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Dendroecological and ecophysiological analysis of gap environments in mixed-oak understoreys of northern Virginia

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Summary

1. Ecophysiological, morphological and dendroecological attributes were examined in species growing in understorey and newly formed gap environments in mixed-*Quercus* forests of northern Virginia.

2. Gap environments were characterized by higher photosynthetic photon flux density (PPFD) but were not different from non-gap control plots in their soil moisture, predawn leaf water potential (Ψ), leaf temperature or leaf to air vapour pressure deficit (VPD). In addition, few significant differences existed between regeneration responses at gap and control sites.

3. Plants in gaps experienced higher rates of net photosynthesis (A) and leaf conductance to water vapour diffusion (g_{wv}) than control plants, although parameters did not differ between early *vs* late successional species. Gap plants also produced leaves with smaller leaf area and greater leaf thickness, leaf mass per area (LMA) and stomatal density than control plants.

4. All gap species experienced accelerated height growth compared to non-gap plants, with early successional *Sassafras albidum* (Sassafras) and *Liquidambar styraciflua* (Sweetgum) exhibiting the highest rates. In contrast, average radial growth in small, understorey trees was not significantly different between habitat type, although *Quercus alba* (White Oak) did respond significantly to the most recent gaps.

5. Many small trees (6–12 cm d.b.h.) were surprisingly old — up to 100 years in age. Despite severe suppression periods in these trees, they experienced release events during their lifetime, although not necessarily to the most recent gaps. This may partially explain the lack of correlation between ecophysiological and growth parameters.

Key-words: Photosynthesis, radial growth, successional status, wind disturbance

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Introduction

Wind is one of the most frequent causes of large- and small-scale disturbance affecting eastern forests and is an intrinsic factor in the determination of structure in many forest types (Bormann & Likens 1979; Foster 1988). In general, creation of single and multiple-tree canopy openings leads to a wide array of microenvironmental, ecophysiological and community changes. The few studies which examined physiological responses to species growing in temperate canopy gaps have reported increased photosynthetic rates (A) and leaf conductances (g_{wv}) (Wallace & Dunn 1980; Reich *et al.* 1990; Ellsworth & Reich 1992). In addition, studies examining species in contrasting light environments including gaps have reported altered leaf morphology in sun leaves owing to acclimation such as thicker leaves, higher stomatal density and smaller leaf area (Carpenter & Smith 1981; Abrams & Kubiske 1990). The degree of physiological and phenotypic response may vary between early *vs* late successional species. Higher A, g_{wv} and respiration rates and more xerophytic leaves have been recorded in early *vs* late successional species (Bazzaz 1979; Abrams 1988; Koike 1988; Kloeppel, Abrams & Kubiske 1993), because late successional species may exhibit more limited physiological plasticity (Bazzaz & Carlson 1982).

Few studies have examined canopy gap processes and colonization dynamics following windthrow in second-growth oak forests (Clebsch & Busing 1989)

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and there is a scarcity of information on the age structure of saplings and small understorey trees (Ross, Sharik & Smith 1982) and their ability to persist and respond to canopy gaps. We also know very little about how sympatric species of differing successional status respond physiologically to gap formation. Therefore, this study assessed the role of windthrow disturbance on the dynamics of *Quercus* (Oak) stands of northern Virginia by linking ecophysiological, morphological and dendroecological attributes of species growing in understorey and newly formed gap environments. We addressed the following hypotheses in this study: (1) newly created treefall gaps will experience higher levels of light, soil moisture, and space availability than control plots; (2) plants in gap environments will exhibit phenotypic plasticity to the light environment resulting in greater photosynthetic and conductance rates than control plants; (3) physiological responses to canopy gaps will vary between early *vs* late successional species, with early successional species exhibiting greater stimulation; (4) leaf structure and physiology will be related to observed growth rates in gap and non-gap plants and between early *vs* late successional species.

Materials and methods

STUDY SITE

The study was conducted within Chancellorsville Battlefield, one of four Civil War battlefields associated with the Fredericksburg and Spotsylvania National Military Park, located near Fredericksburg, VA (38° 15 'N, 77 ° 37 'W). Mean annual temperatures average 13 °C, while winter and summer daily mean temperatures are 2 °C and 23 °C, respectively (Elder 1985). Precipitation averages 102 cm annually and is well distributed throughout the year. The study area is located within the Piedmont Plateau physiographic province and consists of gently rolling topography, elevations of 60–90 m above sea level (US Geological Survey 1984) and deep, well-drained silt loam soils (Elder 1985). Local overstorey vegetation was assessed prior to the wind disturbance and consisted of a mixture of *Quercus alba* L. (White Oak), *Quercus coccinea* Muenchh. (Scarlet Oak), *Liquidambar styraciflua* L. (Sweetgum) and *Pinus virginiana* Mill. (Virginia Pine) (Orwig & Abrams 1994a).

GAP SAMPLING

During a 2 week period in July 1990, several severe thunderstorms with winds in excess of 100 km h^{-1} resulted in many single-tree windthrows of *P. virginiana* and various *Quercus* species within Chancellorsville Battlefield (NOAA 1990). During mid-summer 1993 (the third growing season following the disturbance), 26 gaps within a 20 ha portion of the battlefield were measured for area by using the formula for an ellipse ($a = \pi LW/4$, where L is the length of the longest straight line that will fit in the gap and W is the length of the longest line in the gap that is perpendicular to L) (Runkle 1992). Gaps were defined as canopy openings (>15 m^2) created by the death of one or more trees (gap-makers) and were delimited by vertically projecting the canopy opening to the ground surface. Adjacent non-gap plots of equal area were randomly established within the same stand at a random distance sufficiently far away to exclude the light effects of the gap (i.e. > 20 m). Each established windthrow plot was inventoried for gap-maker species and damage type, while both plot types were sampled for sapling and seedling densities and shrub and herbaceous cover (%).

Growth responses for the last 3 years were determined for a subsample of saplings encountered in the plots by measuring the distance (cm) between terminal bud scars (cf. Runkle 1992). In addition, tree cores were obtained 0·5 m above the ground from saplings and small trees (d.b.h. < 18 cm) when present within gaps and control plots to examine radial growth responses to recent gap formation and to ascertain the extent of past disturbances. All cores were dried, mounted, sanded and aged with a stereomicroscope. Annual growth increments were measured to the nearest 0·01 mm with a tree-ring measuring device (Regents Instruments Inc., Quebec, Canada) and recorded using the MacDendro microcomputer program. Cores were examined for recent abrupt growth releases according to Lorimer & Frelich (1989). The 10 oldest overstorey *Q. alba* cores taken previously from the sampled sites (cf. Orwig & Abrams 1994a) were used to develop a ring-width index or disturbance history. Cores were visually cross-dated, measured as above, standardized via linear regression and division of each measured ring width by the value of the fitted line (Fritts & Swetnam 1989), and averaged to construct the site chronology.

GAS EXCHANGE AND PLANT–WATER RELATIONS

Three gaps ranging in size from 77 to 171 m^2 and three nearby control plots of equal dimensions were selected for ecophysiological study. Each of the six plots contained four to seven understorey seedlings of *Q. alba*, *Sassafras albidum* (Nutt.) Nees (Sassafras), and *Nyssa sylvatica* Marsh. (Blackgum). During the 1993 growing season, predawn (0500 solar time) and diurnal (every 3 h from 0730 to 1800 solar time) leaf water potential (Ψ) measurements were conducted with a pressure chamber (PMS Instrument Co., Corvallis, OR) on one leaf from five seedlings of each species for each habitat type. Diurnal gas-exchange measurements were made four times (9 and 29 June, 14 July and 10 August) during relatively cloud free conditions with a portable photosynthesis unit (LCA-3, ADC Ltd, Herts., UK). Following the final sampling date of 1993, leaf-structure measurements were made on fully expanded leaves from four individuals of each species from each plot following the methods of Abrams & Kubiske (1990). All statistical mean comparisons were accomplished using analysis of variance or general linear models procedures in SAS (SAS Institute Inc. 1985).

Results and discussion

TREEFALL AND GAP CHARACTERISTICS

A total of 45 trees were damaged during the July 1990 windstorms within the 26 gaps examined. The dominant mode of treefall was bole-snap (31 trees) followed by uprooted trees and snags (nine and five trees, respectively). *Pinus virginiana* and *Q. coccinea* comprised 89% of damaged trees and trees which were uprooted. The orientation of downed trees suggests that prevailing winds were from the north-west, as 88% of stems fell in a south-easterly (95–180°) direction. Nearly 90% of sampled gaps were formed by one or two gap-makers and three gap-makers was the maximum number encountered. Canopy gap size ranged from 31 to 196 m^2 with a mean of 95 m^2 (± 9 m^2) and the mean d.b.h. of gap-makers was 38·9 cm (± 1·2 cm, range 18·7–55·8). Gap area was correlated with number of gap makers ($R = 0{\cdot}49$, $P < 0{\cdot}01$, Spearman rank correlation) while the number of gap-makers was negatively correlated ($R = -0{\cdot}38$, $P < 0{\cdot}05$, Spearman rank correlation) with average d.b.h. of gap-makers, suggesting that multiple-tree gaps may have resulted from large trees knocking down smaller trees. All uproots encountered were classified as hinge treefalls according to Beatty & Stone (1986) and pit/mound areas ranged from 4 to 19 m^2 with an average of 10 ± 2 m^2.

MICROENVIRONMENTAL AND ECOPHYSIOLOGICAL RESPONSE

Soil moisture and predawn leaf-water potentials (Ψ) between gap and control habitats were not significantly different for any of the sampling dates (Table 1), which is consistent with some gap studies (Ellsworth & Reich 1992; Kloeppel *et al.* 1993) but not others (Abrams 1986; Abrams & Mostoller 1995). Mean diurnal Ψ was significantly lower (more negative) in gap plants and differed among species (Table 1). *Quercus alba* maintained the lowest values in gap and control plots (–1·54 ± 0·06 and –1·29 ± 0·05 MPa, respectively) while *S. albidum* exhibited the highest leaf Ψ (–0·66 ± 0·04 and –0·65 ± 0·04 MPa, respectively). Gaps received significantly higher PPFD than control sites on all sampling dates and times; however, leaf temperature and VPD were not significantly different between habitats.

Table 1. Mean seasonal microenvironmental and pooled diurnal gas-exchange parameters for species growing in gap and control plots following disturbance in mixed-*Quercus* forests of northern Virginia

Parameter*	Gap	Control
Gravimetric soil moisture (%)	19·4 ± 1·3^a	18·9 ± 1·4^a
PPFD (μmol m^{-2} s^{-1})	479 ± 24^a	110 ± 6^b
Predawn Ψ (MPa)	–0·19 ± 0·01^a	–0·21 ± 0·01^a
Mean diurnal Ψ (MPa)	–1·03 ± 0·04^a	–0·91 ± 0·03^b
Leaf temperature (°C)	28·5 ± 0·2^a	28·3 ± 0·2^a
VPD (kPa)	1·30 ± 0·04^a	1·24 ± 0·03^a
A (μmol m^{-2} s^{-1})	5·10 ± 0·18^a	1·63 ± 0·10^b
A_{max} (μmol m^{-2} s^{-1})	11·48 ± 1·01^a	6·43 ± 0·34^b
g_{wv} (mmol m^{-2} s^{-1})	284 ± 11^a	202 ± 7^b

* VPD = leaf to air vapour pressure difference; A and A_{max} = mean and maximum net photosynthetic rate; g_{wv} = stomatal conductance to water vapour. Values of the same parameter followed by the same letter are not significantly different ($P < 0{\cdot}05$, *t*-test).

No significant ($P < 0{\cdot}05$) differences existed among species' daily gas-exchange means within habitats or within plots on any sampling date, therefore analysis of variance was performed on pooled species data between habitat type. Plants growing in gaps exhibited significantly higher mean and maximum photosynthetic rates, as well as higher conductance rates, than shaded understorey plants (Table 1). Higher gas-exchange rates in gap *vs* non-gap environments have been previously reported (Bazzaz 1979; Wallace & Dunn 1980; Abrams 1988; Ellsworth & Reich 1992). However, several studies also reported species differences in both high and low light environments which were not observed here (Bazzaz & Carlson 1982; Walters, Kruger, & Reich 1993; Abrams & Mostoller 1995). One potential explanation for the lack of successional differences in this study is the greater than expected physiological and morphological plasticity of *N. sylvatica* observed in this study. These findings are consistent with the reputation of *N. sylvatica* as a drought tolerant, gap-facultative species that can effectively utilize small gaps (Latham 1992; Orwig & Abrams 1994b).

All three species adjusted morphologically to gap environments by producing significantly ($P < 0{\cdot}05$, *t*-test) smaller leaf area and greater stomatal density, leaf thickness and leaf mass per area than control plants. *Sassafras albidum* exhibited the largest leaf areas (66–103 cm^2), *N. sylvatica* had the largest guard cell lengths (32·9–33·6 μm) and *Q. alba* displayed the highest stomatal densities in both habitat types (482–584 mm^{-2}) ($P < 0{\cdot}05$, Tukey's multiple comparison test). In both habitats *N. sylvatica* had the thickest leaves (127–165 μm) while *Q. alba* had the thinnest leaves (90–110 μm). This suggests that both early and late successional species can display a high degree of plasticity in response to changing environmental conditions (Carpenter & Smith 1981; Abrams & Kubiske 1990).

Table 2. Summary of 3 year average height growth rates (cm year^{-1} ± SE) following disturbance of saplings (n) sampled in 26 gap and control plots within mixed-oak forests of northern Virginia. Maximum and minimum values are average 1 year values (cm ± SE)

	Gap				Control			
Species	(n)	(3 year)	Max	Min	(n)	(3 year)	Max	Min
Acer rubrum	16	15·2 ± 1·6^{a}	22·3 ± 2·6	8·1 ± 0·9	15	9·9 ± 1·3^{b}	13·9 ± 1·8	7·7 ± 1·3
Liquidambar styraciflua	19	30·0 ± 5·2^{c}	38·3 ± 6·4	21·2 ± 4·4	12	12·2 ± 3·6^{b}	16·0 ± 4·1	7·5 ± 2·7
Nyssa sylvatica	20	15·5 ± 1·6^{a}	18·1 ± 1·9	12·9 ± 1·4	27	11·0 ± 1·2^{b}	13·6 ± 1·4	8·3 ± 1·2
Quercus alba	5	26·0 ± 6·9^{ac}	30·5 ± 8·3	21·9 ± 6·4	2	11·1 ± 2·3^{ab}	13·3 ± 3·3	9·5 ± 2·0
Sassafras albidum	16	33·7 ± 4·3^{c}	46·3 ± 6·1	24·8 ± 3·9	4	13·6 ± 3·5^{b}	17·1 ± 4·4	10·2 ± 2·8

Values in a row or a column with the same letter(s) are not significantly different ($P < 0.05$, t-test between habitats and Tukey's multiple comparison test among species).

HEIGHT AND RADIAL GROWTH RESPONSE

Growth parameters were measured on a larger number and wider array of species than physiological data. In contrast to gas-exchange data, there were differences in height growth among species and between habitats. All species exhibited accelerated height growth in gap *vs* control plots (Table 2). In addition, early successional *S. albidum* and *L. styraciflua* exhibited 3 year average height growth values near 30 cm in gaps while late successional *A. rubrum* and *N. sylvatica* averaged approximately 15 cm. Height growth was not significantly different among species in control plots. All species achieved average maximum 1 year height growth rates of at least 18 cm in gaps following disturbance, and several individuals of *S. albidum* and *L. styraciflua* displayed rates near 1 m per year. It should be noted that relating tree growth to photosynthesis has been problematic owing to the complexity of carbon allocation patterns in plants (e.g. reproduction, above- *vs* below-ground biomass, and leaf chemistry) (Canham & Marks 1985; Fitter & Hay 1987)

A total of 93 saplings and small understorey trees ranging in age from 24 to 108 years old were cored in gap and control plots. In both habitats, *A. rubrum* and *L. styraciflua* displayed the highest radial growth rates, while *Q. alba* and *N. sylvatica* experienced the lowest rates (Table 3). Mean radial growth was not significantly different between gap and control plots for any species prior to gap formation. However, *Q. alba* was the only species responding to recent gaps with accelerated radial growth (Table 3). Our results contrast with those found in northern hardwood forests, where shade tolerant *Acer saccharum* Marsh. (Sugar Maple) and *Fagus grandifolia* Ehrh. (American Beech) saplings exhibited accelerated radial growth as a result of canopy gaps (Canham 1988; Tryon, Lanasa & Townsend 1992; Poage & Peart 1993). Moreover, we found that early successional *L. styraciflua* and *S. albidum* did not respond to recent gaps. Radial growth responses may not emerge until several years following disturbance in suppressed trees, because they typically use photosynthate for foliage production immediately following release, followed by height and then radial growth (Oliver & Larson 1990).

Table 3. Radial growth characteristics of saplings and small trees (n) sampled in 26 gap and control plots following disturbance within mixed-oak forests of northern Virginia

	Gap					Control				
Species	(n)	Average growth (cm ± SE)	% Major release	% Moderate release	% Recent release	(n)	Average growth (cm ± SE)	% Major release	% Moderate release	% Recent release
A. rubrum	5	0·90 ± 0·13^{a}	20	60	0	5	0·83 ± 0·11^{a}	10	40	0
L. styraciflua	11	0·83 ± 0·08^{a}	9	18	0	12	0·69 ± 0·12^{ab}	8	33	0
N. sylvatica	9	0·57 ± 0·06^{b}	33	67	0	7	0·53 ± 0·03^{b}	29	86	0
Q. alba	21	0·53 ± 0·03^{b}	5	52	24	9	0·61 ± 0·03^{ab}	0	33	0
S. albidum	2	0·72 ± 0·10^{ab}	0	0	0	5	0·65 ± 0·03^{ab}	0	10	0

Values in a row or column with the same letter(s) are not significantly different ($P < 0{\cdot}05$, t-test between habitats and Tukey's multiple comparison test among species).

The percentage of cores exhibiting major and moderate releases were defined according to Lorimer & Frelich (1989). A recent release is at least a 100% increase in the mean radial growth of the 3 years following gap formation compared to the mean growth of the 10 years prior to the disturbance.

Table 4. Summary of seedling densities (number $\text{ha}^{-1} \pm \text{SE}$) and ground layer vegetation sampled in 26 gap and control plots within mixed-oak forests of northern Virginia

Species	Gap* ($n = 26$)	Gap pit ($n = 9$)	Gap mound ($n = 9$)	Control ($n = 26$)
Acer rubrum	1918 ± 585^{a}	1451 ± 603^{a}	1453 ± 473^{a}	4444 ± 908^{b}
Amelanchier arboreum	1297 ± 354^{a}	572 ± 384^{a}	985 ± 709^{a}	1684 ± 376^{a}
Castanea pumila	138 ± 89^{a}	0	294 ± 294^{a}	83 ± 61^{a}
Ilex opaca	442 ± 229^{a}	245 ± 245^{a}	780 ± 524^{a}	276 ± 95^{a}
Liquidambar styraciflua	3919 ± 2035^{a}	2416 ± 1210^{a}	1604 ± 807^{a}	3353 ± 1705^{a}
Liriodendron tulipifera	1336 ± 552^{a}	5040 ± 2093^{b}	2298 ± 1570^{a}	814 ± 327^{a}
Nyssa sylvatica	2360 ± 466^{ab}	1259 ± 678^{ab}	495 ± 261^{b}	3436 ± 797^{a}
Pinus virginiana	911 ± 420^{a}	1209 ± 620^{a}	1875 ± 1324^{a}	497 ± 238^{a}
Prunus spp.	1753 ± 899^{a}	0	1223 ± 1015^{a}	1642 ± 723^{a}
Quercus alba	1325 ± 238^{a}	392 ± 269^{a}	844 ± 397^{a}	4206 ± 993^{b}
Quercus coccinea	5214 ± 910^{a}	1352 ± 664^{b}	3270 ± 1421^{ab}	2470 ± 435^{ab}
Quercus falcata	552 ± 156^{a}	0	297 ± 152^{a}	277 ± 98^{a}
Quercus stellata	248 ± 159^{a}	0	0	276 ± 113^{a}
Rhamnus cathartica	0^{a}	0	347 ± 347^{a}	55 ± 55^{a}
Sassafras albidum	7535 ± 1434^{a}	3611 ± 726^{a}	5108 ± 2135^{a}	7645 ± 1905^{a}
Others	1642 ± 148	0	0	1564 ± 145
Totals	28848 ± 3326^{a}	13539 ± 3841^{b}	22294 ± 5545^{ab}	31139 ± 3419^{a}
Richness	8.23 ± 0.5^{a}	4.22 ± 0.9^{c}	5.78 ± 1.0^{b}	7.85 ± 0.5^{ab}
Herb cover (%)	7.37 ± 3.0^{a}	4.37 ± 2.4^{a}	1.67 ± 0.4^{a}	6.14 ± 2.7^{a}
Shrub cover (%)	44.9 ± 4.2^{a}	3.06 ± 1.5^{b}	16.38 ± 6.9^{b}	41.4 ± 3.9^{a}

* Excluding pit and mound densities.
Values in a row with the same letter are not significantly different ($P < 0{\cdot}05$, Kruskal–Wallis test).

DISTURBANCE FREQUENCY AND HISTORICAL DEVELOPMENT

A high percentage of understorey *A. rubrum* and *N. sylvatica* in both environments experienced major and moderate releases lasting at least 10 years (Table 3), which is consistent with radial growth responses reported in overstorey individuals of these shade-tolerant species (Mikan, Orwig & Abrams 1994). To assess whether these releases were associated with previous stand-wide disturbances or localized tree-by-tree events we examined the historical development of the study area (Fig. 1). A moderate release observed in the site chronology during 1894 was associated with a concomitant period of *Quercus* and *N. sylvatica* recruitment seen in the overstorey and understorey figures. A second pulse of understorey recruitment consisting primarily of *Quercus* and *L. styraciflua* occurred from the late 1940s to the early 1960s and coincided with a period of gradually increasing ring-width index. These results provide evidence of continuous understorey recruitment since the 1890s. In addition, the relatively low overstorey basal area and stem density of this xeric site may have resulted in conditions that permitted understorey persistence of these species.

Examples of radial growth indicate individualistic patterns among the overtopped species (Fig. 2). A 60 year-old *Q. alba* exhibited low initial radial growth $<0{\cdot}5$ mm year^{-1}, a moderate release in 1950 and a dramatic increase following the 1990 disturbance (Fig. 2a). In contrast, a 92 year-old *Q. alba* experienced an early moderate release in 1911 followed by an extended period of low growth until a moderate release in 1974 (Fig. 2b). This tree did not respond favourably to the gap after 1990. Following a major release in 1960, a 50 year-old *A. rubrum* displayed low radial growth for 15 years, experienced a moderate release in 1984 and exhibited a spurt of growth following 1990 (Fig. 2c). A *N. sylvatica* tree that became established during the early 1900s experienced a major growth release in 1921 which lasted for 20 years (Fig. 2d). A period of declining growth followed until it was released again in 1963. Figure 2e shows a 75 year-old *L. styraciflua* that had early favourable radial growth followed by a 30 year suppressed period and then a moderate release in 1959. Many *L. styraciflua* trees exhibited a characteristic pattern of high initial growth exceeding 2 mm year^{-1} and then declining radial growth over time with no recent gap response (Fig. 2f). Despite their early successional status, *L. styraciflua* and *Q. alba* endured protracted periods of suppression. This analysis indicates that most understorey trees were capable of experiencing release events during their lifetime. The asynchronous nature of release dates suggests that disturbances were localized and occurred at 20 to 30 year intervals.

GAP REGENERATION

Three years after the wind disturbance there were no

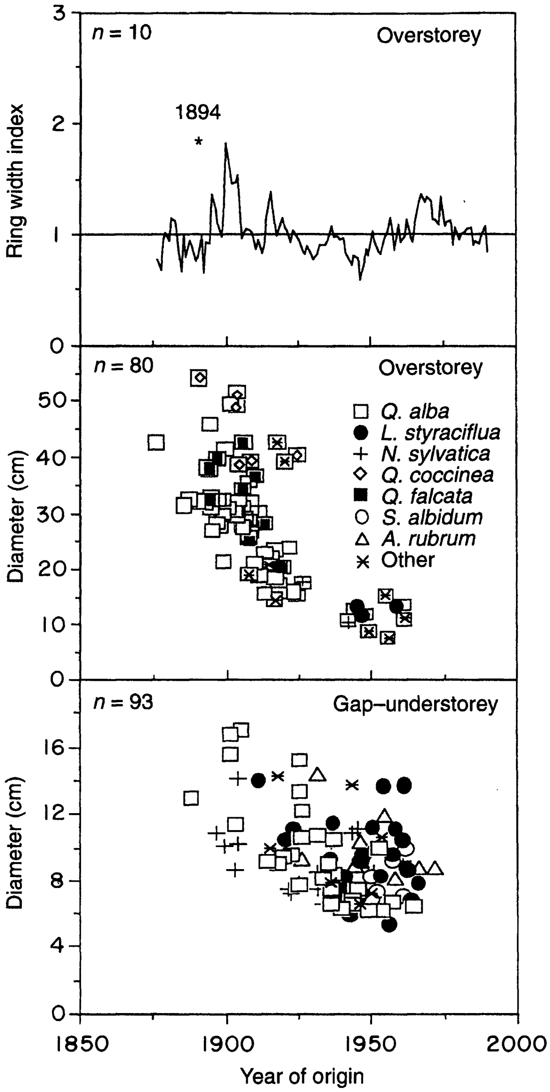

Fig. 1. Present-day overstorey and understorey age–diameter relationships showing date of recruitment and present diameters of sampled trees and ring-width index of the 10 oldest overstorey *Q. alba* in mixed-*Quercus* stands in northern Virginia. Other species include *Carya glabra* (Mill.) Sweet (Pignut Hickory), *Liriodendron tulipifera* (Tulip Poplar), *Ilex opaca* Ait. (American Holly), *Q. stellata* Wanghen. (Post Oak) and *Q. velutina* Lam. (Black Oak). The asterisk indicates a moderate release, as defined by Lorimer & Frelich (1989).

significant differences in average sapling densities between gap and control plots. *Nyssa sylvatica*, *L. styraciflua* and *A. rubrum* exhibited high sapling densities in both plot types, while *S. albidum* densities were significantly higher in gap habitats. Total seedling densities and species richness were similar in gap and control plots but were significantly lower in within-gap microsites (pits and mounds) (Table 4). *Sassafras albidum*, *Q. coccinea* and *L. styraciflua* densities were abundant across all microsites whereas *A. rubrum* and *Q. alba* densities were significantly higher ($P < 0{\cdot}05$, Kruskal–Wallis test) in control plots. Our data indicate rapid colonization and high seedling densities on pit and mound microsites after only 3 years. Light-demanding *L. tulipifera* and *P. virginiana* benefited most from these disturbed microsites, which did not contain the prominent shrub species such as *Vaccinium angustifolium* Aiton (Blueberry) and *Gayluccacia baccata* (Wang.) K. Koch (Huckleberry), common in gap and control sites. Because shrub cover was negatively correlated with gap seedling density ($R = -0{\cdot}67$, $P < 0{\cdot}001$) it may preclude significant seedling establishment despite gap formation (Huenneke 1983).

Conclusions

This study evaluated differences in gap and non-gap microenvironment, leaf morphology, leaf physiology, height and radial growth, and population dynamics. From these measurements we found surprising similarities in leaf temperature, VPD and soil moisture between gap and non-gap environments. Similarly, we found no significant differences among species in gas-exchange parameters in either habitat despite clear leaf morphological differences among species and between light environments. Early successional *S. albidum* and *L. styraciflua* exhibited rapid height growth in gaps and maintained moderate height and radial growth in control plots, whereas late successional *N. sylvatica* exhibited a high degree of physiological and morphological plasticity in response to gap formation. The dendroecological techniques used in this study increased our understanding of gap dynamics and understorey development in second-growth forests. Age structure and individual tree-ring chronologies from this site provided evidence of small-scale disturbances at 20 to 30 year intervals, continuous understorey species recruitment since the 1890s and remarkable persistence of certain species, such as *N. sylvatica* and *Q. alba*, which were still < 10 cm d.b.h. after 70–90 years. This multi-disciplinary approach appears to be a promising tool for examining successional trends and gap events in a variety of forest types.

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References

Abrams, M.D. (1986) Physiological plasticity in water relations and leaf structure of understory *vs* open-grown *Cercis canadensis* in northeastern Kansas. *Canadian Journal of Forest Research* **16**, 1170–1174.

Abrams, M.D. (1988) Comparative water relations of three successional hardwood species in central Wisconsin. *Tree Physiology* **4**, 263–273.

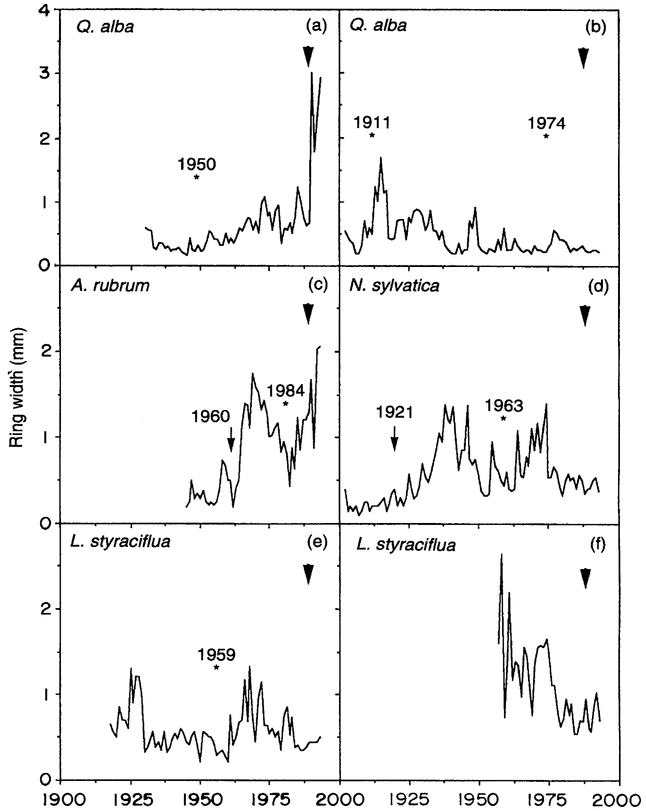

Fig. 2. Characteristic radial growth patterns of overtopped trees growing in gaps in mixed-*Quercus* of northern Virginia. Large arrowheads indicate the 1990 windstorms, while arrows and asterisks indicate the start of major and moderate releases, respectively, as defined by Lorimer & Frelich (1989).

Abrams, M.D. & Kubiske, M.E. (1990) Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. *Forest Ecology and Management* **31**, 245–253.

Abrams, M.D. & Mostoller, S.A. (1995) Drought-year gas exchange, leaf structure and nitrogen in contrasting successional tree species in high and low light environments. *Tree Physiology* **15**, 361–370.

Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**, 351–371.

Bazzaz, F.A. & Carlson, R.W. (1982) Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* **54**, 313–316.

Beatty, S.W. & Stone, E.L. (1986) The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research* **16**, 539–548.

Bormann, F.H. & Likens, G.E. (1979) *Pattern and Process in a Forested Ecosystem.* Springer, New York.

Canham, C.D. (1988) Growth and canopy architecture of shade-tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy gaps. *Ecology* **69**, 786–795.

Canham, C.D. & Marks, P.L. (1985) The response of woody plants to disturbance: patterns of establishment and growth. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett & P. S. White), pp. 197–216. Academic Press, New York.

Carpenter, S.B. & Smith, N.D. (1981) A comparative study of leaf thickness among southern Appalachian hardwoods. *Canadian Journal of Botany* **59**, 1393–1396.

Clebsch, E.E. & Busing, R.T. (1989) Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* **70**, 728–735.

Elder, J.H., Jr (1985) *Soil Survey of Spotsylvania County, Virginia.* USDA and Virginia Agricultural Experiment Station, Washington, DC.

Ellsworth, D.S. & Reich, P.B. (1992) Water relations and gas exchange of *Acer saccharum* seedlings in contrasting natural light and moisture regimes. *Tree Physiology* **10**, 1–20.

Fitter, A.H. & Hay, R.K.M. (1987) *Environmental Physiology of Plants*, 2nd edn. Academic Press, San Diego.

Foster, D.R. (1988) Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, south-western New Hampshire, USA. *Journal of Ecology* **76**, 105–134.

Fritts, H.C. & Swetnam, T.W. (1989) Dendroecology: A tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* **19**, 111–188.

Huenneke, L.F. (1983) Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bulletin of the Torrey Botanical Club* **110**, 170–175.

Kloeppel, B.D., Abrams, M.D. & Kubiske, M.E. (1993) Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open and understory environments. *Canadian Journal of Forest Research* **23**, 181–189.

Koike, T. (1988) Leaf structure and photosynthetic performance as related to the forests succession of deciduous broad-leaved trees. *Plant Species Biology* **3**, 77–87.

Latham, R.E. (1992) Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* **73**, 2129–2144.

Lorimer, C.G. & Frelich, L.E. (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* **19**, 651–663.

Mikan, C.J., Orwig, D.A. & Abrams, M.D. (1994) Age structure and successional dynamics of a presettlement-origin chestnut oak forest in the Pennsylvania Piedmont. *Bulletin of the Torrey Botanical Club* **121**, 13–23.

Oliver, C.D. & Larson, B.C. (1990) *Forest Stand Dynamics.* McGraw-Hill, New York.

Orwig, D.A. & Abrams, M.D. (1994a) Land-use history (1720–1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. *Canadian Journal of Forest Research* **24**, 1216–1225.

Orwig, D.A. & Abrams, M.D. (1994b) Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate *vs* gap-facultative tree species. *Canadian Journal of Forest Research* **24**, 2141–2149.

Poage, N.J. & Peart, D.R. (1993) The radial growth response of American beech *(Fagus grandifolia)* to small canopy gaps in a northern hardwood forest. *Bulletin of the Torrey Botanical Club* **120**, 45–48.

Reich, P.B., Abrams, M.D., Ellsworth, D.S., Kruger, E.L. & Tabone, T.J. (1990) Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology* **71**, 2179–2190.

Ross, M.S., Sharik, T.L. & Smith, D.W. (1982) Age-structure relationships of tree species in an Appalachian oak forest in southwestern Virginia. *Bulletin of the Torrey Botanical Club* **109**, 287–298.

Runkle, J.R. (1992) *Guidelines and sample protocol for sampling forest gaps.* USDA Forest Service Pacific Northwest Research Station PNW-GTR-283.

SAS Institute Inc. (1985) *SAS User's Guide: Statistics*, Version 5 edn. Cary, NC.

Tryon, E.H., Lanasa, M. & Townsend, E.C. (1992) Radial growth response of understory sugar maple (*Acer saccharum*) surrounding openings. *Forest Ecology and Management* **55**, 249–257.

US Geological Survey (1984) *Spotsylvania Quadrangle. 7 1/2" Series.* Reston, VA.

Wallace, L.L. & Dunn, E.L. (1980) Comparative photosynthesis of three gap phase successional tree species. *Oecologia* **45**, 331–340.

Walters, M.B., Kruger, E.L. & Reich, P.B. (1993) Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia* **94**, 7–16.

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