AN EVALUATION OF MECHANISMS PREVENTING GROWTH AND SURVIVAL OF TWO NATIVE SPECIES IN INVASIVE BOHEMIAN KNOTWEED (Fallopia × bohemica, Polygonaceae)1

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Restoring native diversity to habitats dominated by invasive plants requires improved understanding of mechanisms that allow introduced plants to retain dominance. We used a factorial transplant experiment to assess whether light limitation, nutrient limitation, or allelopathic interference by Fallopia × bohemica reduces growth or survival of Eupatorium perfoliatum or Acer saccharinum. Increased light improved A. saccharinum performance but had no effect on E. perfoliatum growth. Increased light had no effect on A. saccharinum survival but improved E. perfoliatum survival. Activated carbon addition had short-term benefits allowing E. perfoliatum plants to grow for 4 wk and increased A. saccharinum leaf width but not biomass. Nutrient addition had no beneficial effect on transplants. These results in combination with the outcome of a cutting experiment suggest that F. × bohemica achieves competitive superiority primarily by limiting access to light. Species-specific effects and significant interaction effects particularly of light and activated carbon suggest additional mechanisms. Allelopathic interference or interaction with microbial soil organisms may contribute to the lack of native species in populations of F. × bohemica. Restoration efforts should combine selective F. × bohemica control with soil amendments (such as activated carbon) to assess their potential to facilitate return of native species to invaded habitats.

Key words: allelopathic interference; carbon addition; central New York; light limitation; plant invasions; Polygonaceae; transplant experiment.

Plant invasions can transform native ecosystems by changing ecosystem processes, disturbance regimes, plant community composition and diversity, nutrient dynamics, and associated food webs (Mack et al., 2000, 2001; National Research Council, 2002). The establishment of an introduced species per se does not necessarily constitute a problem, but negative impacts associated with the usually high abundance of an introduced species do threaten native communities (Levine et al., 2003). Effectively reducing or preventing such impacts is dependent upon our ability to first recognize mechanisms through which introduced species attain their ecological dominance (Levine et al., 2003) and then to develop appropriate management options to reduce invader abundance and impacts.

Recent evidence suggests that invasive species may impact community diversity through reductions in colonization rates of native plants, rather than through competitive replacement of established individuals (Yurkonis and Meiners, 2004). Low colonization rates may be the result of limited arrival of propagules (e.g., through dense canopies), reduced germination rates of available seeds (e.g., through shading, dense litter layers, or allelopathy), or through increased mortality of established seedlings or juvenile plants (e.g., through shading, other resource competition, allelopathy, or interactions with soil pathogens and mutualists) (Klironomos, 2002; Bais et al., 2003; Ehrenfeld, 2003; Reinhart et al., 2003; Reinhart and Callaway, 2004; Eppinga et al., 2006; Stinson et al., 2006). Facilitating the return of native species into ecosystems currently dominated by non-indigenous species (i.e., restoration) will depend upon the effectiveness of management options to reduce the competitive ability of the invader and elimination of any “legacy effects.” For example, mowing, herbicide treatment, or fire may reduce (aboveground) biomass of an invasive species, but if soils retain allelopathic compounds or pathogens, recruitment of native species may still be prevented. Such “legacy effects” may reduce the success of reseeding or transplanting juvenile native plants into areas currently dominated by invasive species (assuming recruitment limitation due to lack of seeds or propagules), even if the invader is selectively weeded, cut, or treated with herbicide to reduce competition for light, water, or nutrients.

We evaluated potential dominance mechanisms of an invasive species using the clonal herbaceous Fallopia × bohemica (Chrt and Chrtková), Bohemian knotweed (for synonyms and details of plant taxonomy, see Materials and Methods, Experimental organisms). This hybrid and its two parental species (Fallopia japonica and F. sachalinensis) are invaders of riparian and disturbed areas in North America and Europe where virtual monocultures develop (Shaw and Seiger, 2002; Pysek et al., 2003; Bimová et al., 2004). Successful restoration and the return of native flora and fauna into habitats currently dominated by F. × bohemica will be facilitated by a better understanding of the mechanisms allowing F. × bohemica to dominate and exclude native species. While light limitation under a tall, dense canopy of F. × bohemica appears the most likely mechanism of competitive superiority, the species may also alter physical, chemical, and biological properties of its surroundings as has been documented for other invasive plants (Ehrenfeld, 2003; Levine et al., 2003; Vivanco

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et al., 2004). Such changes in the abiotic or biotic environment in *F. bohemica* populations may also affect germination and survival of seedlings or juvenile plants of native species and thus prevent their colonization and recruitment. The extensive rhizome system suggests that *F. bohemica* is a good competitor for nutrients (Shaw and Seiger, 2002), but the absence of seedlings of other native species in early spring before canopy closure, near complete absence of shade-tolerant species, and an abundance of bare ground among the *F. bohemica* stems suggest that allelopathic interference (Inderjit and Callaway, 2003; Weston and Duke, 2003) may play a role in maintaining near monocultures of *F. bohemica*.

Riparian areas, which are often invaded by *F. bohemica*, are characterized by efficient dispersal of seeds and plant propagules through hydrochory (Rand, 2000; Boedeltje et al., 2004). We therefore do not consider reduced seed/propagule availability an important factor in limiting recruitment of native species in *F. bohemica*. Assuming sufficient seed or propagule supply, *F. bohemica* can limit recruitment of native species through preventing germination, reducing seedling establishment, or reducing growth and survival of juvenile plants.

We were particularly interested in evaluating the impact of *F. bohemica* on juvenile plant growth and survival. While we consider germination and early seedling growth a critical and important stage for initial plant establishment, by using well-established native juvenile plants rather than seed addition in our experiments, we avoided complications of microsite availability, seedling density, and potential allelopathic interference with germination processes that also affect local recruitment (Münzbergová, 2004; Vivanco et al., 2004). We hypothesized that, even if seeds or propagules of native species arrive and successfully germinate, establish and initiate growth, *F. bohemica* will reduce long-term survival of juvenile plants through interference with their growth requirements. In addition, transplanting juvenile plants is a common practice in wetland and riparian restoration where flooding may wash seeds off the site, and preventing erosion is often an important restoration goal—much easier achieved by using well-established juvenile plants that will grow quickly.

We transplanted juvenile individuals of two native species, silver maple (*Acer saccharinum* L., a deciduous tree) and boneset (*Eupatorium perfoliatum* L., a perennial herb) into a well-established *F. bohemica* population growing in a riparian area. Our treatments consisted of manipulations of resource availability (light, nutrients) and potential allelopathic interference (activated carbon addition) to assess mechanisms of invasive plant impacts in a full factorial field experiment. Although resource competition and allelopathy likely act in concert, for example, through root exudation (Callaway and Aschehoug, 2000; Ridenour and Callaway, 2001; Bais et al., 2003; Vivanco et al., 2004), little is known about their relative importance under field conditions (Inderjit and Callaway, 2003). We tested the following hypotheses: (1) Increased access to light will improve survival and growth of transplants. (2) Increased nutrient availability will improve survival and growth of transplants. (3) Activated carbon addition will improve survival and growth of transplants. (4) Transplant survival and growth will be maximized in treatments in which increased light and nutrient availability are combined with activated carbon addition.

### MATERIALS AND METHODS

**Study site**—Our study site is a 40 × 70 m homogeneous stand of *F. bohemica* occupying a flood plain of Cayuta Creek in central New York, USA (42° 21' 59" N, 76° 26' 43" W). The site lacks conspicuous elevation or moisture gradients. Soils were notable for NO3 limitation (<1 ppm in all samples) as well as low P (5.1 ± 0.78 mg/kg; mean ± 1 SE) and K (47.7 ± 7 mg/kg; mean ± 1 SE) levels (analyzed by Cornell Nutrient Analysis Laboratory). The *F. bohemica* stand is bordered by an old field (dominated by goldenrods, *Solidago* spp.) and riparian trees (*Populus* sp.) and has existed at the site for at least 10 yr (B. Blossey, personal observation). The only other plants occurring within the *F. bohemica* are the invasive *Allaria petiolata* (M. Bieb.) Cavara and Grande and garlic mustard and an onion (*Allium* sp.), and both species occur at low density.

**Experimental organisms**—There is much taxonomic debate about the correct classification of several Asian taxa commonly referred to as Japanese knotweed, and the species are placed in the genera *Reynoutria*, *Polygonum*, or *Fallopia* by various authors (Shaw and Seiger, 2002; Zika and Jacobson, 2003). The most recent volume of the *Flora of North America* confirms the Fallopia designation (Flora of North America Editorial Committee, 2005). Introduced *Fallopia* populations in North America are comprised of Japanese knotweed, *Fallopia japonica* (Houtt.) Ronse Decraene (syn: *Reynoutria japonica* Houtt., *Polygonum cuspidatum* Siebold & Zucc.), giant knotweed, *F. sachalinensis* (F. Schmidt) Ronse Decraene; their common hybrid Bohemian knotweed, *F. bohemica* (Chrek and Chrtkóvá), which may be the most widespread *Fallopia* taxa in the United States (Zika and Jacobson, 2003); and Bokhara fleeceflower, *F. balschuanica* (Regel) Holub. We know relatively little about potential differences in ecosystem function between *F. japonica*, *F. sachalinensis*, and *F. bohemica*, but all are considered serious economic and environmental threats in Europe and North America (Beering et al., 1994; Shaw and Seiger, 2002). On the basis of morphological features (Zika and Jacobson, 2003; Flora of North America Editorial Committee, 2005), plants at Cayuta Creek are *F. bohemica*. Data from Europe suggest that *F. bohemica*, while similar in dispersal and interactions with native species, appears to have increased hybrid vigor and can outcompete both parental species (Pysek et al., 2003; Binnová et al., 2004).

Invasions by Japanese, giant, and Bohemian knotweed create monospecific stands, and native species are competitively excluded as stands expand through growth of an extensive rhizome system (Binnová et al., 2004). The species are particularly abundant along riparian corridors where water can easily transport rhizome or stem fragments and on disturbed grounds. Plants (particularly the roots) contain high concentrations of phenolic compounds (trans-resveratrol and others) (Vastano et al., 2000; Vaheer and Koel, 2003). Rapid stem growth (up to 8 cm/d) begins in early spring (early to mid-May in central New York), and the slightly arching stems can reach 4 m in height, forming a dense canopy and allowing little light to reach the understory. Plants reach their final height in early summer and flower in late August and September. The species are insect pollinated and, at least for *F. japonica*, seedlings are able to establish in spring and grow (Forman and Kesseli, 2003).

We selected two native plant species expected to thrive at Cayuta Creek in the absence of *F. bohemica*. *Acer saccharinum* L. (silver maple) is a native, moderately shade tolerant hardwood deciduous tree that thrives in moist woods and lowlands, including flood plains and stream banks (Burns and Honkala, 1990). The species, often considered important in the restoration of riparian areas, reaches a height of 27 to 36 m at maturity. We obtained bare-root, dormant, 2-yr-old *A. saccharinum* saplings (average height 90 cm, range 74–120 cm) from the Saratoga Tree Nursery (New York State Department of Environmental Conservation, Saratoga Springs, New York, USA).

*Eupatorium perfoliatum* L. (boneset) is a widespread and common native perennial herb (40–150 cm tall). The species is a facultative wetland plant commonly found in floodplains, swamps, bogs, stream banks, and wet meadows. We chose *E. perfoliatum* because the species occurs in the riparian areas at our field site immediately outside the *F. bohemica* stand (4.5 m outside of the stand’s 28 plants within a 20 m2 area adjacent to the creek). We obtained juvenile plants (as 2–3 mo old plugs, average height 12 cm, range 10–18 cm) from JF New native plant nursery (Walkerton, Indiana, USA).

**Experiment 1**—Leaving a 5-m buffer from the edge of the stand bordering the old field, and a 10-m buffer from the edge of the creek, we established a regular grid (cell size 2.5 × 2.5 m) inside the *F. bohemica* population. We then randomly assigned 160 of the 288 possible transplant locations to receive...
either a juvenile A. sacharum or a juvenile E. perfoliatum plant. Each location was also assigned one of four treatments: increased light (L), nutrient addition (N), activated carbon addition (C), or a control (no manipulations) in a complete factorial design (N = 10 replicates/treatment).

Coinciding with spring plant growth in our region, we transplanted 80 A. saccharinum and 80 E. perfoliatum plants into the stand of F. × bohemica (stems approximately 1.5 m tall) on 22 and 23 May 2004. We chose the largest, similar-sized individuals available for each species and recorded their initial height (used as a covariate in the statistical analysis). Before transplanting, we pruned A. saccharinum roots to a 10 cm radius and measured height on 20 additional reference specimens, which were subsequently dried at 50°C for 1 wk to determine initial stem and root biomass. We transplanted E. perfoliatum as plugs but were unable to determine initial biomass due to lack of surplus plants.

To achieve increased access to light, we bent main stems and where absolutely necessary pruned side branches of F. × bohemica, creating a canopy opening of 3–6 m in diameter above our transplants. This treatment, while harvested all 8

and measured maximum leaf width (as a nondestructive measure to determine biomass of

for 7 d in a drying oven and subsequently determined biomass. We were unable to

a 10 cm diameter clump of soil surrounding the roots of the local E. perfoliatum intact to reduce transplant shock. All plantings for experiment 2 occurred on 16 July 2004, and we measured transplant survival weekly for 5 wk and measure light levels at each station on 15 August 2004 (as detailed for experiment 1).

Data analyses—We used SAS 9.1 (SAS Institute, Cary, North Carolina, USA) for all analyses. In experiment 1, we analyzed responses for A. saccharinum and E. perfoliatum separately. Due to early mortality, our analysis of E. perfoliatum growth was limited to the first time interval (22 May to 23 June). We evaluated the relative change in total E. perfoliatum stem length (%) with a three-way ANOVA using PROC MIXED with L (light), N (nutrient), and C (carbon) as fixed and individual plant as a random effect because each plant could have multiple stems. We evaluated the significance of any E. perfoliatum growth by comparing mean growth (Ismeans) to zero using t tests. We determined and compared E. perfoliatum survivorship curves using PROC LIFETEST, the Kaplan-Meier product-limit method.

We used three-way mixed model ANOVAs to analyze A. saccharinum root and aboveground biomass production. We estimated aboveground biomass production by subtracting initial stem biomass (determined by a regression stem biomass relationship in our unplanted references; initial biomass = −5.27 + (0.1542 × initial stem height); SE = 1.69; r² = 0.6153; P = 0.000026) from the final aboveground stem and new aboveground biomass growth values. We analyzed A. saccharinum average leaf width over time using a repeated measures three-way mixed model ANOVA. We used initial stem height as a continuous covariate to account for initial variation in our analysis of average leaf width and root biomass. We used PROC MIXED for all analyses of A. saccharinum growth responses and designated L, N, and C as fixed and individual plant and day as random factors. Differences among treatments and unplanted references were analyzed using Tukey’s HSD test and degrees of freedom were Kenward and Roger adjusted (Kenward and Roger, 1997). We excluded 10 saplings with evidence of deer herbivory casewise from all analyses.

In experiment 2, we used a binary logistic regression model (PROC GENMOD) to evaluate whether E. perfoliatum mortality differed by growing location (within the F. × bohemica stand or outside), treatment (clipped or control), or plant origin (nursery or local). We used survivorship data from day 28 because full mortality in the shade treatments at the end of the experiment (day 38) violated model assumptions.

RESULTS

Experiment 1—Our bending and slight pruning achieved the desired results and increased light levels from 1011 ± 77.25 lux in the control to 8162 ± 469.8 lux (mean ± 1 SE) in the increased light treatments. The juvenile E. perfoliatum survived transplanting well, but only plants in the L×C and the L×N×C treatments had significant positive growth compared to plants in the control treatment (L×C, t = 2.94, P = 0.004; L×N×C, t = 3.38, P = 0.0013, Fig. 1). Carbon addition was the only treatment with a significant effect on E. perfoliatum height (F 1,61 = 14.36, P = 0.0003). After day 31, we observed rapid
Increased access to light survived significantly longer (treatments surviving significantly longer than control plants) leaf loss, a typical symptom for light stress in plants. Increased blackening of branches and eventual premature senescence and individual survived to the end of the experiment and had significant (*Fig. 2). Differences in survivorship among treatments were the E. perfoliatum mortality preventing further growth analyses, and all but two of the E. perfoliatum plants had died by the end of the experiment (Fig. 2). Differences in survivorship among treatments were significant ($\chi^2 = 1.487, P = 0.0377$) with plants in the L×C ($\chi^2 = 5.63, P = 0.0176$) and L×N×C ($\chi^2 = 4.46, P = 0.0347$) treatments surviving significantly longer than control plants (Fig. 2). Across the experiment, E. perfoliatum transplants with increased access to light survived significantly longer ($\chi^2 = 10.06, P = 0.0015$), while carbon addition marginally improved survival ($\chi^2 = 3.24, P = 0.0719$) and nutrient addition had no effect ($\chi^2 = 0.073, P = 0.8954$).

All A. saccharinum transplants (except for a single individual) survived to the end of the experiment and had positive growth. However, plants in the control treatment had blackening of branches and eventual premature senescence and leaf loss, a typical symptom for light stress in plants. Increased access to light ($F_{1,71.1} = 143.3, P < 0.0001$, Fig. 3) and carbon addition ($F_{1,71.3} = 7.51, P < 0.0077$) produced significant increases in mean leaf width of A. saccharinum, but nutrient addition had no significant effect ($F_{1,71.3} = 0.97, P = 0.328$). Leaf width was also significantly affected by day ($F_{3,203} = 37.27, P < 0.0001$), interaction of C×N ($F_{1,71.4} = 3.91, P = 0.0519$), L×day ($F_{3,203} = 3.83, P = 0.0107$), and L×C×day ($F_{3,203} = 4.52, P = 0.0043$).

Initial stem height was a significant predictor of A. saccharinum stem biomass at the end of the experiment ($r^2 = 0.6153, P < 0.0001$). After accounting for the influence of initial stem height, greater light availability increased root ($F_{1,72} = 41.36, P < 0.0001$) and aboveground biomass ($F_{1,86} = 55.27, P < 0.0001$, Fig. 4), but neither nutrient nor carbon addition showed any significant effect on A. saccharinum biomass ($P > 0.05$). We also found a significant interaction of C×N for aboveground biomass ($F_{1,86} = 5.1, P = 0.027$).

Experiment 2—In our second experiment, plants in the unmanipulated control treatments within F. ×bohemica showed significantly lower survivorship ($\chi^2 = 7.49, P = 0.006$) with only 11 (30%) survivors compared to the cutting treatment and plants transplanted into the riparian area where 24 (80%) survived to day 28. By day 38, none of the plants in the control treatment were alive compared to 81% survivorship in the cutting treatment and in the riparian area. There was no significant difference in survival of E. perfoliatum transplants ($\chi^2 = 0.01, P = 0.928$) between the cutting treatment inside the F. ×bohemica stand (82%, N = 11) and in the unmanipulated riparian area (85%, N = 13). There was no significant difference ($\chi^2 = 0.66, P = 0.415$) in survival of nursery plants (65%, N = 20) and local E. perfoliatum (71%, N = 14). Interestingly, midday light levels (at the height of our transplants) in the riparian area and in the F. ×bohemica cutting treatment were similar (9000 to 10000 lux).

**DISCUSSION**

A lack of well-designed field experiments and bioassays currently limits our understanding of the role of allelopathy and its interaction with biotic and abiotic factors and resource availability in shaping natural plant communities (Inderjit and
Callaway, 2003). We used a full factorial field experiment to simultaneously evaluate contributions of resource availability and potential allelopathic interference that may facilitate the lasting dominance of an invasive over native species by reducing colonization rates (Yurkonis and Meiners, 2004). To the best of our knowledge, this is the first field experiment to simultaneously vary resource availability and potential allelopathic interference.

Our transplanting worked well, and we had extremely little immediate mortality, probably aided by frequent rain events eliminating the need to water experimental plants. We found strong support for our first hypothesis that increased access to light improves survival of transplanted juvenile native plant species. However, this increased survival was temporary and only realized for E. perfoliatum. Regardless of treatment, catastrophic mortality over the next 2 mo eliminated all but two individuals in the L×C and L×N×C treatments. In contrast, all transplanted A. saccharinum individuals survived to the end of our experiment, although plants growing in unmanipulated control treatments had symptoms of light stress and performance decreases. Their long-term survival under a F. ×bohemica canopy is questionable. Increased access to light improved A. saccharinum performance (measured as leaf width and biomass production) supporting the second part of our first hypothesis. However, no performance increase as a function of light increase was evident for E. perfoliatum. Clearly, increased light availability had species-specific effects.

Nutrient addition in combination with carbon or light improved growth of juvenile E. perfoliatum or A. saccharinum transplants, but we found no support for our second hypothesis that increased nutrient availability alone will improve survival and growth. We found limited support for our third hypothesis that carbon addition will improve survival and growth of juvenile transplants. In the first 4 wk, carbon addition allowed E. perfoliatum plants to grow, and carbon addition increased A. saccharinum leaf width (but not overall biomass). We found no support for our fourth hypothesis that combinations of increased light, nutrient, and carbon addition will maximize survival and growth of native juvenile plants growing in F. ×bohemica, although E. perfoliatum plants in L×C treatments survived longest.

It is not surprising that light limitation may reduce the ability of native plant species to colonize F. ×bohemica populations. This hybrid and its two parental species are known for their dense, closed canopies in their introduced ranges (Beerling et al., 1994). In contrast, in its native range in Japan, F. japonica is a pioneer species colonizing new soils, for example, after eruptions of Mt. Fuji (Adachi et al., 1996). Relatively short-lived F. japonica patches act as nurseries for later successional species unable to colonize bare ground (Adachi et al., 1996). These important differences in growth and community impacts of Fallopia spp. between the native (facilitation of diversity) and introduced ranges (suppression of colonization and reduction in diversity) suggest that either (1) recipient communities and its members are ill adapted to co-exist with the new arrival or (2) through introduction and selection/hybridization Fallopia spp. have obtained traits allowing them to exclude native species.

The enemy release hypothesis (Keane and Crawley, 2002), the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold, 1995) and the novel weapons hypothesis (Callaway and Ridenour, 2004) all may offer explanations for these observations. With the exception of introduced Japanese beetles (Popilia japonica Newman) F. ×bohemica is essentially herbivore-free in North America (B. Blossey, personal observation), while native species are attacked by multiple herbivores and pathogens, thus giving a competitive advantage to F. ×bohemica. We continuously surveyed all transplants for aboveground pathogens and herbivores in our experiment. A few A. saccharinum individuals were browsed by mammals (most likely by white-tailed deer, Odocoileus virginianus), which we excluded from our analyses. We noticed that E. perfoliatum stems were attacked by a pathogen (identified as a generalist Fusarium sp. by the Plant Disease Diagnostic Clinic at Cornell University, but only plants inside F. ×bohemica were attacked, turned black, and died. While the fungus may have contributed to mortality of E. perfoliatum, we consider it unlikely that it was the cause of the poor plant performance because this opportunistic fungus colonized already weakened individuals. We also consider it unlikely that aboveground herbivores or pathogens contributed to poor survival and growth of E. perfoliatum or A. saccharinum at our site, weakening the role of natural enemies, at least in our experimental setup. However, we are unable to exclude the possibility that soil pathogens facilitated by F. ×bohemica may have caused the observed catastrophic mortality of E. perfoliatum. Such facilitation of soil pathogens by invasive plants to the detriment of native plant species has been recently reported for A. petiolata (Stinson et al., 2006).

The apparent lack of specialized natural enemies of F. ×bohemica, which can be quite damaging in Japan (Shaw and
addition could not prevent major *E. perfoliatum* mortality, suggesting the existence of other important mechanisms (such as facilitation or suppression by soil microbial communities) that contribute to the success of *F. ×bohemica* in the introduced range.

Overall, our data support findings (Yurkonis and Meiners, 2004) that recruitment limitation by invasive species (through light limitation, potential allelopathic interference, and other mechanisms) may facilitate the long-term dominance and development of near monocultures of *F. ×bohemica*. Manipulation of light availability appears an obvious choice (for example, by repeated cutting) to restore diverse communities. Our second experiment clearly established that cutting of *F. ×bohemica* alone allowed *E. perfoliatum* to survive. It also established that conditions at Cayuta Creek were suitable for *E. perfoliatum* to grow and that *F. ×bohemica* invasion has an important negative impact on site conditions. However, while the improved *E. perfoliatum* survival rates in our second experiment offer some hope for restoration efforts using repeated selective cuttings, we cannot exclude the possibility that cutting of large areas changed more than access to light. The removal of a substantial amount of *F. ×bohemica* biomass and the redirection of resources to regenerate aboveground tissues is likely to have affected plant chemistry or the ability to produce root exudates and their potential impact on *E. perfoliatum* survival and growth. In addition, cutting would have to be maintained for extended periods, and our experiment was terminated after 5 wk. Although transplants appeared healthy, our experiment was comparatively short (for a field experiment) and long-term survival of transplants uncertain (particularly if *F. ×bohemica* recovers). Canopy gaps to improve access to light for *E. perfoliatum* seedlings also had to be substantial to prevent mortality (7.5 × 7.5 m clearing in our second experiment), and bending and light pruning were not sufficient to prevent near total mortality, even under improved light conditions (Fig. 2).

Most importantly, our field experiment established that no single mechanism appears solely responsible for the competitive exclusion of colonization of native species by *F. ×bohemica*. While light limitation appeared clearly to have dramatic impacts for juvenile plants, many newly germinated seedlings may not even make it this far in a dense *F. ×bohemica* population. Our field experiment also demonstrated species-specific responses of native species to conditions created by an invader and showed that different performance measures (survival vs. growth) may give different answers. Ultimately, the goal of restoration of invaded riparian areas is the return of native diversity (fauna and flora). In light of our results, it appears that experiments using different integrated restoration techniques (cutting or selective herbicide treatments or biological control plus potential soil amendments and seeding and planting of different native species) as attempted for *Phalaris arundinacea* (Perry et al., 2004) may be more productive in developing successful long-term management of *F. ×bohemica* and its parental species.

**LITERATURE CITED**


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