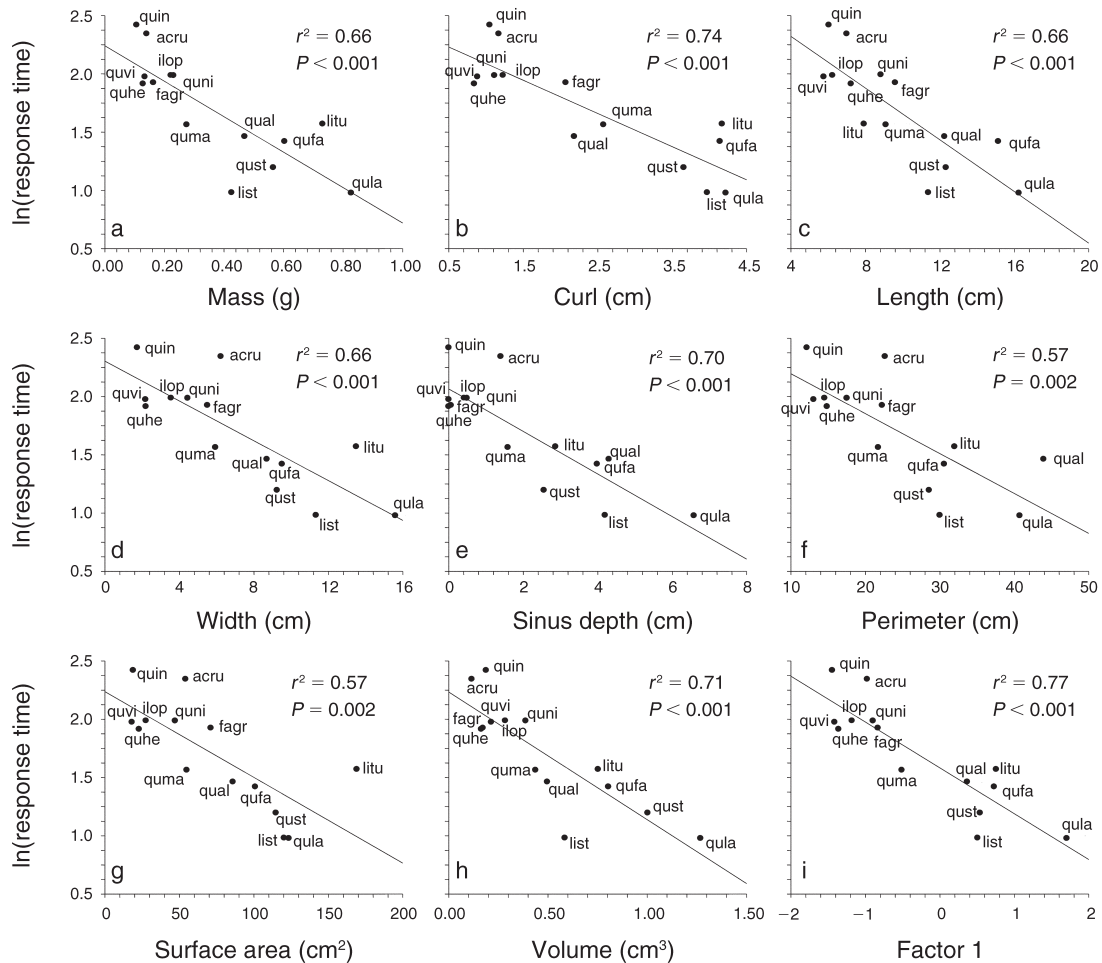
FIG. 4. Relationship between litter drying rates (ln[response time]; measured in hours) and the following leaf level characteristics across 14 common southeastern U.S. tree species: (a) leaf mass, (b) leaf curl, (c) leaf length, (d) leaf width, (e) leaf sinus depth, (f) leaf perimeter, (g) leaf surface area, (h) leaf volume, and (i) a composite of these characteristics from PCA. See Appendix B for species codes.

strongly, an important characteristic in determining fuel bed bulk density.

Litter absorptive capacity was controlled primarily through leaf properties associated with thickness. Thinner leaves were higher in both SA : V and density, and retained more moisture when they comprised litter beds. Differences in initial moisture content indicate that the fire-sensitive mesophytes with these characteristics

TABLE 3. Correlation matrix of leaf measurements across 14 southeastern U.S. broadleaved tree species and correspondence values between leaf characteristics loading into factor variables using PCA.

Variable	Mass	Curl	Length	Width	Thickness	Sinus depth	Perimeter	Surface area	Volume	SA : V	Density	Factor 1	Factor 2
Mass	1.00	0.77	0.77	0.88	0.11	0.79	0.73	0.89	0.92	−0.18	−0.06	0.89	0.01
Curl	0.77	1.00	0.70	0.80	−0.06	0.72	0.61	0.81	0.72	−0.06	0.08	0.72	0.00
Length	0.77	0.70	1.00	0.75	0.07	0.81	0.77	0.70	0.81	−0.07	−0.11	0.77	0.00
Width	0.88	0.80	0.75	1.00	−0.13	0.89	0.81	0.90	0.81	0.02	0.05	0.90	0.02
Thickness	0.12	−0.06	0.07	−0.13	1.00	0.01	−0.15	−0.21	0.30	−0.72	−0.66	0.00	0.78
Sinus depth	0.79	0.72	0.81	0.89	0.01	1.00	0.84	0.72	0.77	−0.11	−0.03	0.83	0.00
Perimeter	0.73	0.61	0.77	0.81	−0.15	0.84	1.00	0.73	0.64	0.08	0.15	0.71	0.05
Surface area	0.89	0.81	0.70	0.90	−0.21	0.72	0.73	1.00	0.81	0.08	0.06	0.83	0.04
Volume	0.92	0.72	0.81	0.81	0.30	0.77	0.64	0.81	1.00	−0.30	−0.31	0.83	0.08
SA : V	−0.18	−0.06	−0.07	0.02	−0.72	−0.11	0.08	0.08	−0.30	1.00	0.84	0.01	0.86
Density	−0.06	−0.08	−0.11	0.05	−0.66	−0.03	0.15	0.06	−0.31	0.84	1.00	0.01	0.83

Note: Factors 1 and 2 are described in the notes of Table 2.

(e.g., *L. tulipifera*, *F. grandifolia*, and particularly *A. rubrum*) may enhance moisture absorption in the forest floor following precipitation. Results from these mesophytes (with the exception of *L. styraciflua*) contrast sharply with the low absorptive, rapid drying litter from the pyrophytes that historically dominated these fire-prone landscapes.

Increased forest floor moisture absorption and retention have important consequences for fire regimes. Moisture retention in surface litter reduces susceptibility to ignition and subdues fire spread and intensity when fires do occur (Rothermel 1972). Reduction of fire frequency and intensity allows invasion and growth by fire-intolerant species that can further enhance moisture retention by influencing canopy structure and litter input that reduce long-term fire susceptibility (Abrams 2005, Nowacki and Abrams 2008). The frequency and intensity of fires influence both species composition and vegetation structure in fire-prone ecosystems (Glitzenstein et al. 1995, 2003, Peterson and Reich 2001, Govender et al. 2006, Hiers et al. 2007, Alexander et al. 2008, Green et al. 2010). Increased canopy cover, from invasion, may reduce surface winds and solar radiation, thus slowing the drying process and reducing fuel temperatures (Agee and Skinner 2005), ultimately reducing fire frequency and intensity (Abrams 2005, Nowacki and Abrams 2008, Hoffman et al. 2012). In addition, moisture retention through the incorporation of litter by invading tree species, as observed here, likely initiates this process. The combined effects of canopy cover and surface litter composition on moisture dynamics is likely an important mechanism in the mesophication of eastern forests where anthropogenic influences have reduced historical fire return intervals.

The implications of litter moisture retention following invasion of mesophytes into historically fire-prone ecosystems include the potential for an alternative stable state (Scheffer and Carpenter 2003) to develop where restoration of fire-prone ecosystems may be difficult (Abrams 2005, Nowacki and Abrams 2008). Maintaining species composition and open-canopied structure in these ecosystems requires frequent fires. As this study suggests, litter beds created from pyrophytes historically prevalent in fire-prone ecosystems likely promote flammability by shedding moisture readily, increasing opportunities for burning through increased ignition probability and enhancement of fire spread. The suppressive influence of fuel moisture on flammability, however, would be enhanced through the incorporation of moisture-retaining litter from mesophytes that would lower the probability of ignition and inhibit or reduce fire spread when ignition occurs. A feedback may ensue by lowering fire-induced mortality of those species with high moisture retention potential, thus resulting in an alternative stable state where fire is unlikely to occur and where fire-sensitive species dominate. At this point, we don't know how widespread this phenomenon may be in other formerly fire-prone ecosystems.

In addition to the effects of moisture regimes on flammability, retained forest floor moisture may influence other important ecological processes. High moisture retention capacity of forest litter may subdue moisture loss and heating of soils (Bussiére and Cellier 1994) that may influence decomposition rates (Gholz et al. 2000) and nutrient dynamics (Fabio et al. 2009). Alexander and Arthur (2010) observed increased stem-flow and subsequent increases in soil moisture, nutrient input, net nitrification, and net ammonification beneath invading mesophyte *A. rubrum* compared with pyrophytic upland oaks. The considerable moisture retention capacity of *A. rubrum* litter observed here may enhance these effects across the forest floor. Increased litter and soil moisture, lower soil temperatures, and potential increases in nutrient availability may increase productivity, but may also enhance mesophyte seed germination and seedling survival (Clinton and Vose 1996, Hane 2003). Potential alterations to these ecological processes, in addition to the influence of moisture retention on fire susceptibility, may be primary components in the shifting ecological states and suggestive of the proximate mechanism for the resistance of these communities to reintroduction of fire.

Species with high litter moisture retention capacity were those primarily associated with the invasion of previously fire-prone forests in the eastern United States. The mesophytes *Quercus virginiana*, *Q. hemisphaerica*, *Q. nigra*, and *Acer rubrum* were higher in initial moisture content and dried more slowly than the pyrophytes *Pinus palustris*, *Quercus laevis*, *Q. falcata*, *Q. margaretta*, and *Q. stellata* (Myers 1985, 1990, Abrams 1992). *Fagus grandifolia*, *L. tulipifera*, and *A. rubrum* had the highest initial moisture of all species and both *F. grandifolia* and *A. rubrum* were slow in drying response, all markedly higher in moisture retention capacity than *Q. alba*, a dominant presettlement pyrophyte in forests of the mid-Atlantic, where *F. grandifolia*, *L. tulipifera*, *A. rubrum* have increased in the absence of frequent fire (Abrams and Downs 1990), and in the southern Piedmont region, where *A. rubrum* has increased (Christensen 1977). In terms of invasion and establishment into forests of eastern North America, *A. rubrum* is the most ubiquitous (Abrams 1998). *A. rubrum* has a large range over most of the east, occurring across a variety of site conditions and successional stages, but was apparently uncommon in upland ecosystems prior to settlement (Abrams 1992, 1998, 2005). Although its ecophysiological characteristics allow *A. rubrum* to thrive across diverse ecological conditions (Abrams 1998), it is sensitive to fire (Peterson and Reich 2001, Alexander et al. 2008, Green et al. 2010) and has likely assumed dominance due to fire exclusion (Abrams 1992, 2005). *A. rubrum* was highest in initial moisture content and the second slowest in drying rates of all species observed in this study. The changes in forest floor (observed here) and stand structure (Nowacki and Abrams 2008) caused by *A. rubrum* invasion likely facilitate continued

invasion and dominance of *A. rubrum* across historically fire-prone eastern forests.

Increases in potential moisture retention, where invasion and establishment of fire-sensitive species have occurred, may be an important initiation of a mesophication feedback cycle within historically fire-prone ecosystems. Fire regime characteristics are a function of both climate and fuel characteristics and species community control over litter flammability may be an important component of the perpetuation of ecological stable states in fire-dependent or fire-sensitive ecosystems (Gagnon et al. 2010, Trauernicht et al. 2012, Veldman et al. 2013). Restoration efforts aimed at shifting these ecosystems to a previous ecological state may be difficult. The exclusive use of prescribed burning for restoration may leave managers with few windows of opportunity for success due to a reduction in flammable conditions conducive for both fire spread and intensity sufficient to cause desired mortality to those species responsible for enhanced mesic conditions (Peterson and Reich 2001, Arthur et al. 2012). To enhance forest floor flammability, other treatments in concert with silvicultural methods (e.g., thinning or removing mesophytic species via mechanical or chemical means), may be required in these landscapes (Arthur et al. 2012, Brose et al. 2013). The potential for shifts in ecological stable states due to mesophication may continue in areas where both forest structure and species composition are altered due to past fire exclusion.

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Supplemental Material

Appendix A

Leaf characteristics of 17 southeastern tree species (*Ecological Archives* A023-097-A1).

Appendix B

Species codes used in Figs. 2, 3, and 4 (*Ecological Archives* A023-097-A2).