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Growth strategies of main trees and forest architecture of a *Fagus-Magnolia* forest in Florida, USA

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Abstract

Growth strategies of six species of trees are compared and used to analyze forest architecture. They included the overstory species *Fagus grandifolia*, *Magnolia grandiflora*, *Pinus glabra* and *Liquidambar styraciflua*, and the understory species *Ostrya virginiana* and *Ilex opaca*. The six species were abundant in Woodyard Hammock, an old-growth forest in northern Florida, USA. Height, stem diameter, crown projection and radial growth were measured in trees between 5 and 35 m tall. Three different, but non-exclusive, growth strategies were identified for the tree species: 'survival' (*Fagus grandifolia*, *Magnolia grandiflora*, *Ilex opaca*), 'occupy open space' (*Fagus grandifolia*, *Ostrya virginiana*, *Ilex opaca*), and 'reach above competitors' (*Liquidambar styraciflua*, *Pinus glabra*). In two transects (0.42 ha) and one quadrat (1 ha), heights of dominant trees were used to distinguish different phases of forest development, which were mapped. In the quadrat, juvenile canopy trees in the undergrowth were mapped. The combination of presence of different developmental phases, presence of juveniles in the undergrowth, growth strategies of main tree species, and disturbance regime was used to assess forest development in the near future. *Fagus grandifolia* is predicted to become the main dominant species, but the frequent hurricanes open the forest canopy and provide opportunities for understory species (*Ostrya virginiana* and *Ilex opaca*), and light-demanding overstory species (*Liquidambar styraciflua* and *Pinus glabra*).

Introduction

In the northern hemisphere, mixed evergreen-deciduous forests occur in a transition zone between deciduous broad-leaved forests of the cool temperate zone and evergreen broad-leaved forests of the subtropical zone (Braun 1950; Knapp 1965; Greller 1980; Platt & Schwartz 1990). In these warm temperate forests, *Fagus* is typically co-dominant with evergreen broad-leaved trees, usually members of the Magnoliaceae or Fagaceae. For example, *Fagus grandifolia* dominates with *Magnolia grandiflora* in hardwood forests in the coastal plain of the southeastern United States (Braun 1950; Blaisdell *et al.* 1974; Harcombe & Marks 1977, 1978; Platt & Schwartz 1990). Similarly, in the mountains of central Mexico, *Fagus grandifolia* subsp. *mexicana* Camp ex Shen forms mixed-species stands with evergreen *Quercus* spp. and *Magnolia schiedeana* Schlecht. (Miranda & Sharp 1950; Puig 1976; Rzedowski 1981; Peters 1995). In hardwood forests in mountains of southern China, *Fagus lucida* Rehd. et Wils. and *F. longipetiolata* Seem. dominate with *Castanopsis* spp., *Lithocarpus* spp. *Cyclobalanopsis* spp. and *Manglietia chingii* Dandy (Wu *et al.* 1980; Wang & Li 1986; Cao 1995).

Mixed evergreen-deciduous forests are rich in tree species (Marks & Harcombe 1975; Platt & Hermann 1986; Platt & Schwartz 1990). Poulson and Platt (1989) suggest that a diversity of overstory species can be maintained in *Fagus grandifolia - Acer saccharum* forests by species-specific differences in response to spatial and temporal differences in light regimes caused by variability in the scale, intensity, and frequency of disturbance. Platt & Hermann (1986) estimated that any given location on the forest floor of the *Fagus - Magnolia* forest in Woodyard Hammock in northern Florida, would, on the average, be directly below a canopy gap about once a century, but that increased illumination from partial openings and proximity to other gaps would result in increased light at any given point about once a decade. Moreover, at any given time, a wide range of gap sizes might be present in such forests.

Species of trees in such forests with highly heterogeneous light regimes might exhibit different growth strategies. For example, a tree that invested relatively more resources in height growth than in stem diameter and crown growth (i.e., a larger tree-height/ stem-diameter (*h*/*d*) ratio, but a smaller crown projection on the forest floor) might reach higher light levels in the forest canopy more quickly. In contrast, a tree that invested relatively more energy in crown expansion and stem-diameter growth than in height growth (i.e., a lower *h*/*d* ratio, but a larger crown projection) might occupy space in a gap more quickly.

We compared growth strategies of six species of trees abundant in Woodyard Hammock, an old-growth mixed species forest in warm temperate northern Florida, USA (Batista & Platt, in press), by comparing tree height, stem diameter, crown projection and stem-diameter growth rates. We examined four overstory species, two of which are deciduous [*Fagus grandifolia* and *Liquidambar styraciflua*], and two of which are evergreen [*Magnolia grandiflora* and *Pinus glabra*]. We also included two smaller-statured species that do not reach the forest canopy: the deciduous *Ostrya virginiana* and evergreen *Ilex opaca*. Below, only genus names of the six species are used. We used the comparative data on growth strategies to analyze forest architecture. These analyses enabled us to project whether current diversity of this old-growth forest is likely to be maintained over time (as projected by the disturbance dynamics theory, sensu Platt & Schwartz 1990) or whether there is any directional change towards a 'climax' with one or two dominant species (*Fagus* and *Magnolia*, sensu Braun 1950 and Quarterman & Keever 1962).

Study site and methods

Study site

Woodyard Hammock is an old-growth mixed species forest located within headwaters of the drainage basin of Lake Iamonia in northern Leon County, Florida (30°40′N). Situated about 40 m above mean sea level, the stand is located on a gentle (1°) south-facing slope. The species composition of the forest was described initially by Blaisdell *et al.* (1974). In 1978, a 4.5-ha plot was established in the central region of the forest where anthropogenic disturbance was minimal. Locations were mapped and diameters measured for all trees $\geq$ 2 cm dbh. Between 1978 and 1994, diameters have been remeasured and survival recorded every two years; these data have been used to describe stand structure and forest dynamics (Platt & Hermann 1986; Platt & Schwartz 1990). This forest was affected by hurricanes in 1919 and 1941 (E.V. Komarek, pers. comm.). The right eye of Hurricane Kate passed over Woodyard Hammock on November 21, 1985 (Batista & Platt in press).

Two transects, each 70 $\times$ 30 m, were established in the region of the 4.5-ha study plot in 1989. The site covered by the transects was not strongly affected by Hurricane Kate. Although crown parts of several overstory trees were broken, no treefalls were recorded in the transects. The transects were selected so that patches of forest trees were present that differed in composition of the dominant overstory species. We distinguished four patch types: 1) *Fagus* (F), 2) *Magnolia* (M), 3) other overstory tree species (O), and 3) understory tree species (U) (no overstory species present). Each patch was in one of four phases of development, i.e., innovation, aggradation, biostatic, and degradation. A patch in the innovation phase is dominated by tree seedlings or sprouts; in the aggradation phase by juvenile trees; in the biostatic phase by mature trees; and in the degradation phase by senescent trees (Oldeman 1990; Peters 1992).

We defined the difference between juvenile and mature trees using the relation between height, stem-diameter and crown-projection. For juvenile trees height growth towards the light is important, and for mature trees crown expansion is important. Whereas in juvenile trees height-growth rate is strong compared to stem-diameter or crown-expansion growth rate, in mature trees height-growth rate becomes relatively weak. The result is that the height/diameter ratio becomes smaller in mature trees. In this definition the transition between juvenile and mature trees is gradual. Overstory trees that had reached a height at which they could no longer be suppressed by neighbor trees, had reached the mature phase. This was used in determining the threshold for mature trees. The forest canopy is defined by mature trees of tall tree species.

In each transect all trees taller than 5 m were recorded, and, in a sub-transect (50 m $\times$ 4 m) in the center, all trees and shrubs from 0.5 m to 5 m tall were recorded. Along the center line in 28 quadrats (5 m × 5 m) cover was estimated for trees and shrubs from 0.5 m to 5 m tall and for vegetation below 0.5 m. Height, diameter (at 0.5 m height), position and crown projection were measured for all trees. Crown projections were determined by checking the positions of about 10 to 20 points, depending on the crown size, vertically below the edge of the crown on a grid laid out in the field.

Tree growth strategy

For the six tree species studied, we analyzed relations between height (*h*), diameter (*d*) and crown projection (*cp*) in individuals taller than 5m. Using empirical parameters a, b and c, regression analysis was carried out, and the multiplicative model gave the best descriptions for relationships between height & diameter ($d = a * h^b$), diameter & crown projection ($cp = a * d^b$), and height & crown projection & diameter ($d = a * h^b * cp^c$). With a one-tailed F-test, we tested whether *h-d*, *d-cp* and *h-cp-d* relations were significantly different by comparing residual sums of squares (RSS) from regression curves for individual species (I & II) and their combination:

$$F = [RSSI\&II-(RSSI+RSSII)]/2 \\ * \ 1/[(RSSI+RSSII)/(nI+nII-4)].$$

Coefficients of variation were calculated from the estimated values from the *h-d* and *h-cp-d* regression curves, which is the variance not explained by the regression curves. For the regression curves that estimated diameter from height and/or crown projection, the coefficient of variation was the mean square of residuals divided by the average diameter and multiplied by 100. The larger the coefficient of variation, the weaker is the predictability of the regression curve. A large coefficient of variation is also an indication of a larger flexibility within a tree species, e.g., variation among individuals in relative investment in height and diameter growth.

We compared radial growth of suppressed trees, released-growing juvenile trees and mature trees for the six tree species. A juvenile tree was defined as suppressed if more than 50% of its crown projection was covered by the crown of a taller tree.

Forest Architecture

In April and May 1985 (prior to hurricane Kate), a crown projection map was made of all recorded trees in a 1-ha section of the 4.5-ha mapped plot (see Platt & Hermann 1986 for methods). In this map, trees were divided into three classes based on heights of crowns: taller than about 25 m, about 15 m to 25 m tall, and less than about 15 m. We analyzed the presence of tree species in the three height classes (>25 m, 15–25 m, <15 m) of the 1-ha mapped quadrat and the two transects, and in the understory ($\geq$5 m) of the two transects.

The occurrences of the four patch types differing in the dominant species (*Fagus*, *Magnolia*, other overstory trees, and no dominant overstory trees) were determined on the crown-projection map, and the areas encompassed by these different patches were measured. To predict the direction of change in composition of different patch types in the near future (assuming no disturbance), we also measured the area under mature trees occupied by juvenile trees taller than 5 m.

Results

Tree Growth

Ranges of stem diameters and crown projections were much larger for overstory trees taller than 25 m than for smaller trees of these same species (Table 1). Most of the overstory trees taller than 25 m had reached a height at which they could not be suppressed by a neighbor tree. Hence, height thresholds used to separate juvenile trees from mature trees were set at 25 m for overstory trees (Table 2). The understory trees did not show a change in height-diameter relations with increasing height; an empirical threshold was set at 15 m.

While the ranges in heights and diameters of mature trees were similar for the overstory species, there were different ranges in the crown projections (Table 2). Both minimum and maximum crown projections for mature *Fagus* trees were much larger than those of the other three overstory species examined. The maximum crown projections for mature *Liquidambar* trees were much smaller than those of the other species. *Liquidambar* trees much larger than those in the transects are present in Woodyard Hammock; the largest has a diameter of 90 cm, a height of 35 m, and a crown projection of 150 m^2, putting the largest sizes of this

Table 1. Variances of diameters (d in cm) and crown projections (cp in m^2) for different height ranges in overstory tree species.

Height range (m)	*Fagus* d	*Fagus* cp	*Magnolia* d	*Magnolia* cp	*Pinus* d	*Pinus* cp	*Liquidambar* d	*Liquidambar* cp
5–9	5	63	--	--	--	--	0	1
10–14	12	56	--	--	--	--	2	2
15–19	31	310	28	9	--	--	0	0
20–24	26	133	63	159	13	9	15	12
25–29	234	1370	140	230	34	60	29	19
30–35	243	2205	222	570	102	784		

Table 2. Sizes ranges of mature trees, i.e., trees taller than h_{min} (bold numbers). For overstory species, this h_{min} is based on position in canopy and $h - d$ relationship. For understory species, this h_{min} is based on the h_{min}/h_{max} ratio observed in overstory species.

Species	Height (m) h_{min}	Height (m) h_{max}	Diameter (cm) range		Crown projection (m^2) range	
Fagus	**25**	35	31	97	45	229
Magnolia	**25**	33	29	91	15	89
Pinus	**25**	35	22	71	*	92
Liquidambar	**25**	35	32	43	10	22
Ostrya	**15**	21	14	24	11	68
Ilex	**15**	24	15	35	7	35

Table 3. One-tailed F-test analyzing whether residual sums of squares from regression curves of a population are significantly larger than those of subpopulations. Significance level: - p>0.05; * p<0.05; *** p<0.001.

Subpopulations	sign. level *h-d*	*d-cp*	*h-cp-d*
overstory versus understory	*	*	**
Fagus & *Magnolia* versus *Lquidambar* & *Pinus*	***	*	***
Fagus versus *Magnolia*	–	***	***
Liquidambar versus *Pinus*	–	–	*
Ostrya versus *Ilex*	***	***	***

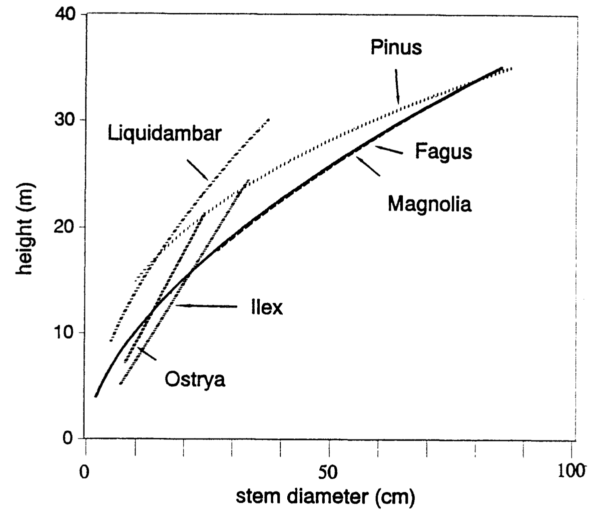

Fig. 1. Regression curves for height (h) and stem-diameter (d) relations: $d = a * h^b$. Although d is the 'dependent variable' in the models it is presented on the x-axis for comparison with other studies.

species in the ranges of the largest-sized trees of the other overstory species. Maximum heights for mature trees of understory species were smaller than threshold heights of mature trees of overstory species.

Regression curves for height-diameter (*h-d*), diameter-crown projection (*d-cp*), and height-crown projection-diameter (*h-cp-d*) differed significantly among the species (Table 3). Exception were *h-d* curves, which were similar for *Fagus* and *Magnolia*, and for *Liquidambar* and *Pinus*. Also, *d-cp* curves were similar for *Liquidambar* and *Pinus*.

Fitted *h-d* regression curves for *Fagus* and *Magnolia* were lower than the curves for *Pinus* and *Liquidambar*, indicating that the latter species had larger increases in height per unit increase in diameter (Fig. 1). The regression for *Ostrya* and *Ilex* were virtually straight lines, again underlining the difficulty of setting a height threshold for mature trees of these understory species. The *d-cp* relation analyses produced correlations that were strong for *Fagus*, less strong for *Magnolia* and *Pinus*, and weak for *Liquidambar*, *Ostrya* and *Ilex* (Table 4).

The *h-cp-d* curves were compared with the h-d curves from Fig. 1 (Fig. 2). Reference *h-cp-d* curves were calculated for crown projections of 5, 10, 25, 50, 100 and 200 m^2. The *h-d* curve crosses these reference *h-cp-d* curves. If these reference *h-cp-d* curves were far apart, like in *Fagus* or *Magnolia*, then cp changes gradually with *h-d*. If the *h-d* curve runs more parallel to the reference curves, then *cp* size is not related to *h* and *d*. If the *h-d* curve ascends quickly across reference curves for large crown projections, then the tree species tends to have large crown projection with low

Table 4. Coefficients of determination (R^2, %) and coefficients of variation (V, %) for regression analysis of *h-d*, *d-cp*, and *h-cp-d* relationships. For *Fagus* and *Liquidambar*, juvenile trees were analyzed separately.

Relationship:			*h-d*		*d-cp*		*h-cp-d*	
Coefficients:	Species	N	R^2	V	R^2	V	R^2	V
All trees	*Fagus*	54	87	33	87	37	92	26
	Magnolia	36	47	23	63	56	66	19
	Pinus	12	83	23	68	59	97	10
	Liquidambar	22	83	18	46	43	83	18
	Ostrya	34	67	19	38	52	76	16
	Ilex	36	81	21	39	43	86	18
Juvenile trees	*Fagus*	36	91	20	79	35	94	18
	Liquidambar	18	81	14	37	45	81	14

height and/or diameter. For a given height, *Fagus* trees tended to have larger crown projections than the other trees (Fig. 2). *Pinus* and *Magnolia* trees had similar *h-cp-d* relations and *Ostrya* trees tended to have a larger crown projections than *Ilex* trees. In *Liquidambar*, crown projections tended to be smallest among canopy species, and were less related to tree height and stem diameter (Table 4). However, only a limited range of sizes of *Liquidambar* were examined, so a different pattern might occur if larger trees had been examined. The coefficient of variation for *h-d* and *h-cp-d* was largest in *Fagus* among all trees, indicating large variation among *Fagus* trees (Table 4).

Radial growth was larger for mature trees than juvenile trees, regardless of whether those latter trees were released or suppressed (Table 5). Standard deviations were large, however. Among suppressed and released growing juvenile trees, *Fagus* had the largest radial growth rates. Among mature trees, *Pinus* had the largest radial growth rates, followed by *Liquidambar* and then *Fagus*. *Magnolia* had the slowest growth rates of the overstory species. Unless suppressed, *Magnolia* was still growing faster than the understory tree species, even those that were released.

Forest architecture

In the quadrat and the transects, the woody species were divided into four groups: overstory *Magnolia* dominant in the canopy, overstory *Fagus* dominant in the 15 to 25 m height layer, other overstory species, and understory species (Table 6; Fig. 3). Overstory tree species had a maximum height of more than 25m, and for understory tree species this was less than 25m. *Magnolia* and *Pinus* occurred almost exclusively in the canopy, while *Liquidambar* and *Fagus* were present in many different strata. *Ilex* and *Ostrya* were among the dominant species in the understory.

In both the quadrat and the transects, the four distinguished patch types comprised 88% of the area on the average. The remainder, about 12%, was in innovation to very early aggradation, with no trees at least 2cm dbh and/or 5 m tall. The understory species patch comprised 5% of the area on the average; this area was split between aggradation and biostatic phases. Many canopy gaps were dominated by understory species, which were often present as large trees without any overstory species present. Each of the three overstory-tree patch types, which together comprised 83% of the cover, was divided into three different phases: early aggradation (trees 5 m to 15 m tall), late aggradation (trees 15 m to 25 m tall), and biostatic (trees > 25 m tall) (Fig. 4). Early aggradation phases (3%: *Fagus* 2%, *Magnolia* 0%, others 1%) comprised less of the cover than late aggradation phases (12%: *Fagus* 6%, *Magnolia* 1%, others 5%). Most of the overstory-tree patches were in the biostatic phase (68%: *Fagus* 17%, *Magnolia* 31%, others 20%).

The projected replacement of canopy trees in the one-ha quadrat and in the transects by juvenile trees between 5 and 25 m tall is presented in Table 7. Half of the area under the canopy was without juvenile trees taller than 5 m. In this part of the one-ha quadrat there will be space for new trees to become established after disturbance. About one-fourth of the area beneath overstory trees contained juvenile trees of *Fagus* that ranged in size from 5 to 25 m in height. Only 4% contained *Magnolia* (all large subcanopy trees) and 7% contained juvenile trees of other overstory species. About 15% of the area contained understory tree species; death of overstory species in these areas probably would result in the understory species forming an patch dominated by mature trees of these species. Because *Magnolia* comprised almost half of the overstory patches, it appears likely that death of large trees of this species are much more likely to result in *Fagus* or understory species becoming the dominant species rather than replacement by other *Magnolia*.

The 0 to 5 m height layer of the areas containing the transects was rather open (c.f. Braun, 1950; Platt & Hermann, 1986; Platt & Schwartz, 1990). Trees and shrubs from 0.5m to 5m tall covered less than 10% of the area, and also the vegetation below 0.5 m covered less than 10% of the area. Between 0.5 and 5 m shrubs

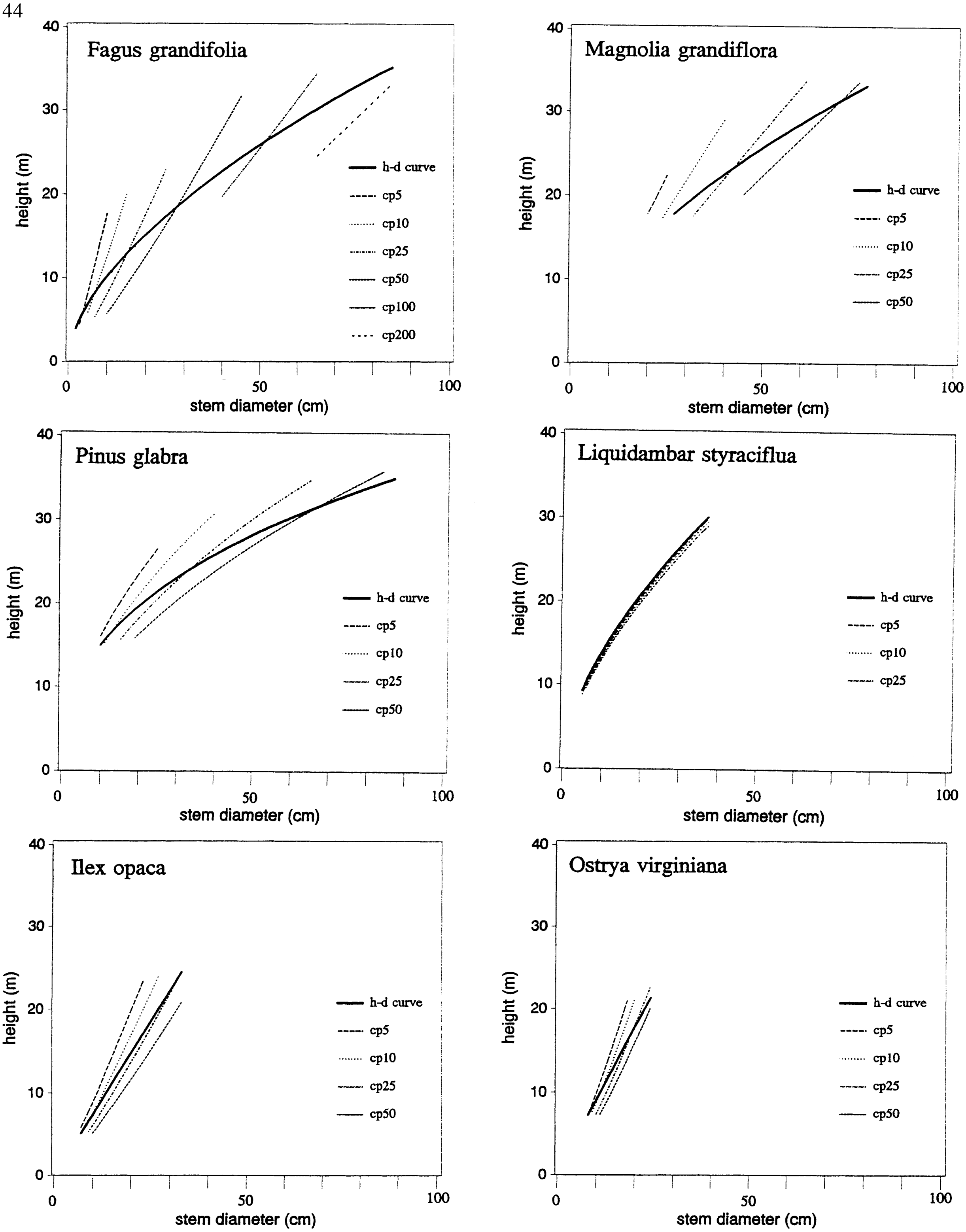

Fig. 2. Regression curves showing the height (h) and stem-diameter (d) relations for given crown projections (cp): $d = a * h^b * cp^c$. For reference the height-diameter regression lines from figure 1 are given. Although d is the 'dependent variable' in the models it is presented on the x-axis for comparison with other studies.

Table 5. Average annual radial growth measured in tree census (quadrat, 1978–1986). Standard deviations and sample sizes are given in parentheses.

	Juvenile trees suppressed (mm)		Juvenile trees released growing (mm)		Mature trees (mm)	
Fagus	0.85	(0.62; 95)	1.51	(0.91; 17)	2.17	(0.76; 8)
Magnolia	0.41	(0.44; 8)	1.16	(2.12; 2)	1.04	(0.61; 54)
Pinus	– –		1.34	(1.52; 11)	3.06	(1.46; 14)
Liquidambar	0.31	(0.50; 53)	0.84	(0.59; 21)	2.26	(0.93; 25)
Ostrya	0.49	(0.44; 16)	0.94	(0.70; 14)		
Ilex	0.30	(0.39; 23)	0.31	(0.00; 1)		

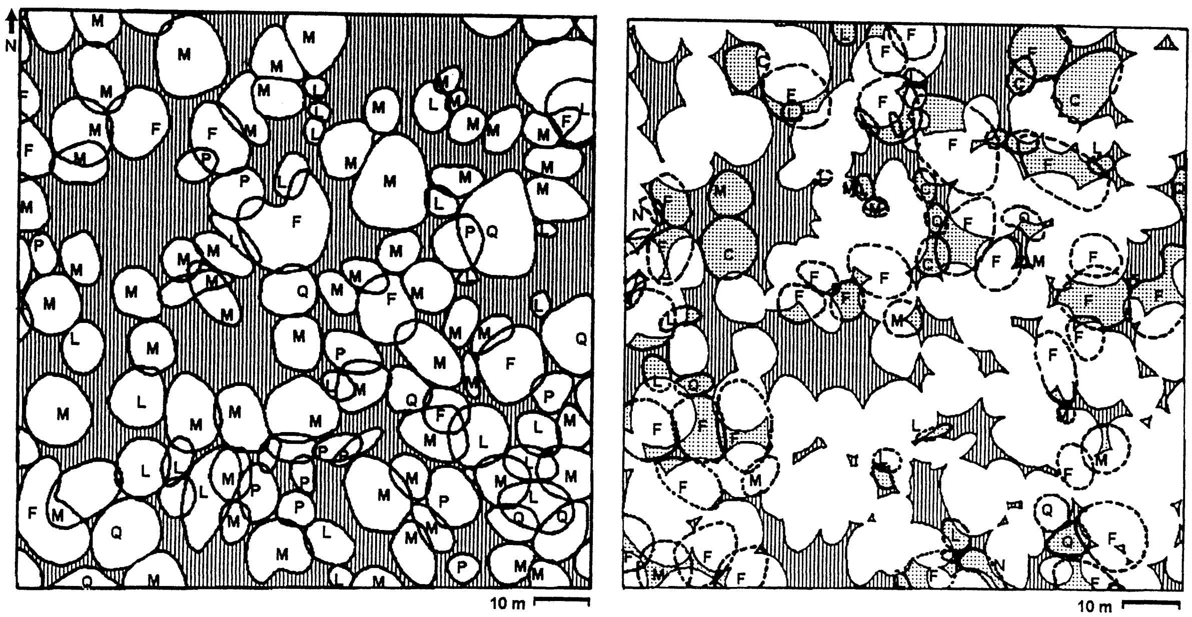

Fig. 3. The 1-ha quadrat showing stem position (letters) and crown projection of different tree species in different phases of development. Left (>25 m): mature overstory trees; Right (15–25 m): understory trees and juvenile overstory trees (broken lines if underneath mature overstory trees). The mature overstory trees are white (= biostatic phase), canopy gaps are hatched and juvenile overstory trees in the canopy gaps are dotted (= aggradation phase). F = *Fagus grandifolia*; M = *Magnolia grandiflora*; P = *Pinus glabra*; L = *Liquidambar styraciflua*; N = *Nyssa sylvatica*; Q = *Quercus* spp.; C = *Carya* spp.

were not abundant and overstory and understory trees were about equally important, with *Pinus* and *Ostrya* dominant. The cover of juveniles of tree species below 0.5 m was low; it was highest for *Fagus* (1%) and *Pinus* (1%). No juveniles of *Magnolia* were present.

Discussion

Tree growth

Three different, but non-exclusive growth strategies can be identified for the tree species in Woodyard Hammock: 'survival' (*Fagus grandifolia*, *Magnolia grandiflora*, *Ilex opaca*), 'occupy open space' (*Fagus grandifolia*, *Ostrya virginiana*, *Ilex opaca*), and 'reach above competitors' (*Pinus glabra*, *Liquidambar styraciflua*).

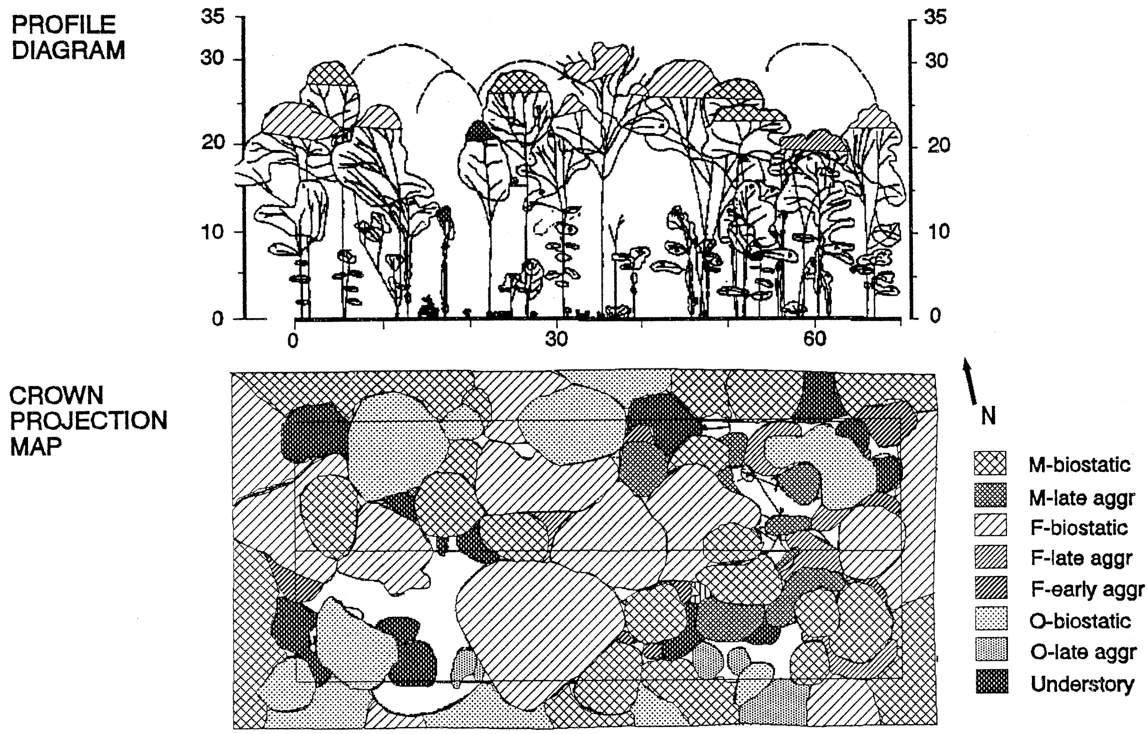

Fig. 4. Transect showing the four patch types (M, F, O, U) and their different phases of development. Above is a profile diagram and below is a crown projection map of the same area. In the crown projection map, the rectangle shows the outer boundary of the 70 × 30 m transect. Patches are dominated by *Magnolia* (M), *Fagus* (F), other overstory tree species (O) or understory tree species. Where present, three phases of development (biostatic, late aggradation and early aggradation; aggr = aggradation) are indicated for these four patch types.

Growth patterns of *Fagus* were more flexible than those of other species (Table 4). *Fagus* exhibited greater diameter growth relatively to height growth (low h/d) and larger horizontal crown expansion compared to the other species. Also, when suppressed, *Fagus* had the largest diameter growth rates. These characteristics suggest a strategy of survival in the shade and growth into open space containing increased light levels. A somewhat similar growth pattern appears to characterize large *Magnolia*, which also had a low h/d ratio. Small trees of this species were not sampled, however.

Our data suggest that both *Liquidambar* and *Pinus* have growth patterns that involve rapid height growth, with trees reaching the forest canopy before the crown expands and substantial increments occur in trunk diameter (Figs 2 & 3). Both *Pinus* and *Liquidambar* have high h/d ratios when trees are small, suggesting rapid growth to tall tree size. In this study, the h/d ratio of *Pinus* decreased rapidly with increasing size, suggesting a shift to greater diameter growth as trees reached the canopy. This was observed as mature *Pinus* trees had much larger diameter-growth rates than juvenile *Pinus* trees (Table 5). Large *Liquidambar* trees were not sampled in the current study, but small *Liquidambar* trees had high h/d ratios, with relatively little diameter growth. Fowells (1965) also indicated that *Liquidambar* saplings may grow fast in height, more than 1.5 m in the first 5 years. Root sprouts of *Liquidambar* have especially rapid initial height growth (W.J. Platt, personal observation). Both *Pinus* and *Liquidambar* had smaller coefficients of variation than *Fagus*, which indicates that they were less flexible in the relative allocation of energy to height, diameter and crown growth. Although *Pinus* and *Liquidambar* have similar growth patterns, they have very different life histories. *Liquidambar* is very long lived, reaching ages of about 300 yr (Platt 1984). *Pinus* tend to be much shorter lived (Hirsh & Platt 1981). Also, *Liquidambar* is clonal, and genets may be very old.

Table 6. Species presence (number of stems) in different height layers in the quadrat and the two transects (1.42 ha).. Groups are F. *Fagus*, M. *Magnolia* and O. other overstory tree species, U. understory species.

Height layer species	>25 m	15–25 m	<15 m	group
Fagus grandifolia Ehrh.	30	41	132	F
Magnolia grandiflora L.	87	19	1	M
Pinus glabra Walt.	23	5	0	O
Liquidambar styraciflua L.	28	30	42	O
Nyssa sylvatica Marsh.	8	5	3	O
Quercus shumardii Buckl.	2	1	0	O
Quercus nigra L.	2	0	6	O
Carya glabra (Mill.) Sweet	2	1	0	O
Quercus michauxii Nutt.	3	7	62	O
Carya cordiformis (Wangenh.) K. Koch	0	8	2	O
Oxydendrum arboreum DC	0	1	4	O
Acer rubrum L.	0	0	1	O
Ilex opaca Ait.	0	18	33	U
Cornus florida L.	0	0	14	U
Ostrya virginiana (Mill.) K. Koch	0	22	66	U
Carpinus caroliniana Walt.	0	0	66	U
Total	121	71	334	

Table 7. Percentage of area under the canopy occupied by juvenile trees between 5 and 25 m tall. F = *Fagus*; M = *Magnolia*; O = other overstory tree species. (+ = < 0.5%)

	1-ha quadrat			transects			Total
Patch type	F	M	O	F	M	O	
Understory:							
Fagus							
$15 \leq H < 25$m	2	14	9	3	7	4	19
$5 \leq H < 15$m	+	5	4	1	1	1	6
Magnolia							
$15 \leq H < 25$m	1	+	2	3	0	1	4
$5 \leq H < 15$m	0	+	+	0	0	0	+
Other overstory species	0	4	4	1	1	4	7
Understory tree species	+	4	1	9	9	7	15
No juvenile trees	11	27	12	31	10	7	49
Total	14	54	32	48	28	24	100

The understory species, *Ostrya* and *Ilex*, had low diameter growth and large h/d ratios. When suppressed, *Ilex* often dies back and regrows from basal sprouts (W.J. Platt, personal observation). Neither *Ostrya* nor *Ilex* showed a clear decrease in h/d ratio with increasing height. Other understory trees may exhibit decreases in h/d ratios, e.g., in tropical rain forests in Surinam where the h/d ratio was less than 50 in 22 m tall trees of the understory *Eschweilera*, while *Couratari* and *Quala* trees formed a canopy at about 40 m height (Schulz 1960). *Ilex* and *Ostrya* appear to be fugitive rather than persistent subcanopy species (Platt & Schwartz 1990). Their recruitment and growth are associated with canopy gaps (W.J. Platt, unpublished data), but in these gaps they usually become overgrown by taller canopy trees. Therefore, *Ilex* and *Ostrya* may not remain very long in a mature phase, even if they reach this phase.

Regeneration and dominance

The old-growth forest in Woodyard hammock can be considered a mosaic of patches in different phases of development. Although *Magnolia* trees were most frequently the dominant tree in biostatic patches, they were rare in aggrading patches. *Fagus* and light-demanding species dominated both early and late aggrading patches; continued recruitment by these species into the forest canopy is likely to occur. Early aggrading patches covered less area of the forest than late aggrading, but this is compensated by older juvenile trees having larger crown projections. Not all light-demanding species were equally present in the different phases. *Pinus* was only dominant in biostatic phases, while *Liquidambar* dominated both early and late aggradation, as well as biostatic phases. Because the *Pinus* and *Liquidambar* entered the canopy following the 1941 hurricane, the differences in size distribution and patch phases dominated by each species appear attributable to faster height growth of *Pinus* and/or larger size at the time of the hurricane.

Few juvenile *Magnolia* trees were present in Woodyard Hammock (Blaisdell *et al.* 1974; Platt & Hermann 1986), although seedlings are abundant (Platt & Hermann 1986). Apparently the *Magnolia* seedlings recorded by Blaisdell *et al.* (1974) did not survive and form juvenile trees. Prior to Hurricane Kate, *Magnolia* seedlings were present in plots both beneath the canopy and in gaps (Platt & Hermann 1986), but seedlings survived no more than 3–4 yr in either microhabitat. Almost no seedlings were found for several years after Hurricane Kate; but this appeared to be a result of extensive damage to large *Magnolia* trees and, hence, reduced seed production (Platt, pers. obs.). Platt and Hermann (1986) and Platt and Schwartz (1990) suggest that higher light intensities than those occurring at the current time in Woodyard Hammock may be needed for growth and survival of seedlings, which would result in *Magnolia* being less shade tolerant than *Fagus*. In contrast, Glitzenstein *et al.* (1986) suggest that *Magnolia* may even be more shade-tolerant than *Fagus*, because only small saplings of *Magnolia* showed net recruitment and substantial height growth in the understory of the mixed *Fagus-Magnolia* forest of Weir Woods in Texas. Furthermore, *Magnolia* does not always occur above *Fagus* in the canopy; in other forests *Magnolia* may be present in all layers or even as juveniles in forest dominated by *Fagus* (Quarterman & Keever 1962; Harcombe & Marks 1977; Glitzenstein *et al.* 1986; White 1987). In Weir Woods, Harcombe and Marks (1978) found low densities of *Magnolia* and *Fagus* saplings, but small juveniles of both species were present. This means that tolerance of understory conditions is not very high in *Magnolia* seedlings. Because *Magnolia* is evergreen, seedlings may photosynthesize and profit from warm days in the winter when the leaves are off the deciduous canopy trees. A difference in abundance of deciduous trees in the canopy may cause some difference in survival of *Magnolia* seedlings.

The relationship between *Magnolia* and *Fagus* in Woodyard Hammock, which involves at least some degree of shade tolerance in both species, appears different from the relationships between *Fagus* trees and evergreen broad-leaved species in other forests. While *Fagus grandifolia* appears capable of recruitment beneath an largely evergreen overstory, large disturbances appear necessary for establishment of *Fagus* in China (Peters 1992) or *Nothofagus* in Chile (Veblen 1985). In these other forests, evergreen broad-leaved trees are present in the canopy or understory, and the *Fagus* species tend to be less shade tolerant than these evergreen broad-leaved species. In contrast, in the southeastern United States, *Fagus* appears capable of reaching the canopy beneath *Magnolia*.

In the undergrowth of biostatic patches, juvenile trees of *Fagus* were most abundant, whereas light-demanding species were uncommon (Table 7). *Fagus* occurred underneath all tall tree species, but the light-demanding species were more common beneath *Magnolia* or other light-demanding trees. On the other hand, in a substantial part of the area beneath biostatic patches there were few or no juvenile trees (Tables 8 & 9), which suggests that only after gap formation are light-demanding species likely to grow into the small tree category (see Platt & Hermann 1986). Because *Fagus* dominated most of the aggradation phases and was most frequent in the undergrowth of biostatic phases (Table 7), we would expect *Fagus* to increase in dominance in the forest canopy, replacing *Magnolia* trees that die.

Pinus seedlings survive only if they are located in gaps (Platt & Hermann 1986). Juveniles in gaps survive for several years, but do not reach the forest canopy in those gaps unless there is a second disturbance that results in increased light levels (Platt & Schwartz 1990). As a result of increased light levels following Hurricane Kate, *Pinus* became the most abundant tree species in the layer below 5 m (Batista & Platt, in press). The age distribution of *Pinus* reveals that most trees of this species in Woodyard Hammock regenerated in gaps created by a hurricane in 1941 (Hirsh & Platt 1981). The age distribution of *Liquidambar* also indicates that the most recent successful establishment of this species occurred after the hurricane of 1941 (Platt 1984).

The future relative importance of light-demanding tree species is uncertain. The higher ratio of aggradation area to biostatic area in the mapped plot suggests that light-demanding overstory species will increase in importance relative to more shade-tolerant overstory tree species (Table 7). Conversely, the paucity of regeneration by light-demanding species in the biostatic phases (Table 8) suggests a decrease in importance, but the presence of large areas in biostatic phases without any juvenile trees indicates that light-demanding overstory species might regenerate following large disturbances. Changes in species abundances following Hurricane Kate reveal that while all species have been recruited during the past seven years, *Pinus* and *Ostrya* have been recruited in vastly disproportionate numbers (Batista & Platt, in press). The disturbance regime is clearly an important factor determining the future composition of the forest stand. The relatively large (6%) annual probability of hurricanes along the Florida panhandle coastline (Simpson & Lawrence 1971; Van der Leeden & Troise 1974) favors creation of large canopy gaps in which regeneration of light-demanding overstory species can occur. The most recent disturbance prior to 1985, the hurricane of 1941 resulted in establishment of both *Pinus* and *Liquidambar* (Hirsh & Platt 1981; Platt 1984).

The combination of forest architecture and disturbance regime makes an assessment of future forest development possible. In the absence of large disturbances, like hurricanes, *Fagus* will become more dominant relative to *Magnolia*. Frequent hurricanes open space, providing the opportunity for understory species and light demanding species like *Pinus* and *Liquidambar* to become established and grow into the forest canopy.

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