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Shoot damage effects on regeneration of maples (*Acer*) across an understorey-gap microenvironmental gradient

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Summary

1 We measured whole-plant survival, frequency of leader (mainstem terminal bud) damage among survivors and growth responses of intact and damaged juveniles of three *Acer* species over 3 years along a microenvironmental gradient represented by the understorey and two sizes of artificially created canopy gaps in central Massachusetts, United States of America.

2 For all species combined, survival decreased while the frequency of leader damage among survivors increased across the gradient of microsite exposure. *Acer rubrum* L. (red maple) showed the highest survival (65–93%) but also very high leader damage (80–97%). *Acer pensylvanicum* L. (striped maple) showed fairly high survival (81–93%) in all but the most exposed microsites (24–36%) and had the lowest leader damage overall (17–44%). *Acer saccharum* Marsh. (sugar maple) was intermediate for both survival (25–86%) and leader damage (55–96%).

3 Growth differed significantly among sites and species. Both intact and damaged plants showed greater growth in gaps than in understorey, particularly in large gaps. For most growth variables in most microsites, *A. pensylvanicum* ≥ *A. rubrum* > *A. saccharum* when plants were intact, but *A. rubrum* ≥ *A. pensylvanicum* > *A. saccharum* when damaged. Species differences in growth varied among sites, with large gaps producing more pronounced effects than small gaps and understorey for both intact and damaged plants.

4 Growth recovery was inversely related to leader damage frequency among species, and thus at least partially offset the effects of damage on net growth across the populations.

5 The microsite- and species-specific responses to leader damage may influence gap regeneration and forest composition. *A. pensylvanicum* may be favoured by its regrowth advantage over *A. rubrum* and *A. saccharum* in the understorey, where damage is likely to occur during prolonged pre-gap periods. In contrast, *A. rubrum* shows a decisive advantage over its congeners in regrowth in the centres of large gaps, where the probability of a juvenile tree capturing canopy gap space is highest.

Key-words: canopy gaps, forest regeneration, microclimate, shoot damage, *Acer*

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Introduction

Significant advances have been made over the last decade in understanding the principles of morphological and architectural variation among tree species (Kohyama & Hotta 1990; Brown & Sommer 1992; Ford 1992; Niinemets 1996), including the roles they play in determining species success in response to different forest environments (e.g. Pickett & Kempf 1980; Newell *et al.* 1993) and the mechanisms of physiological and architectural plasticity shown by early- vs. late-successional species or understorey- vs. large-gap specialists (Walters & Field 1987; King 1991; Riddoch *et al.* 1991; Bazzaz & Miao 1993; Walters *et al.* 1993; Kitajima 1994; DeLucia *et al.* 1998; Huante & Rincon 1998). However, most studies have either eliminated shoot damage (e.g. glasshouse and chamber experiments) or have not measured it separately and included it in the interpretation of growth response. Under natural regeneration processes few juvenile trees reach reproductive maturity without experiencing damage or death in portions of their woody tissues as a result of microclimatic extremes, chemical injury, physical breakage (by falling debris, animal

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contact, wind or snow/ice loads), herbivory, parasitism or pathogens (Clark & Clark 1989, 1991; Putz & Brokaw 1989; Holopainen 1990). Experiments imposing shoot damage on trees have focused more on simulated folivory (e.g. Heichel & Turner 1984; Nuñez-Farfan & Dirzo 1991; Cornelissen 1993; Krause & Raffa 1996) than removal of buds or stem tissue (Canham *et al.* 1993). Large mammals browse on woody tissue, but research has generally emphasized forage availability, herbivore diet preferences, spatial-temporal patterns of damage, and community-level impacts of browse on the regeneration stratum, rather than the details of recovery by individual plants (e.g. Nixon *et al.* 1991; Strole & Anderson 1992).

Although some species differences have been documented in the sprouting abilities of saplings and larger trees (Powell & Tryon 1979; Cooper-Ellis *et al.* 1999; Paciorek *et al.* 2000), we know relatively little about how recovery mechanisms following stem and bud damage to juvenile trees differ among species and across different forest environments. Such recovery, however, may play a significant role in overall forest regeneration, particularly through dieback and regrowth of seedlings and saplings, or through basal and lateral sprouting from larger trees that have been snapped, windthrown or cut (Hara 1987; Glitzenstein & Harcombe 1988; Putz & Brokaw 1989; Peterson & Pickett 1991; White 1991; Paciorek *et al.* 2000).

The probability of shoot damage increases when juvenile trees experience stress during major changes in their microenvironments, such as those caused by canopy gap formation. Juveniles of shade-tolerant overstorey species that have acclimated to the understorey (advance regeneration) may encounter stresses that exceed their physiological tolerance ranges or increase their susceptibility to herbivore or pathogen attack. Photoinhibition, leaf dehydration and senescence, and decreased seedling survival and growth have been documented following gap formation for juveniles of many tree species, particularly shade-tolerant taxa (e.g. Tubbs 1977; Hibbs *et al.* 1980; Turner & Newton 1990; Osunkoya & Ash 1991; Kamaluddin & Grace 1992; Naidu & DeLucia 1998). Advance regeneration may give established juveniles a competitive advantage over other species that colonize gaps only after the gaps have formed (Bicknell 1982; Brown & Whitmore 1992; Palik & Pregitzer 1991; Clinton *et al.* 1994; Tuomela *et al.* 1996), but this depends on whether the advance-regenerated trees are able to adjust to the markedly different gap environments. The breadth of the microenvironmental gradient from understorey to gap, and the degree of environmental shift experienced by advance-regenerated juveniles, increase with gap size (e.g. Sipe 1990; Brown 1993). Significant microenvironmental gradients may also occur within gaps, with the greatest exposures to high irradiances and temperatures skewed towards the north or south gap edges, especially at higher latitudes (Canham *et al.* 1990). Gap-phase regeneration processes are important in many temperate and tropical forest types, and differences among co-occurring species in their susceptibility and/or response to shoot damage across understorey and gap environments may therefore affect forest regeneration.

We conducted a 3-year study of the response of three shade-tolerant species of maple (*Acer*) to the understorey and to experimentally created, cleared gaps of two sizes (75 m^2, 300 m^2) in central Massachusetts, United States of America (USA) (Sipe & Bazzaz 1994, 1995). We asked the following questions:

1 Do the frequencies of whole-plant survival and leader (mainstem terminal bud) damage vary among microsites across the understorey-gap microenvironmental gradient?

2 Do the three types of sites (understorey, small gap, large gap) differ overall in growth by intact or damaged individuals?

3 Do the three species differ overall in growth by intact or damaged individuals?

4 Do differences among species in growth vary across or within sites for intact or damaged individuals?

5 What is the overall significance of leader damage and recovery across the entire populations of intact and damaged individuals?

6 What are the implications of these patterns for gap regeneration and forest composition in this system?

Methods

STUDY SITE AND SPECIES DESCRIPTION

We conducted our study in a mixed deciduous-conifer stand at the Harvard Forest in central Massachusetts (42°30′ N, 72°15′ W). The stand originated after clear-cutting in 1890 and is relatively mature. It is dominated by *Quercus rubra* L., *Acer rubrum*, *Fagus grandifolia* Ehrh., *Betula allegheniensis* Britton., and *Betula papyrifera* Marsh., with scattered individuals of *Betula lenta* L., *Prunus serotina* Ehrh., *Fraxinus americana* L., *Pinus strobus* L. and *Tsuga canadensis* (L.) Carr. The site exhibits modest local relief (*c.* 5 m), with three main areas of slightly higher ground that are separated by narrow, shallow ravines with small intermittent streams. The soils are derived from granitic glacial till and are dominated by coarse stony loams that are well-drained, shallow, prone to drought and generally infertile.

The geographical distributions of our three study species (*A. pensylvanicum* L., striped maple; *A. rubrum* L., red maple; *A. saccharum* Marsh., sugar maple) overlap across much of the eastern USA, including New England, the Great Lakes Region, and higher elevations in the Appalachians as far south as Georgia (Burns & Honkala 1990). They co-occur in greatest abundance in moist forests where small gaps dominate the disturbance regime. They are prominent throughout New England, including the Harvard Forest (Sipe 1990). Some germination and establishment may occur after disturbance, especially for *A. rubrum*, but advance regeneration is thought to be more important for canopy recruitment and/or reproductive maturity in all three species (Marquis 1982; Canham 1985; White 1991).

A. saccharum is one of the most shade-tolerant North American broad-leaved species, and it is the largest and longest-lived of our species (Burns & Honkala 1990). *A. saccharum* saplings can survive extended understorey suppression and respond well to small canopy gaps (Barden 1983; Canham 1985; Ellsworth & Reich 1992a,b), but may not perform as well in larger silvicultural gaps (Tubbs 1977). *A. rubrum* is intermediate in longevity and mature size, is widely thought to be less shade-tolerant than *A. saccharum*, and responds well to larger canopy openings (Wallace & Dunn 1980; Burns & Honkala 1990; White 1991; Clinton *et al.* 1994). *A. pensylvanicum* is primarily a subcanopy tree that can reach reproductive maturity in the understorey. Opinions differ on its shade tolerance, ranging from very tolerant (Hibbs 1979; Lei & Lechowicz 1990) to intermediate (Bormann & Likens 1979). Wilson & Fischer (1977) suggested that it should be able to respond well to small canopy gaps, and rapid growth by *A. pensylvanicum* has been documented in whole-watershed clearcuts by (Bicknell 1982) and in a catastrophic blowdown by Peterson & Pickett *et al.* (1995).

GAP CREATION AND SEEDLING PLOTS

Three large gaps (300 m^2, 16 m × 24 m), three small gaps (75 m^2, 8 m × 12 m) and three understorey sites were positioned across the 4-ha study area in 1986. All gaps were elliptical and the long axis was orientated east–west to generate the greatest diurnal differences in within-gap microclimatic patterns. The gap sizes and shapes (length : width ratio, 1.5) were chosen as characteristic of the most commonly encountered gaps in mature forests of eastern North America (Barden 1983; Runkle 1985). All gap and understorey sites were located on the higher topographic positions with minimal to no slope. Gaps were located where overstorey trees could be felled to create canopy openings with the desired size and shape, and the understorey sites were then positioned to maximize distance from gaps. Although the locations of the understorey sites were not randomized, all were under full canopy and were representative of the diversity of overstorey composition in the study area.

Five 1 m × 2 m seedling plots were positioned in each site a year before gap creation. In future gaps, plots were placed in the centre and where the subcardinal axes (NW, NE, SW, SE) would intersect the expected elliptical margin of the gap. Careful selection of gap-maker trees and controlled felling resulted in all subcardinal plots being on or very close to the vertically projected gap canopy edges. Plots in the understorey sites were spaced to match the large gap dimensions.

No seedling plots contained coarse woody debris. Woody root competition was prevented by slicing the plot margins vertically to a depth of 25 cm using flat spades to sever roots from surrounding trees, and chopping the soil to the same depth inside the plots with mattocks. Care was taken to minimize inversion of the soil profile. Small and large woody roots, herbaceous and shrubby perennials and any rock fragments > 2.5 cm diameter were removed. The surface layer (*c.* 5 cm deep) was raked and smoothed across the plots to homogenize the upper soil. The plot margins were re-spaded annually in late spring, and the plots were weeded by hand regularly during the growing season. These treatments were deemed necessary to quantify non-competitive responses of our species to the basic patterns of microclimates generated by gap geometry, given the potential effects of heterogeneous soil conditions and low site replication ($n = 3$) on statistical power (Sipe & Bazzaz 1994, 1995).

After leaf senescence, naturally established seedlings (15–30 cm tall, 4–20 years old, 720 per species) were collected with a small soil ball (typically < 15 cm deep) from various understorey locations in the Harvard Forest. All seedlings were unbranched with an intact leader. The seedlings from various source locations were non-systematically randomized across the 45 prepared plots and transplanted with bare roots over a 3-week period in October 1986. Each plot contained 12 seedlings of each species, randomized by position in four rows of nine seedlings each, with 25-cm spacing in all directions. All seedlings were grown in the understorey for 18 months (October 1986–April 1988) to allow adjustment to transplant shock before the first exposure to high irradiances in gaps in the 1988 growing season. Survival over the pre-gap period was > 95% (Sipe & Bazzaz 1995).

We created all gaps between 25 September and 2 November 1987. Plot margins were surrounded with cordwood, so that no seedlings were damaged during tree felling. All boles and branches were then removed, and all regrowth in the gaps was cut back regularly to 0.5 m high in mid-summer each year to maintain exposed ground-level conditions. Naturally falling leaf and fine woody litter were left in place in plots, but larger branches were removed if they fell on seedlings. We could therefore measure the effects of gap size and geometry on spatial microenvironmental patterns and species responses near the forest floor without the confounding effects of structural heterogeneity in the downed and recovering gap community. Extrapolation of the results to natural, uncleared gaps must be done with caution.

The entire study area was protected from herbivory by white-tailed deer (*Odocoileus virginianus*) by installing a five-stranded electric fence around the perimeter and maintaining the fence year-round. Deer were never seen in the area during the experiment, although a few hoof prints were found inside the fence on one occasion late in the study.

The pre-gap age (terminal bud scar counts), height (to the nearest 0.1 cm with a metre stick) and basal diameter (to the nearest 0.01 mm with precision dial calipers 1 cm above root collar) of each seedling were measured in September 1987. Survival and growth were recorded at the end of the 1988 and 1989 growing seasons. We analysed eight growth variables. The first three were for plant status at the end of the experiment in 1989: (i) stem height (highest living meristem, regardless of whether it was of leader or branch origin); (ii) number of leaves per plant; and (iii) total leaf area per plant (calculated through regressions of area on laminar length). The remaining five variables were for cumulative growth across the entire 1987–89 period: (i) total leader growth (terminal extension by the dominant vertical axis, either the original leader or the tallest new one following loss of the original); (ii) total branch growth (terminal extension by all lateral axes); (iii) total stem growth (leader plus branches); (iv) net stem height change; and (v) net basal diameter change. Negative values were possible for the last two variables because only live stem axes were measured and a stem resulting from regrowth following dieback could be smaller than its dead precursor. The analysis of cumulative growth included all survivors as of October 1989. Data were grouped for analysis according to whether the original leader at the time of transplanting in fall 1986 was still intact 3 years later. A seedling that lost its original leader but then developed a new, vigorous one was still classified in 1989 as damaged. Positive leader growth could occur on a stem that lost its original leader as measurements of leader extension were made on the tallest new leader emerging as a lateral or basal sprout.

Differences among the three site types and among species in survival (numbers of stems) and leader loss percentages (transformed by square root arcsin) were analysed using two-way analysis of variance (ANOVA). The data for growth variables could not be normalized, so Kruskal–Wallis one-way ANOVA was performed separately on intact vs. damaged plants for growth differences among sites overall (species lumped), among species overall (sites lumped), and among species for each combination of leader damage status and site (e.g. damaged plants in small gaps). Post-hoc multiple comparisons were done using pairwise Dunn's tests.

MICROCLIMATIC MEASUREMENTS

We measured microclimates simultaneously in all seedling plots in one large gap (291 m^2), one small gap (74 m^2) and one understorey site every other week across the 1988 and 1989 growing seasons (Sipe 1990). Photosynthetic photon flux (PPF) was measured with a home-built silicon photodiode quantum sensor on a 30-cm arm extending out over each seedling plot at a height of 50 cm. The quantum sensors were based on the design by Biggs *et al.* (1971), as modified by R. Pearcy and R. Chazdon (personal communication). Air temperature was measured 40 cm above the ground on the main support column with a WVU-7 ventilated psychrometer (Delta-T Instruments, Cambridge, England). Surface soil temperature (1 cm) and 'deep' soil temperature (15 cm) were measured directly below the PPF sensor with 107 and 107B thermistors, respectively (Campbell Scientific, Logan, UT, USA). The 15-cm depth encompassed the primary rooting zone for our seedlings. One microclimate station was placed midway along the north edge of each seedling plot position, and the five stations at each site were connected to a 21X datalogger and AM32 channel multiplexer (Campbell Scientific). The sensors were scanned at 10-s intervals and data were stored as 10-min means continuously over 4–5-day periods. Average microclimatic patterns across the season were calculated for constant 12-h intervals symmetric around solar noon on 5 clear days and 5 overcast days, spread as evenly as possible between May and September 1988. Means and standard errors were calculated separately for the 5 clear days, 5 overcast days, and the combined set of 10 clear and overcast days. We also checked for consistency of microclimatic patterns among the replicates of each gap size by occasionally measuring microclimates simultaneously in the three large gaps or three small gaps.

In addition to direct measurements of microclimate, we also calculated for each gap the expected durations of diurnal and seasonal direct beam radiation on clear days for each plot position. Predictions of these durations were made by making detailed measurements of gap geometry, including the heights of gap edge trees, and modelling solar movement diurnally and seasonally. The predictions were tested by mapping the locations of ground-level shade arcs in each gap at various times during the day and season.

A consideration of gap geometry, solar movement and seedling plot positions suggests there should be at least seven distinct microenvironments across the three site types. Both gaps should show a south to north gradient of increasing irradiance, with large gaps experiencing much greater levels overall (Canham *et al.* 1990). The small gap south microsites, although quite shaded, should be brighter than the full understorey due to increased diffuse radiation penetrating the gap (Nakashizuka 1985). The small gap north microsites should receive greater total radiation than the large gap south microsites due to direct beam striking the former and not the latter, especially near the summer solstice. As a result, seasonal means and maximums for irradiance, air temperature and soil temperature should vary from least to most exposed in the following order: understorey, small gap south, small gap centre, large gap south, small gap north, large gap centre and large gap north.

Our microclimate data suggest that there were indeed seven distinct microsites along the understorey-gap gradient (Table 1). Hereafter, mean clear day PPF values are used as a convenient index of microsite 'exposure' as variation in incident radiation largely drives changes in other microclimatological variables, such as air and soil temperature and relative humidity. However, we

Table 1 Microclimatological data across the experimental understorey-gap gradient. Direct beam data refer to how long beam radiation could potentially shine on each plot position across the growing season (seasonal duration) and on days near the summer solstice (diurnal duration), and are averaged across all three replicates for each site type. The remaining variables are means for continuous data (10-s sample interval) on 5 clear, 5 overcast or 10 combined clear and overcast 12-h sample days spread across the growing season in one replicate set of large gap (LG), small gap (SG) and understorey (U) sites. N = north plots, C = centre plots, S = south plots. Surface soil = – 1 cm, deep soil = – 15 cm. PPF = photosynthetic photon flux (μmol m^{-2} s^{-1})

Site/plot	Seasonal direct beam (week)	Diurnal direct beam (h)	Mean PPF (clear days)	Mean PPF (combined days)	Duration PPF > 800 (clear days) (min)	Mean air temp (clear days)	Mean air temp (combined days)	Duration air temp > 25 °C (clear days) (min)	Mean surface soil temp (clear days)	Mean deep soil temp (clear days)
LG Mean			434	285	147	23.7	22.2	287	24.4	19.2
SG Mean			171	113	47	22.2	21.0	155	18.2	15.9
U Mean			50	33	1	21.2	20.4	128	17.2	15.7
LGN	27.6	5.0	612	375	237	24.8	22.6	340	24.2	18.6
LGC	12.7	3.8	565	365	216	24.8	23.0	314	25.2	20.3
LGS	0.2	0	190	154	23	22.1	21.4	318	23.4	19.1
SGN	5.5	2.1	280	164	93	22.8	21.4	172	19.4	16.4
SGC	0.3	0	144	106	16	22.4	21.1	157	19.1	15.9
SGS	0	0	74	64	1	21.5	20.6	138	16.2	15.4
U	0	0	50	34	1	21.2	20.4	128	17.6	15.7

note that doing so simplifies a more complex microclimatological pattern by ignoring diurnal and seasonal dynamics (including east–west differences in gaps), the occurrence of potentially damaging extreme irradiance and temperature values (e.g. durations of high PPF or temperature, Table 1), the temporally asynchronous effects of multiple environmental variables, and distinctive whole-site differences among the three site types on overcast days, all of which could influence leader damage or recovery (Sipe 1990).

Results

FREQUENCIES OF WHOLE-PLANT SURVIVAL AND LEADER DAMAGE ACROSS THE GRADIENT

Survival over the 3 years following transplant (1 year before and 2 years after gap creation) differed significantly overall among site types ($P = 0.001$, with understorey = small gaps > large gaps) and species ($P = 0.013$, *A. rubrum* > *A. saccharum* but neither significantly different from *A. pensylvanicum*), but there was no significant site–species interaction ($P = 0.126$). In contrast, percentage leader damage differed significantly among species ($P < 0.001$, *A. rubrum* > *A. pensylvanicum* > *A. saccharum*), but not for sites ($P = 0.14$) or the site–species interaction ($P = 0.73$).

For all species combined, survival decreased across the gradient while the frequency of leader damage among survivors increased (Fig. 1). Neither variable showed a consistent trend from the understorey to small gaps and to the south sides of large gaps. However, survival dropped and leader death increased dramatically in the centre and north plots of large gaps

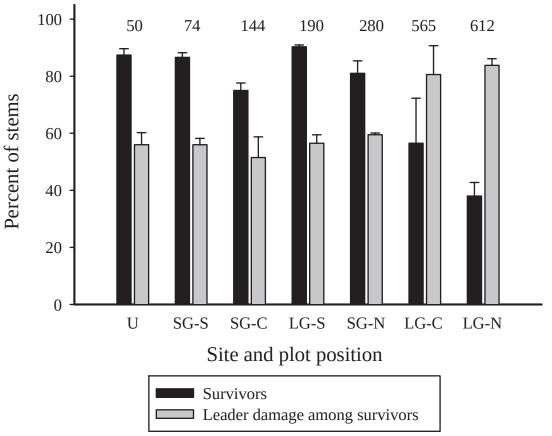

Fig. 1 Survival and frequency of leader damage (mean ± 1 SE) among survivors across all species for each site-plot combination. Site and plot abbreviations are as follows: U = understorey, SG = small gap, LG = large gap, N = north plots, C = centre plots, S = south plots. The numbers above the bars are mean seasonal clear day photosynthetic photon flux for each microsite (μmol m^{-2} s^{-1}; see Table 1). Sample sizes are three for the centre plots, six for the north and south plots, and 15 for the understorey plots.

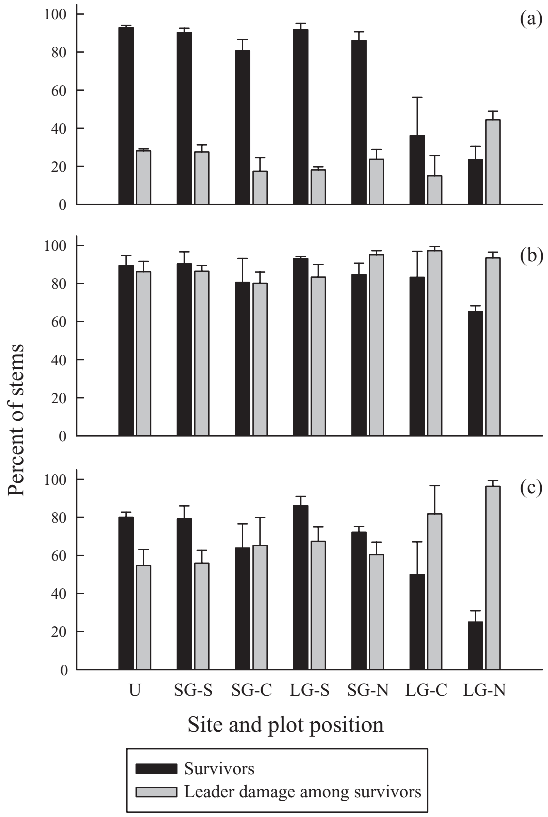

Fig. 2 Survival and frequency of leader damage (mean ± 1 SE) among survivors for (a) *A. pensylvanicum*, (b) *A. rubrum* and (c) *A. saccharum*. Site-plot sequence and PPF values same as in Fig. 1.

(when PPF > 300 mmol m^{-2} s^{-1}). Interestingly, survival and leader death tended to parallel each other across the less exposed half of the gradient (PPF < 200 μmol m^{-2} s^{-1}), but exhibited an inverse relationship across the more exposed half. The three species showed distinctive patterns of survival and leader damage (Fig. 2). *A. pensylvanicum* exhibited high survival (81–93%) and low leader damage (17–28%) in the five least exposed microsites, and even when survival dropped to 24% in the most exposed microsite, leader damage rose to only 44% (Fig. 2a). *A. saccharum* showed fairly high survival (64–86%) but significant leader damage (55–67%) in the less exposed microsites. It survived poorly (25%) and showed nearly complete leader damage (96%) in the large gap north microsites (Fig. 2c). *A. rubrum* survived best (65–93%), particular in the large gap centre and north, but leader damage was very high (80–97%) across the entire gradient (Fig. 2b).

There was a significant linear relationship between percentage survival and percentage leader loss for all species combined ($P = 0.005$; Fig. 3a) and for *A. saccharum* ($P = 0.004$; Fig. 3b), but not for *A. pensylvanicum* ($P = 0.40$) or *A. rubrum* ($P = 0.38$).

SITE DIFFERENCES IN GROWTH

There were highly consistent results across the three main site types for all growth variables (Table 2; Figs 4, 5). Intact large gap and small gap plants were similar and both showed greater growth than intact plants in the understorey. Damaged plants generally had more leaves, greater branch growth and greater total stem growth (leader plus branch) than intact plants in all three sites, but damage reduced stem height and total leaf area in both small gaps and understorey. Damaged plants exhibited negative net height change in all sites. Though damaged plants showed net positive increases in basal diameter, these increases were substantially lower than for intact plants.

In general, large gap plants recovered better than plants in either small gaps or understorey (Figs 4, 5). Understorey plants recovered better than small gap plants for stem height, leaf number, leader growth and total stem growth, but the sites were similar for total leaf area, net height change and net basal diameter change.

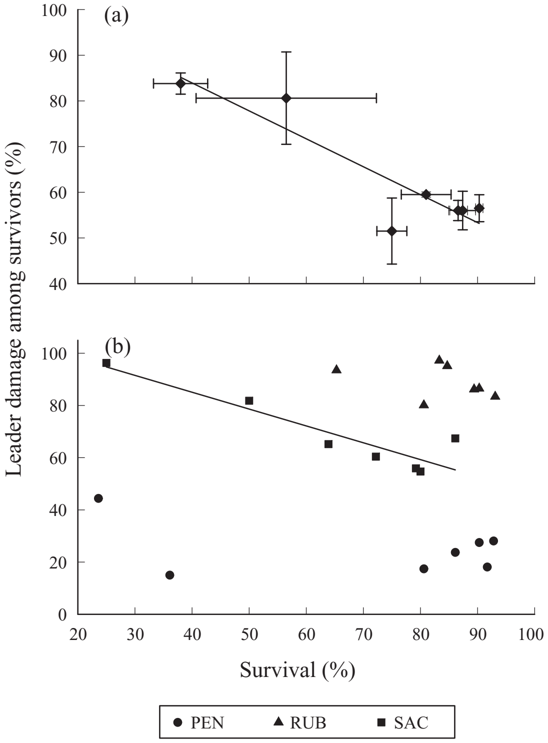

Fig. 3 Leader damage vs. survival across the seven microsites in the experimental understorey-gap gradient for (a) all species combined and (b) each species. The lines indicate significant linear regressions for all species combined ($P = 0.005$, $R^2 = 0.82$) and for *A. saccharum* ($P = 0.004$, $R^2 = 0.83$). Regressions for the other species were not significant. PEN = *A. pensylvanicum*, RUB = *A. rubrum*, SAC = *A. saccharum*. $n = 3$ for all data points. Error bars in (a) are ± 1 SE.

SPECIES DIFFERENCES IN GROWTH

There was a strong pattern among the species in overall growth by intact plants (Table 2; Figs 4, 5), with *A. pensylvanicum* ≥ *A. rubrum* > *A. saccharum* for all variables except number of leaves and branch growth (*A. rubrum* > *A. pensylvanicum* ≥ *A. saccharum*). All species showed reductions in net height and basal

Table 2 Differences among sites and species for growth by intact and damaged seedlings, based on Kruskal–Wallis one-way ANOVA and Dunn's multiple pairwise comparisons. LG = large gap, SG = small gap, U = understorey, pen = *A. pensylvanicum*, rub = *A. rubrum*, sac = *A. saccharum*, NS = no significant difference at $P = 0.05$. Site and species rank comparisons are in order of declining mean values, with differences significant at $P = 0.05$ for each pairwise test. Ranks for non-significant differences are shown in parentheses to indicate the trends

		Site comparisons		Species comparisons	
Variable	Leader status	*P*-value	Pattern	*P*-value	Pattern
Stem height	Intact	< 0.001	LG = SG > U	0.516	(rub > pen > sac)
	Damaged	0.138	(LG > SG > U)	< 0.001	pen = rub > sac
No. leaves	Intact	< 0.001	LG = SG > U	< 0.001	rub > pen > sac
	Damaged	< 0.001	LG > SG > U	< 0.001	rub > pen > sac
Total leaf area	Intact	< 0.001	LG = SG > U	< 0.001	pen > rub = sac
	Damaged	< 0.001	LG > SG = U	< 0.001	pen > rub > sac
Leader growth	Intact	< 0.001	LG = SG > U	< 0.001	pen = rub > sac
	Damaged	0.044	LG = SG = U	< 0.001	rub > pen = sac
Branch growth	Intact	< 0.001	LG = SG, SG = U	< 0.001	rub > pen = sac
	Damaged	< 0.001	LG = SG > U	< 0.001	rub > pen > sac
Total stem growth	Intact	< 0.001	LG = SG > U	< 0.001	pen = rub > sac
	Damaged	< 0.001	LG = SG > U	< 0.001	rub > pen > sac
Net height change	Intact	< 0.001	LG = SG > U	< 0.001	pen = rub > sac
	Damaged	0.262	(LG > SG > U)	< 0.001	pen = rub > sac
Net basal diameter change	Intact	< 0.001	LG = SG > U	< 0.001	pen > rub > sac
	Damaged	< 0.001	LG = SG > U	< 0.001	rub = pen > sac

diameter for damaged plants in most sites, despite increases in the number of leaves, branch growth and total stem extension.

However, the species did not behave in parallel across the three site types for any of the eight growth variables, implying complex species-specific patterns of response to leader damage (Figs 4 and 5). *A. rubrum* demonstrated the greatest growth recovery, particularly in large gaps where it showed much larger gains or smaller losses than either of the other species for all eight variables. For example, damaged *A. rubrum* in large gaps showed striking relative increases in number of leaves (> 60%), total leaf area (> 250%), total stem growth (> 250%) and net basal diameter change (> 120%) compared with intact plants. *A. pensylvanicum* was generally intermediate in recovery ability but tended to recover better than both *A. rubrum* and *A. saccharum* in the understorey. *A. saccharum* was mostly unresponsive to the gradient for both intact and damaged plants. The clearest demonstration of spatial differences in recovery by the three species occurred for net height growth by damaged plants (Fig. 5c), which declined for *A. rubrum*, increased for *A. saccharum* and showed little change for *A. pensylvanicum* across the gradient.

Discussion

SPATIAL PATTERNS AND LEVEL OF MORTALITY

Strong spatial patterns in both whole-plant mortality and leader damage among survivors occurred across our experimental understorey-gap gradient. The lowest survival and the greatest leader damage occurred in the most exposed portions of the large gaps (centre and north plots). Several studies have noted significant mortality and/or spatial patterns of mortality in gaps (Howe 1990; Ashton *et al.* 1995; Gray & Spies 1996) but mortality has generally not been compared with measured microenvironmental patterns. The exception is Brown & Whitmore (1992), who found that mortality of three advance regenerant dipterocarp species increased across a 10–1500 m^2 range in gap size, representing an eightfold range of mean daily photosynthetically active radiation and a 10–20% increase in maximum daily air and soil temperature. Higher mortality in the centre and on the north sides of our large gaps is consistent with the occurrence of dramatically higher radiation loads in these microsites, especially diurnal and seasonal durations of direct beam radiation (Table 1; Canham *et al.* 1990). Mean daily photosynthetic photon flux (PPF) in the seedling plots increased over 10-fold across the gradient, from 34 to 375 $\mu mol\ m^{-2}\ s^{-1}$, including marked differences within both large and small gaps. The irradiance gradient was even broader on clear days, ranging from 50 to 612 $\mu mol\ m^{-2}\ s^{-1}$. Furthermore, the mean daily PPF values do not reflect the very high irradiances experienced by the north and centre plots in large gaps for several hours on clear days in June and July (> 1600 $\mu mol\ m^{-2}\ s^{-1}$; Sipe 1990).

We stress that our artificial, cleared gaps produced greater exposure of small seedlings to high irradiances and temperatures than would often be the case in most natural treefall gaps, where downed boles, crowns and upgrowth would partially ameliorate increases in ground-level irradiance and air and soil temperatures. Gradual gap formation due to progressive standing death would also provide more time for advance

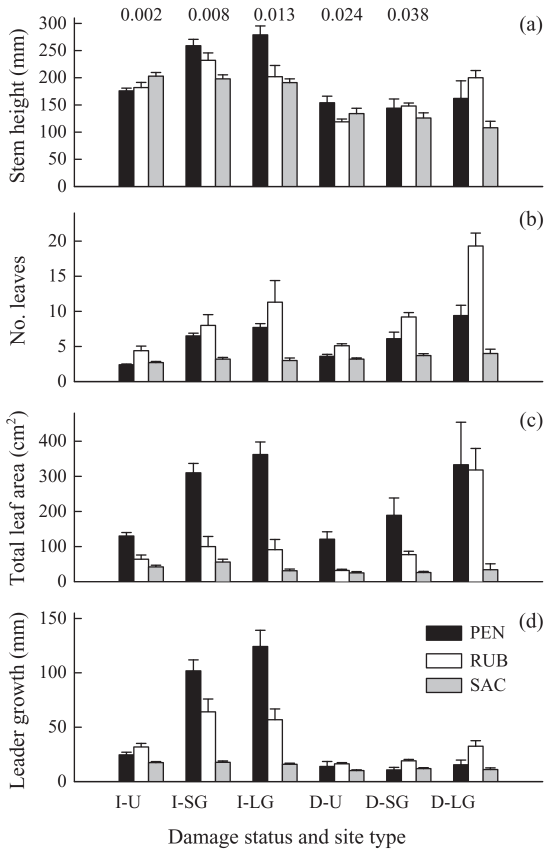

Fig. 4 Growth responses (mean ± 1 SE) by intact and damaged plants for all species in each site: (a) absolute stem height at the end of 1989; (b) total number of leaves per plant in 1989; (c) total leaf area per plant in 1989; (d) leader growth over 1987–89. I = intact plants, D = damaged plants. Plot and species abbreviations as in Figs 1 and 3, respectively. $n = 3$ for all data points. Species comparisons within each damage-site category were significant at $P < 0.0001$ based on Kruskal–Wallis one-way ANOVA, unless otherwise indicated by a different P-value above a group of bars. See Table 2 for results of Kruskal–Wallis ANOVA on sites overall and species overall.

regenerated juveniles to adjust to more slowly increasing irradiance and temperatures (Krasny & Whitmore 1992). Conversely, our data may be applicable to canopy openings caused by logging, which often exposes juveniles to a greater degree than natural treefall gaps (e.g. Marquis 1982).

We are aware of no published data specifically focused on naturally occurring levels of shoot damage and regrowth for juvenile trees in north-eastern USA forests. Our observations in the Harvard Forest system over the last 16 years suggest that the majority of juveniles (perhaps > 60%) experience some leader loss in the understorey before they reach 0.5 m in height.

AGENT OF MORTALITY

Although leader damage for survivors was clearly greater in the north half of large gaps (> 80%), there was still a surprising level of leader damage (50–60%) in all other microsites, including the understorey (Fig. 1). The reason for extensive leader death in our study was not obvious. Deer removed a few buds from three *A. rubrum* in one large gap centre plot later in the study after these plants had already experienced leader damage and were exhibiting extensive regrowth. There was no evidence of damage by small mammalian herbivores. Several researchers have measured gap-related patterns of insect herbivory or pathogen activity (Nuñez-Farfan & Dirzo 1988, 1991; Howe 1990; Khan & Tripathi 1991). Although we noted several types of insect damage sporadically on foliage and stems, none was clearly related to the leader damage. In most cases, the terminal meristems died in place with no removal or external signs of damage by any identifiable source.

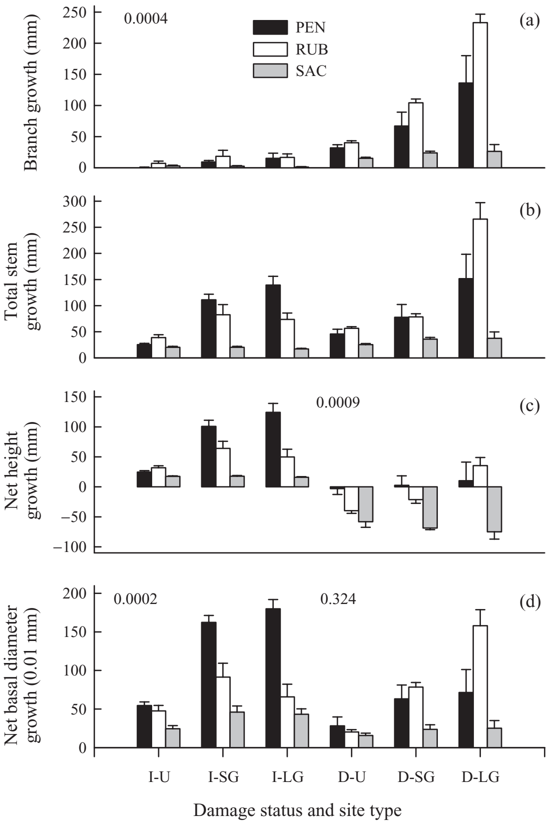

Fig. 5 Cumulative growth responses (mean ± 1 SE) by intact and damaged plants for all species and sites: (a) branch growth over 1987–89; (b) total stem growth (leader plus branches) over 1987–89; (c) net stem height change over 1987–89; (d) net basal diameter change over 1987–89. Abbreviations and statistics as in Fig. 4.

A pathogen could have been partially responsible. We observed abrupt leaf wilting and necrosis in the centre and north plots of large gaps during a warm, wet period in July 1988, particularly by *A. pensylvanicum* and *A. saccharum* (Sipe 1990). Small gap north plots were also affected, though much less so, but there was no wilting in the understorey. Marquis (1982) also noted browning and some leaf loss by exposed seedlings of these three species during midsummer in a large clearcut in Pennsylvania. The spatial pattern of wilting generally corresponds to the plot-specific and species-specific data on whole-plant mortality and leader damage among survivors in large gaps (Fig. 1), suggesting a link, but does not account for the substantial levels of leader damage in the understorey.

A number of non-pathogenic physiological processes could be involved, including transplant shock, thermal load, photodestruction (e.g. UV-B exposure), dehydration, and extreme high or low temperatures. Some transplant shock must have occurred, especially since the dormant seedlings were bare-rooted when transplanted. However, seedling survival in the understorey during the 18 months prior to gap formation was > 95%, and survival in the understorey was consistent across pre-gap and post-gap years (Sipe & Bazzaz 1995), implying that transplant shock was not serious. Our diurnal microclimatic and gas-exchange data suggest that high irradiances, air temperatures and water stress could have acted synergistically to dehydrate and overheat developing meristem tissues in large gaps in late summer, particularly on the well-drained soils in our site (Sipe & Bazzaz 1994, 1995). While this may explain the high levels of leader damage in the most exposed microsites, it does not readily account for the substantial levels of leader damage in the understorey. Thus the explanation for extensive leader damage in our study system remains unclear and may involve several factors, such as an interaction between physical stress and pathogen activity.

SITE DIFFERENCES IN GROWTH AND RECOVERY

Numerous studies of gap regeneration show that tree densities and growth rates increase with gap size (Popma & Bongers 1988; Brown & Whitmore 1992; Clinton *et al.* 1994) and with increasing exposure across locations within natural gaps (Ashton *et al.* 1995; Gray & Spies 1996). This is generally due to higher irradiance and soil moisture, plus the tendency of fast-growing shade-intolerant species to colonize and dominate large gaps and gap centres.

None of these studies has distinguished performance by damaged vs. undamaged plants, but it is logical to predict that recovery of damaged plants should be greatest in places supporting fastest growth by intact plants. As a combined group, our three species recovered best in large gaps, the same sites that had the lowest survival, greatest leader damage and highest irradiances. Greater growth has also been linked to higher irradiance in gap microsites that experience higher mortality (Gray & Spies 1996) or herbivore damage (Khan & Tripathi 1991). In contrast, Canham *et al.* (1993) found that the effect of simulated browsing on seedling stem tips (including *A. rubrum*) was greater for seedlings growing in full sun compared with 8% full sun. They showed that, unlike the shaded plants, full sun plants were placing most of their stored carbohydrates in stems rather than roots, which resulted in a more detrimental impact on carbon balance when stems were removed.

SPECIES DIFFERENCES IN SURVIVAL, DAMAGE AND RECOVERY

We found strong differences among species in whole-plant survival and leader damage (Figs 1, 2), and in the relationship between survival and damage frequency (Fig. 3). Recent work on the importance of juvenile tree growth and mortality in forest dynamics has emphasized larger saplings (e.g. Kobe *et al.* 1995) and few data exist on comparative mortality for smaller juveniles of these species. However, our results agree with Houle (1991), who found greater survival by *A. saccharum* than *A. rubrum* for young seedlings in the understorey, and with Marquis (1982), who documented better survival by *A. pensylvanicum* (58%) and *A. rubrum* (55%) than *A. saccharum* (37%) after release of advance regenerant, small (6–9 cm tall) seedlings in a clearcut. There are no published data on leader damage for *Acer* except for Bartlett *et al.* (1991), who documented various sources of injury prior to whole-plant mortality in 1-year-old *A. saccharum* seedlings along a cliff-edge microenvironmental gradient. Terminal bud loss was highest along the cliff edge and declined towards the forest interior, but the authors indicate that the loss was probably caused primarily by herbivory and not by exposure.

Ecophysiological and growth differences have been reported for these species from both controlled environment and field studies and are discussed in Sipe & Bazzaz (1994, 1995), but no studies have compared growth by damaged vs. undamaged stems for more than one species. However, documented differences in shoot development and architectural flexibility, sprouting and shoot regrowth ability, and physiological plasticity, may help explain why *A. rubrum* was more capable of recovery from shoot damage than the other species, especially in large gaps.

First, these species differ in shoot development and architecture in ways that could be relevant to damage recovery. Sakai (1990) has distinguished three main branching models for Japanese species of *Acer*: (i) sympodial-spread, determinate extension; (ii) monopodial-spread, indeterminate extension; and (iii) elongate, indeterminate extension. *A. rubrum* clearly shows indeterminate shoot extension, while *A. saccharum* and *A. pensylvanicum* are partially determinate with limited neoformation and heterophylly (Critchfield 1971; Steingraeber 1982a). Indeterminate growth offers greater flexibility in shoot development during the growing season and may help explain the more extensive branching and flushing of sizeable numbers of new leaves by damaged *A. rubrum* during the two post-gap years. *A. pensylvanicum* appears to be sympodial in the understorey (Lei & Lechowicz 1990) and if the sympodial form was always determinate, this would limit responses to altered environments or damage. *A. pensylvanicum*, however, showed a dramatic transformation to rapid, elongate growth in our small gaps, including the south sides where irradiance levels were only slightly higher than in the understorey, implying significant plasticity in growth form and perhaps a greater ability to respond to leader damage in suitable environments (Wilson & Fischer 1977).

Brown (1993) and Endler (1993) have documented striking differences in spectral quality of radiation, including red : far-red ratios, between the understorey and gaps of different sizes, and it is possible that *A. pensylvanicum* is using spectral cues to alter shoot development. *A. saccharum* shows some architectural plasticity in response to irradiance levels (Steingraeber 1982b; Bonser & Aarssen 1994) and more responsiveness to canopy gaps than its frequent codominant, *Fagus grandifolia* (Canham 1988), but it is widely regarded as less flexible architecturally than *A. rubrum*, which shows substantial shifts in allocation to branches and leaves in response to increases in irradiance (Wallace & Dunn 1980).

Secondly, some evidence suggests that *A. rubrum* is more capable of sprouting or recovering from simulated bud/stem loss than the other species. Powell & Tryon (1979) showed that *A. rubrum* is better than *A. saccharum* at producing seedling sprouts from stems < 2 cm in diameter. Cooper-Ellis *et al.* (1999) found that *A. rubrum* was more effective than *A. saccharum* at resprouting from damaged larger trees or saplings (> 30 cm tall but < 5 cm in diameter at breast height) in response to a simulated blowdown at another site in the Harvard Forest. Many of the *A. rubrum* seedlings that lost leaders in our study died back completely and resprouted from basal buds, whereas *A. pensylvanicum* and *A. saccharum* were less likely to recover if the entire stem died back. The ability to maintain populations of dormant buds is essential to recovery from damage (Tuomi *et al.* 1994). For shade-tolerant tree species, which tend to be slow-growing, large numbers of suppressed lateral buds may accumulate on stems that are no more than 20–30 cm tall. However, data on interspecific differences in dormant bud populations and the ease with which they can be induced to grow are generally lacking (Critchfield 1971). Nor is the degree of apical dominance well documented for these species. Our results strongly suggest that dominance declines in the order *A. pensylvanicum* > *A. saccharum* > *A. rubrum* for both damaged and intact plants across all sites. Remarkably, damaged *A. rubrum* sprouted effectively and grew more than intact individuals in our large gap centres. This is consistent with Canham *et al.* (1993), who found that *A. rubrum* seedlings from which terminal stem segments were removed in the winter showed more shoot growth than the undamaged control plants in full sun treatments the following summer.

Thirdly, these species differ in overall ecophysiological plasticity. *A. rubrum* is fairly plastic in photosynthetic biochemistry and rates, response to water stress, biomass and dimensional growth rates, root : shoot allocation and shoot architecture across a wide range of irradiance (Wallace & Dunn 1980; Bazzaz & Miao 1993). Although *A. saccharum* shows some physiological adjustment to higher irradiance, most researchers have concluded that it survives and grows better in small gaps than large gaps (e.g. Barden 1983; Runkle 1990), perhaps due to conservative responses to water stress (Ellsworth & Reich 1992a,b), and is thus relatively insensitive to gap size beyond fairly small canopy openings (Canham 1985; McClure & Lee 1993). *A. pensylvanicum* shows better photosynthetic acclimation to the understorey than *A. saccharum* (Lei & Lechowicz 1990; Sipe & Bazzaz 1994). In our study, *A. rubrum* had consistently higher photosynthetic rates per unit leaf area than *A. pensylvanicum* and *A. saccharum* for the north and south plots of all three site types. However, *A. pensylvanicum* showed greater total photosynthesis when scaled to the shoot level in all but the large gap north plots, and shoot photosynthesis was correlated with greater growth by this species across most of the gradient (Sipe & Bazzaz 1994). It has been shown that leaf biochemistry and photosynthesis may change significantly when simulated defoliation occurs on species such as *A. rubrum* and *Quercus rubra* (Heichel & Turner 1984). We have no such data for damaged individuals of our species since we measured gas-exchange only on intact plants. However, if the relative pattern among species for photosynthetic rates per unit leaf area were to remain the same for damaged plants as for intact plants, then damaged *A. rubrum* would be likely to show higher shoot-level photosynthesis than either of the other species in large gaps, and this would also help explain its recovery advantage in microsites with higher irradiance.

POPULATION-LEVEL SIGNIFICANCE OF LEADER DAMAGE AND RECOVERY

Judgements about the impact of leader damage on regeneration of maples in our system must combine the frequencies of leader damage with its effects on growth compared with intact plants. Our data show that *A. rubrum* was more resilient in response to damage, with smaller declines or larger gains in growth than the other species in all sites (Figs 4, 5). However, the *A. rubrum* population suffered far more leader damage as a whole. *A. pensylvanicum* was less resilient to damage than *A. rubrum* but was more successful in avoiding leader loss in the first place. *A. saccharum* was intermediate on both accounts. Intact plants clearly grew better than damaged plants for the key variables of height and basal diameter increase with *A. pensylvanicum* > *A. rubrum* > *A. saccharum* (Fig. 5). Thus the greater resilience of *A. rubrum* was not able to overcome fully the widespread occurrence of leader damage, and *A. pensylvanicum* showed better performance as a population (Sipe & Bazzaz 1995).

MICROSITE-SPECIFIC RECOVERY AND IMPLICATIONS FOR FOREST REGENERATION

There are at least two ways in which microsite-specific differences in the occurrence of leader damage and regrowth among our species could influence future forest composition. First, juveniles of shade-tolerant trees may grow very slowly for decades in the shade before canopy gaps form overhead (Canham 1985; Runkle 1990; Clark & Clark 1992) and it is highly probable that some leader damage will occur during these long pre-gap periods (Clark & Clark 1989, 1991; Paciorek *et al.* 2000). Consequently, the ability to recover from damage in the shade will affect the status of juveniles and their ability to respond to gaps when the openings finally occur. Our data suggest that in the understorey *A. pensylvanicum* responds somewhat better following damage than *A. rubrum*, at least for the most important growth variables (total leaf area, net height change, net basal diameter change), and that *A. saccharum* fares poorly in this regard. Secondly, juvenile trees located in the centres of gaps have the greatest chance of capturing canopy space as the margins close in through lateral crown growth. Our data show that *A. rubrum* outperforms the other species in large gaps where it exhibits substantially higher survival (Figs 2 and 3) and growth (Figs 4 and 5) in spite of the greater frequency of leader damage. This is mostly due to its dramatic response in large gap centres (Sipe & Bazzaz 1995; also see McClure & Lee 1993). It may realize a competitive advantage in capturing canopy gap space over other less-resilient, advance-regenerating species when leader damage is extensive. Some studies have shown that released, advance-regenerant species may be overtopped by faster-growing pioneer species which can establish in large gaps, generally > 500 m^2 (e.g. Bicknell 1982; Tuomela *et al.* 1996), and the gap centre advantage for advance regenerants may therefore apply only to medium-sized gaps (200–500 m^2).

Our results may relate to the widely documented increase of *A. rubrum* in both the understorey and overstorey throughout the eastern USA (Abrams 1998). Palik & Pregitzer (1992) noted the importance of *A. rubrum* sprouts in achieving the overstorey in aspen-dominated stands in northern Michigan, while Abrams (1998) concluded that *A. rubrum* is a ‘super-generalist’ with a suite of traits that collectively give it an advantage in many sites and forest types in the absence of fire. To this list of traits we would add the ability to recover following leader damage caused by natural or anthropogenic disturbance.

Many forests in eastern North America are currently under heavy browse pressure due to high densities of white-tailed deer. Deer selectively remove terminal buds, may seriously suppress juvenile tree survival and growth, and may have substantial impacts on overstorey regeneration (e.g. Tilghman 1989; Gill 1992; Strole & Anderson 1992). Within forested landscapes, deer are often attracted to disturbed areas with greater densities of woody regrowth and available browse, such as canopy openings caused by logging. We are not aware of any published work comparing these three maple species in their susceptibility or response to deer browsing. We have observed browse damage on all three species in and around the Harvard Forest, but deer densities and browse pressure outside the fence in our study area were generally low compared to other areas in Massachusetts and the north-eastern USA.

Although the leader damage we documented was not due to deer, it does resemble deer browse in the selective death of meristems followed by sprouting from lateral or basal buds. If species-specific recovery following light deer browse (i.e. removal of one to several terminal buds) parallels the patterns we documented in our study, then deer pressure may favour *A. pensylvanicum* in the understorey and *A. rubrum* in larger gaps, at least for smaller juveniles (25–50 cm tall). The presence of deer is likely to increase the frequency of leader damage overall, placing even more significance on the role of damage and recovery processes and strongly suggesting that further research needs to be done on microsite- and species-specific responses to leader loss.

In summary, there were significant differences in spatial patterns of whole-plant survival and leader damage for advance-regenerated juvenile trees across the understorey-gap gradient, and these patterns differed for our three species of *Acer*. Damaged plants grew more in gaps than in understorey, particularly in large gaps, and the species differed significantly, with *A. rubrum* showing the greatest growth overall by damaged stems. Growth differences among species varied among sites for both intact and damaged plants, with large gaps producing the most pronounced species differences. Differences among species in recovery ability were offset by inverse patterns in the frequency of leader damage at the population level. Although *A. rubrum* was more resilient to damage, it suffered very high leader losses and was less successful as a population than *A. pensylvanicum*, which was much better at maintaining intact stems. Finally, some microsite-specific differences in growth recovery among these species may influence gap regeneration processes and forest composition, particularly through (i) cumulative damage and recovery episodes during prolonged pre-gap understorey periods, where *A. pensylvanicum* may have a modest advantage, and (ii) successful recovery in the centres of large gaps, where capture of canopy gap space is most likely to occur and where *A. rubrum* shows the most decisive advantage over its congeners.

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