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Age and age structure of an invasive plant, Lythrum salicaria

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AGE AND AGE STRUCTURE OF AN INVASIVE PLANT, *LYTHRUM SALICARIA*

BY

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Bachelor of Science, University of New Hampshire, 2001

THESIS

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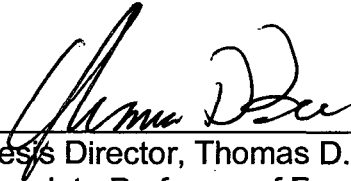
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ABSTRACT

AGE AND AGE STRUCTURE OF AN INVASIVE PLANT, *LYTHRUM SALICARIA*

by

Kimberly L. Therrien

University of New Hampshire, May 2010

My objective was to determine whether purple loosestrife (*Lythrum salicaria* L.) individuals could be aged using the pattern of ramet production. Assuming current year loosestrife ramets produce new basal ramets only in the following year, plant age could be estimated by counting ranks of sequentially produced ramets. I found that in four New Hampshire wetlands the assumptions of the method were generally met, although some ramets were not produced sequentially. Using ramet counts I was able to estimate minimum age for individuals in each of the four populations. All populations were dominated by individuals > 1 year old. I tested whether mechanical damage to ramets releases lateral buds, inducing production of more than one rank of new ramets in one growing season and thus affecting age estimates. Clipped ramets produced lateral ramets (from leaf axils) that were morphologically distinct from basal ramets that characterize normal annual growth.

INTRODUCTION

Background

Commerce, transportation, and cultivation have led to the expansion of species distribution beyond natural barriers, such as oceans, mountains and climatic zones. The naturalization and continued expansion of non-indigenous species, a process called invasion, may alter fire regimes, nutrient cycles, hydrology, and soil structure (Mack et al. 2000). Approximately 5000 introduced plant species now exist in natural habitats in the US (Morse et al. 1995). Invasive plants present serious economic costs of $33 billion annually in agricultural losses (Pimentel et al. 2005). In the northeast, 1/3 of the plant species are introduced (Oehler et al. 2006).

Although invasive species are well documented, relatively little is known about why they are able to succeed. Some researchers believe that a community's tolerance to invasion relates to community structure. According to Elton (1958), invasion should be less likely in communities with high species richness. Fewer species means less competition and thus more resource availability, which lowers a community's biological resistance to invasion. Experimental studies have found support for Elton's hypothesis (Kennedy et al. 2002, Naeem et al. 2000). However, correlational studies often support the idea

that species richness may not be an effective barrier to invasion (Lonsdale 1999, Stohlgren et al. 2003).

Disturbance maintains species diversity by preventing competitive exclusion and, for the same reason, can facilitate invasion of non-indigenous species (Burnham and Lee 2010, Hobbs and Huenneke 1992). Burke and Grime (1996) found that abundance of introduced species increased from less than 25 percent to greater than 40 percent as levels of vegetation removal and fertilization increased. Recent studies have shown, however, that disturbance may not be a factor for all invasive species. For instance, a shade-tolerant invasive shrub, *Rhamnus frangula* (Gleason and Conquist 1991), is able to colonize undisturbed forest (Burnham and Lee 2010, Frappier et al. 2003a). Martin and Marks (2006) found that even though its rate of invasion was suppressed, *Acer platanoides* (L.) was able to colonize intact forests.

According to Blossey and Notzold (1995), reduced levels of herbivory can lead to an increase in plant vigor. As natural predators of invasive plants often do not occur in an invader's new environment, there is less herbivory, thus increasing invasion success (Keane and Crawley 2002). Recent studies on *Acer platanoides* support this "enemy release hypothesis" (Adams et al. 2007, Cincotta et al. 2009). However, research conducted by Agrawal and Kotanen (2003) determined that the occurrence of herbivory on non-indigenous species was similar or greater than that experienced by native plants.

Age and Age Structure

Some insight into the causes of invasion might be gained by observing the timing and pattern of the invasion process. Unfortunately, we often become aware of invasions only after they have occurred (e.g., Cunard and Lee 2009, Wangen and Webster 2006). Thus, we have little knowledge of the timing and pattern of invasion or of the population dynamics of the invading species. Understanding the timing and temporal pattern of invasion might provide insight into the roles competition, disturbance, and herbivory have in controlling plant invasions. The age and age structure of an invasive plant population may provide insight to the mechanisms underlying the invasion.

The ability to determine the age structure of a population may be useful to characterize demography, estimate the rate of spread, and develop hypotheses about the processes and factors controlling the invasion. It may be possible to approximate time of invasion based on the current age structure (Dietz 2002 Frappier et al. 2003b, Perkins et al. 2006, Wangen & Webster 2006).

Population dynamics can provide insight to the life history characteristics and mechanisms that provided the opportunity for invasion, such as disturbance, dispersal, or community structure. Burnham and Lee (2009) were able to age invasive glossy buckthorn (*Frangula alnus*) and this allowed them to show that,

while buckthorn invasion of a hemlock-pine forest began prior to canopy opening, most individuals established afterward. Wangen & Webster (2006) used age structure to determine that seed dispersal and canopy gaps governed invasion of *Acer platanoides.* Perkins et al. (2006) studied the relationship between population age and both disturbance and environmental gradients.

In addition, age structure may also allow for the prediction of future population size (Bullock et al. 1996). Growing populations are characterized by age structures with large numbers of juveniles and few adults (Hett 1971, Leak 1975). If recruitment is high and the population is growing then it may be necessary to implement a control method. Conversely, a declining population often may have many adults but few if any juveniles (Leak 1975). In such a case there may be no need to apply control measures. However, the ability to predict future population sizes accurately relies upon knowledge of the survivorship of individuals. For example, the assumption that a population with a high percentage of juveniles is growing may be inaccurate if there is a high rate of juvenile mortality.

In an effort to identify age structure and invasion patterns of invasive forbs, Dietz (2002) investigated the possibility of aging individuals by counting annual growth rings in a select group of invasive species. Using perennial plants that grow in seasonal climates and that produce annual growth rings in the root structures, he found temporal patterns of population development. Recently, the

spatial and temporal invasion pattern of *Rhamnus frangula*, was determined by aging and mapping individual stems (Frappier et al. 2003b). Individuals were aged using annual wood rings.

Purple Loosestrife (*Lythrum salicaria* L.)

I studied invasive *Lythrum salicaria* (purple loosestrife). Demographics of purple loosestrife have not been well investigated despite major efforts to control spread. Age structure of purple loosestrife may provide information on which to base control procedures for land managers as well as allow assessment of the long-term environmental impact of the invasion.

The history of purple loosestrife invasion as well as the key life history characteristics of the plant were reviewed by Thompson et al. (1987) and are summarized here. Purple loosestrife, an aquatic plant species of Eurasian origin, was introduced to North America in the early 1800's. Ship's ballasts, livestock bedding, and the horticulture industry were largely responsible for purple loosestrife's introduction. Within a few decades of introduction, purple loosestrife was observed forming monospecific stands and having detrimental impacts to wetland ecosystems along the New England coast. The early expansion coincided with the construction of canals in NY and later enhanced by the development of road systems. Currently, purple loosestrife has been declared a

noxious weed in 19 states and occurs in 48 states in the US and in 9 Canadian provinces (Blossey et al. 2001).

Today, purple loosestrife occupies freshwater marshes, alluvial floodplains, and stream margins in the northeastern and north-central United States (Thompson et al. 1987). Optimum site conditions include a moist soil with a slightly acid pH and experiments have shown temperatures between 15 – 20°C are optimum for germination (Shamsi & Whitehead 1974b). Purple loosestrife reaches 2 m in height with 30-50 ramets that form a dense canopy. Perennial rootstocks provide energy for the production of new shoots. Purple loosestrife produces long-lived seeds that are dispersed via water, wind, and wildlife. Temperature limits growth and expansion in northern distributions in North America. Purple loosestrife forms monospecific stands that may persist for at least 20 years within wetland communities. Purple loosestrife is often associated with communities of cattails (*Typha* spp.), reed canary grass (*Phalaris arundinicaea*), sedges (*Carex* spp.), bulrushes (*Scirpus* spp.), willows (*Salix* spp.), and horsetail (*Equisetum fluviatile*) (Thompson et al. 1987).

Purple loosestrife's impact on wetland ecosystems has been the topic of many studies resulting in conflicting conclusions. Some assert that purple loosestrife out-competes native wetland species, reducing biodiversity (Thompson et al. 1987). The plant's perennial habit and ability to adjust to a wide range of environmental conditions enable it to thrive in disturbed habitats in

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temperate climates. Weihe and Neelly (1997) found purple loosestrife to replace *Typha latifolia* (broad-leaved cattail) in both shaded and unshaded conditions. In a laboratory experiment, purple loosestrife suppressed the biomass of all the forty-four herbaceous wetland species tested (Gaudet and Keddy 1988). In conjunction with its competitive ability, another factor commonly attributed to the invasiveness of purple loosestrife is the absence of natural enemies to regulate population growth (Malecki et al. 1995). Blossey and Notzold (1995) tested the effect of herbivory on purple loosestrife growth, concluding that plant height and biomass increased in the absence of herbivores. In addition, Anderson (1991) found purple loosestrife responded to herbivory by producing multiple lateral ramets near the point of damage.

Some believe that there is a lack of quantitative evidence supporting the theory that purple loosestrife reduces native biodiversity. Anderson (1995) disputes claims that purple loosestrife reduces species diversity. He suggested that the long-lived individuals with increasing stem density might be deceiving. Purple loosestrife may be increasing in percent coverage but may not reduce species richness as previously thought. Anderson (1991) found no correlation between species richness and purple loosestrife abundance in the wetland he studied. In addition, he suggests that purple loosestrife is used by native fauna such as insects, muskrats, and deer (Anderson 1995). Mahaney et al. (2006) found that loosestrife invasion might not negatively impact undisturbed wetlands with low diversity. Others have rejected the hypothesis that purple loosestrife

reduces species diversity (Hager and McCoy 1998, Lavoie et al. 2003, Treberg and Husband 1999). Similarly, Morrison (2002) concluded that purple loosestrife did not form monospecific stands in two sites located in lowland meadows in New York. In addition, Hager and Vinebrook (2004) found an increase in plant diversity in the presence of *L. salicaria.*

According to Thompson et al. (1987), the occurrence of disturbance increases the colonization of purple loosestrife by providing a favorable habitat. In a comparison of *L. salicaria* seedling germination among plots which *P. arundinacea* was removed and undisturbed plots of *Phalaris arundinacea,* Rachich and Reader (1999) concluded that disturbance allowed purple loosestrife to establish through the removal of a vegetative barrier.

Some have attempted to age herbaceous perennials using morphological indicators that mark annual growth (Dietz 2002, Harper and White 1974). Anderson (1991) studied the age structure of purple loosestrife individuals by examining its pattern of annual ramet production. Anderson harvested entire loosestrife individuals in the field and, based on careful examination of relationships among ramets, he developed hypotheses about patterns of ramet production. He hypothesized that every year a loosestrife individual produces one or more new ramets, each of which dies back to its base at the end of that year. He then hypothesized that, in the following year, each such ramet produces a new ramet or ramets only at its base. As one ramet may give rise to more than

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one ramet in the next year, whole plants may show a sequential pattern of ramet production that radiates out from a central point (Figure 1). Based on the morphological relationships among ramets, Anderson estimated that, of 152 current year's stems, 90% arose from the base of a previous year's ramet. He also estimated that a single ramet originated from the previous year's ramet in 78% of the ramets produced. Less than 5% of the ramets produced did not originate from the basal portion of the previous year's ramet. These ramets originated on either current year stems or on stems greater than 1 year old.

Based on the inferred pattern of ramet production, Anderson (1991) further hypothesized that the age of an individual plant could be estimated by counting backward across sequentially produced ramets, from the current year's ramet to the oldest available ramet (Figure 1). Applying this method to his populations he found evidence for episodic recruitment of purple loosestrife with low densities of new genets per year (Anderson 1991).

Anderson's aging method assumes that the current year's ramets do not produce additional ramets in that year, but only produce new basal ramets in the following year. In addition, he assumed 1 year old ramets would not produce new ramets in subsequent years. However, Anderson did not test his aging method directly as the consistency of the numbers of stems produced was not monitored across growing seasons; Anderson's inferences were made solely from an interpretation of spatial ramet relationships made at one point in time.

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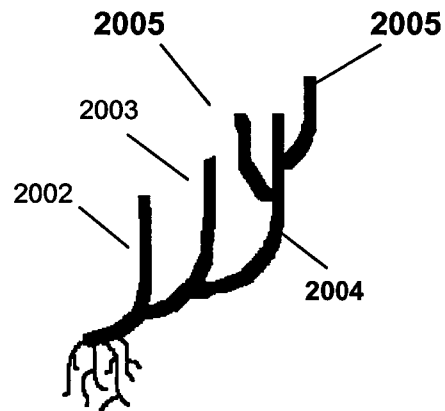
Figure 1. Stems of *Lythrum salicaria* depicting: the yearly production of basal ramets originating from the base of an existing stem.

Anderson (1991) believed that there was one major uncertainty about his proposed aging method. He worried that herbivory to the upper parts of loosestrife ramets might release basal buds on those ramets, thus causing the production of a second rank of ramets in the same year. If one assumed that one set or rank of ramets was produced per year and estimated age by counting backwards from the current year's ramet, a year in which herbivory occurred might be tallied as two years.

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I.   OBJECTIVES

The main objective of this study was to test and apply Anderson's (1991) method of aging purple loosestrife. First I tested the hypotheses that (a) current year ramets of purple loosestrife produce new basal ramets only in the following year, (b) that this pattern can be used to estimate the age of the purple loosestrife individuals, and c) that damage to ramets does not interfere with the method of aging. The second objective was used to determine the age structure of four purple loosestrife populations.

II.   METHODS

A.   <u>Study Sites</u>

This study was conducted in four, freshwater emergent wetlands in the New Hampshire seacoast region: Upper Peverly Pond, Bellamy Reservoir, Pease Tradeport, and Brown Mill Pond (Figure 2).
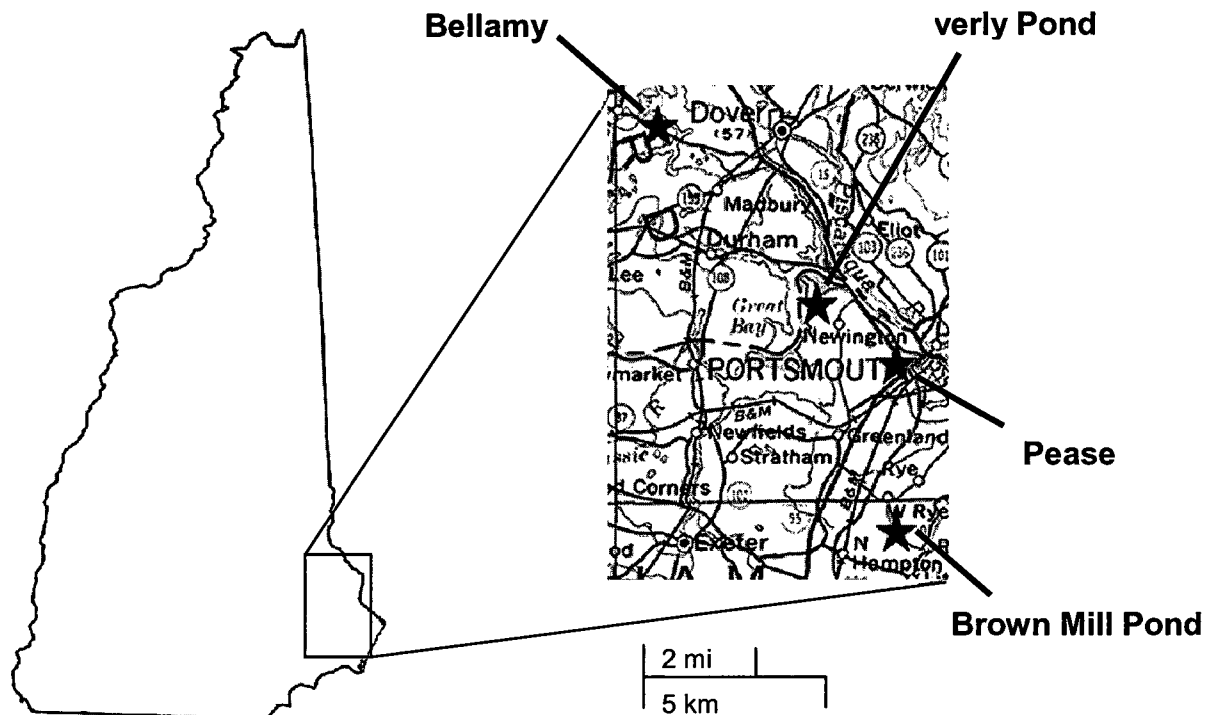
Figure 2. Four emergent freshwater wetlands in the New Hampshire seacoast region: Upper Peverly Pond Bellamy Reservoir, Pease Tradeport, and Brown Mill Pond.

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The Brown Mill Pond site (herafter 'Brown'), owned and managed by The Nature Conservancy, was located west of Love Lane in Rye, Rockingham County (42° 59.202' N lat. 70° 46.613' W long.). Brown Mill Pond and associated littoral habitat was created by an earthen dam constructed before 1800. Soil was Chocorua mucky peat (Soil Survey Staff) and the site had a well developed hummock-hollow microtopography. Elevation was 12 m above sea level. The sampled loosestrife population was located on the northern edge of the pond, in emergent palustrine vegetation dominated by tussock sedge (*Carex stricta*), Canada bluejoint (*Calamagrostis canadensis*), cattail (*Typha latifolia*), and poison ivy (*Toxicodendron radicans*).

The Upper Peverly Pond site (hereafter 'Peverly') was on the 1089 acre Great Bay National Wildlife Refuge, which is located along the eastern shore of the Great Bay Estuary in Newington, Strafford County (43° 05.235' N lat. 70° 50.406' W long.). Upper Peverly Pond was constructed around 1900 as a water supply for the City of Portsmouth. The soil adjacent to the pond was an Eldridge silt loam (Soil Survey Staff). Elevation was 10 m above sea level. The sampled loosestrife population was located within a littoral habitat with palustrine vegetation dominated by cattail (*Typha latifolia*), and Canada bluejoint (*Calamagrostis canadensis*).

Bellamy Reservoir (hereafter 'Bellamy'), located in the town of Madbury, Strafford County (43° 11.843' N lat. 70° 57.137' W long.), is fed by the Bellamy

River and Mallego Brook. Bellamy Reservoir is a 420 acre impoundment created in 1960 and is the drinking water supply for the City of Portsmouth. The study site was located just northwest of the Route 9 bridge, which bisects the reservoir. The soil was a Swanton, fine, sandy loam (Soil Survey Staff). Elevation was 13 m above sea level. The sampled loosestrife population was located in palustrine vegetation dominated by cattail (*Typha latifolia*).

The Pease site (hereafter 'Pease'), owned by the Pease Development Authority, was located in the town of Newington, Strafford County (43° 04.241' N lat. 70° 46.613' W long.). The site was located 100 m east of an abandoned school building. The site was impacted, and perhaps created, during the construction of interstate 95 during the 1960s. The soil was a Squamscott fine sandy loam (Soil Survey Staff). Elevation was 12 m above sea level. The palustrine vegetation is dominated by cattail (*Typha latifolia*), Canada bluejoint (*Calamagrostis canadensis*), purple loosestrife and silky dogwood (*Cornus amomum*).

B.   Growth Patterns

During June – August, 2004, at all four sites, I selected purple loosestrife individuals along evenly spaced transects using restricted random sampling. The sample area at each site ranged from 0.04 – 0.1 ha. Distance between transects varied from site to site but was generally 2.5 to 5 m. The loosestrife population at

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Peverly was highly fragmented, occurring in small patches along the shore of the pond. Consequently, at Peverly, I established one transect per patch, oriented along the long axis of the patch. At all sites, each transect was divided into segments of equal lengths (1 - 5m, depending on site) and a random point was chosen along each segment. The loosestrife individual closest to the point was selected for study.

An individual was defined as a single plant consisting of one or more living ramets all derived vegetatively from the same primary ramet. I identified each plant with an aluminum tag. Thirty plants each were chosen at Peverly and Brown. At Bellamy and Pease, I selected 60 plants, 30 of which were randomly designated as control plants, with the remaining 30 as experimental (manually clipped) plants. On each individual, all current year ramets (2004) were marked with flagging. I recorded the number of current year live ramets per plant. I monitored the plants monthly through October 2004, noting the occurrence of stem damage and mortality.

During the months of June – October of the following year, I examined each ramet tagged in 2004 on the control plants and marked new ramets produced in 2005 with flagging, recording the total number of new ramets per plant and noting plant mortality and any damage to ramets produced in 2004 and 2005. In September and October of 2005, I used a shovel to extract the 30 control plants at each site and cleaned the soil and debris from their roots and

lower ramets. In the laboratory, I re-counted the total number of new (2005) ramets produced per plant and determined the location on the plant where each new stem originated.

I analyzed the spatial pattern of the production of 2005 ramets in two ways. First, on each plant, I randomly selected 3 ramets produced in 2004. For each of these "2004 ramets", I recorded the number of new ramets produced in 2005. All 2005 ramets originating from the base of a 2004 ramet were said to be of the same "rank". When the 2004 ramets produced multiple new ramets in 2005, I noted whether the ramets originated from the 2004 stem (same rank) or from one of the other ramets produced in 2005 (different rank) (Figure 3).
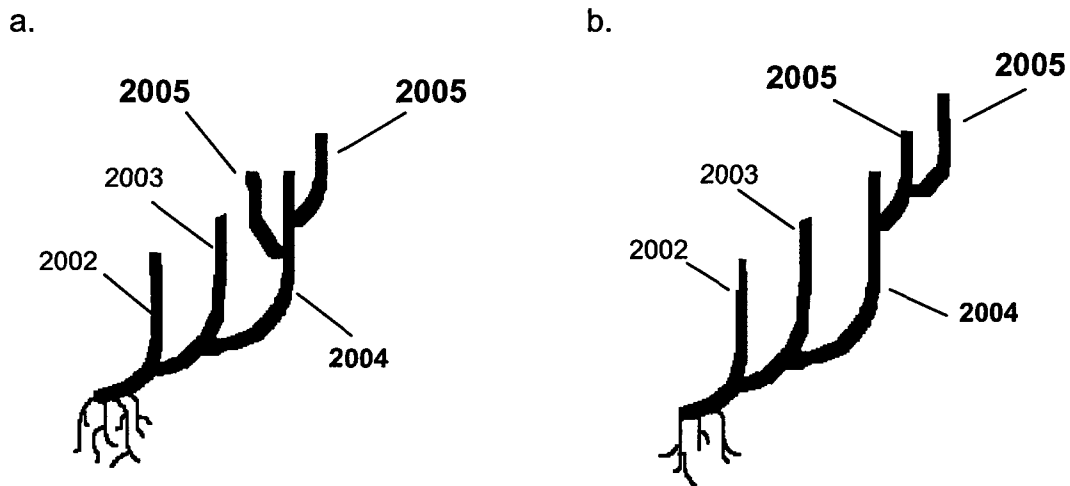
Figure 3. Stems of *Lythrum salicaria* depicting: a) ramets originating from the base of an existing stem (same rank) and b) ramets originating from the base of a stem produced in the same year (different rank).

I also randomly selected 3 ramets produced in 2005 on each plant and recorded whether each originated from a) a 2004 stem, b) an untagged stem

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(one that either lost its tag or was produced before 2004), c) an older stem (produced before 2004), d) root tissue, e) or could not be determined.

C.   Estimation of Age

The method of aging (Anderson 1991) assumes that each current year ramet arises from the basal portion of a ramet that was produced in the previous year. Using the extracted and cleaned plants, I estimated the minimum age of purple loosestrife individuals by counting the number of ranks of ramets, starting with the most recently produced ramet (2005) and working backwards to the oldest rank (Figure 3a). Some plants were branched, meaning that at one or more times in the past a single stem gave rise to two or more new ramets in the following year. At least two of the daughter ramets produced new ramets and proliferated further. In branched plants, I estimated the age by counting backwards from two or more current year ramets (each on a different branch) to the oldest available stem. In some plants, the oldest available stem appeared to be the original stem tissue while in others it was a broken stem.

In some cases, I clipped the ramets close to the rootstock to clearly see the pattern of ramet proliferation and in some cases I dissected the plant to get a better view. Some plants were already in pieces due to breakage during extraction or cleaning. In these cases, I pieced the plants back together if possible.

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D.   Effects of Clipping

During the first two weeks of July, 2004, at the two sites selected for the clipping experiment (Bellamy & Pease), all ramets produced per selected plant (n = 30 per site; see above) were tagged. From each plant, half of all the ramets were selected haphazardly and clipped using pruning shears at 16 cm above water level. The 16 cm height was chosen to allow plants to respond by making either basal or lateral ramets. Between August and September 2004, the sites were visited, and all marked ramets (clipped and not clipped) were checked for the production of new lateral ramets. On each marked ramet, the number of new ramets produced and location at which they were produced along the marked stem were recorded.

E.   Data Analysis

To test whether the number of ramets per plant varied across the four sites, a Kruskal-Wallis non-parametric ANOVA was run. The data were not normally distributed and so a parametric test was not run. To test whether survival of plants from 2004 to 2005 varied among sites, I ran a χ^2 test of independence. Individual plants varied greatly in the number of ramets produced and, as whole plants were the independent study units, I elected to examine performance of individual ramets based on a random sample of 3 ramets per plant. Thus, bias due to plants with large numbers of ramets would be avoided.

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To assess variation across the four sites in the production of ramets in 2005 by ramets produced in 2004, the location of stem origin, and the propensity of ramets to develop single or multiple ramets I ran χ^2 tests of independence. To compare the percent of ramets producing lateral ramets across treatments in the clipping experiment, I ran a Kruskal-Wallis one way ANOVA.

III.   RESULTS

Characteristics and Fate of Tagged Control Plants

In total, I tagged 121 plants and over 700 ramets in 2004. The mean number of living ramets per plant in 2004 ranged from 3.10 at Peverly to 9.07 at Pease, with both Bellamy and Brown having intermediate values (Table 1). The number of ramets per plant varied significantly among sites (Kruskal-Wallis non-parametric ANOVA, $\chi2$ = 10.9, d.f. = 3, P = 0.012). At all four sites, the minimum number of ramets per plant was 1, but the maximum number of ramets ranged from 9 at Peverly to 28 at Pease (Table 1).

Table 1. Sample size and characteristics of *Lythrum salicaria* control plants at four southeastern New Hampshire sites in 2004 and 2005.

	Number of plants	Mean Number of ramets per plant tagged in 2004 (St. Dev.)	Minimum number of ramets per plant in 2004	Maximum number of ramets per plant in 2004	Plant Survival 2004-05 (%)	Mean Number of ramets per plant in 2005 (St. Dev.)
Peverly	31	3.10 ±1.83	1	9	45	2.87 ±1.30
Pease	30	9.07 ±8.10	1	28	100	8.07 ±5.90
Bellamy	30	6.40 ±4.38	1	17	93	6.54 ±4.44
Brown	30	6.20 ±5.79	1	24	73	3.86 ±3.56

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Most of the plants tagged in 2004 survived to 2005, but survival was site dependent ($\chi 2$ test of independence, $\chi 2$ = 32.1, d.f. = 3, P < 0.001; Table 1). Plants that were tagged in 2004 but not recovered in 2005 were assumed to have not survived. However, the apparent absence of a plant could have been due to lost tags. Survival at Peverly was lowest; only 45% of the plants were recovered in 2005. At all other sites survival exceeded 73%. In most plants that did not survive, cause of death was not possible to discern. At Peverly, however, some plant death was associated with herbivory. These plants were visibly grazed and trampled, with some ramets grazed near the base. The pattern of cutting combined with nearby tracks suggested white-tailed deer (*Odocoileus virginianus*) as a major herbivore. Survival at Brown may have been impacted by the release of the biological control beetle (*Galerucella* sp.) in 2005.

In 2005, the 94 remaining plants produced over 500 new ramets. The mean number of ramets produced per control plant was greater than 6 at both Bellamy and Pease and less than 4 at Brown and Peverly (Table 1). These values are generally similar to those obtained at these sites in 2004. The maximum number of ramets produced per plant in 2005 ranged from a high of 22 at Pease to a low of 5 at Peverly.

A.   Growth Patterns

Production of New Ramets by the Previous Year's Ramets

The focus of this next section turns from the whole plant to individual ramets (regardless of what plant they were part of) and the ability of 2004 ramets to produce new ramets in 2005 (Figure 4). Most of the 2004 ramets produced at least one new ramet in 2005. At the Pease site, an average of 67.8% of the ramets produced at least one new ramet in 2005. Corresponding values for Brown, Peverly, and Bellamy were 81.1%, 61.9%, and 71.4%, respectively. The fraction of 2004 stems producing one or more new ramets in 2005 (71.7% overall) did not differ among sites (χ^2 test of independence, χ^2 = 4.56, d.f. = 3, P = 0.207).
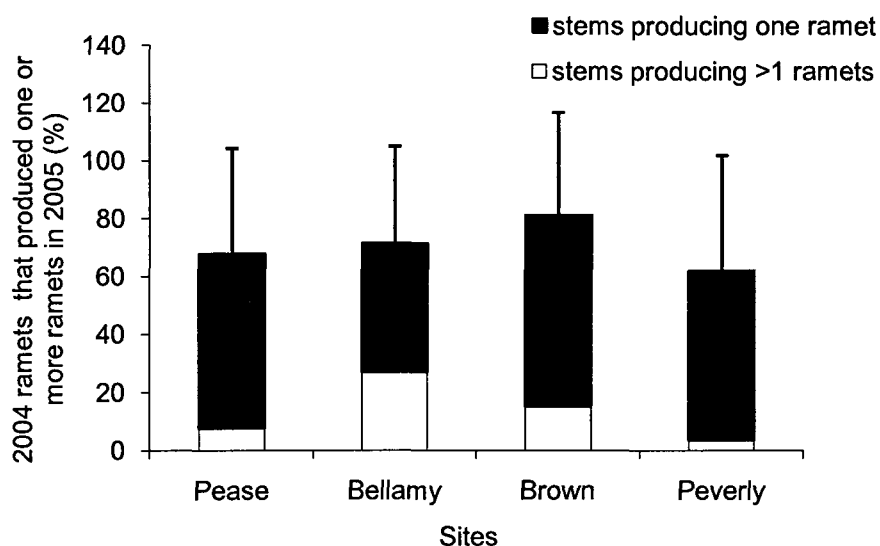
Figure 4.   Percent of *Lythrum salicaria* ramets in 2004 that produced new ramets in 2005 at four southeastern New Hampshire sites (st. dev.).

At all four sites, some flagging on 2004 ramets were lost prior to sampling in 2005. If ramets losing tags were more or less likely to produce new ramets than ramets with tags, there could have been bias in the data. Consequently, over all four sites, I analyzed the data from all 2004 plants that were *not* missing tags to see if lost tags had biased the results. In this reduced, pooled sample (n = 32 plants), 72.9% of the 2004 ramets produced one 2005 ramet, similar to the overall mean for plants all plants (71.7%).

Of those 2004 ramets producing one or more ramets in 2005, most produced a single new ramet in 2005 (Figure 3a, Figure 4). At the Pease site, a mean of 90.2% of 2004 ramets that produced ramets in 2005 produced only one new ramet in 2005. Corresponding values for Brown, Peverly, and Bellamy were 84.6%, 93.3%, and 63.2% respectively. In the reduced/pooled sample of plants that did not lose tags (n = 32 plants), 77.9% of 2004 ramets produced only one 2005 ramet.

In some cases, a 2004 ramet produced multiple (2, 3, 4, or 5) ramets in 2005 (Figure 4). The maximum number of 2005 ramets produced by a 2004 ramet was 5. At the Pease site, an average of 9.8% of all 2004 ramets produced multiple ramets in 2005. Corresponding values for Brown, Peverly, and Bellamy were 15.4%, 6.7%, and 36.8%. The propensity to develop multiple ramets differed across sites (χ^2 test of independence, $\chi^2 = 16.367$, d.f. = 3, P < 0.001).

In the reduced/pooled sample that included only plants that did not lose tags (n = 32 plants), 22.1% of the 2004 ramets produced multiple ramets in 2005.

Origin of New Ramets

When 2005 ramets were produced, they generally originated from buds near the base of 2004 ramets (Figure 3a). These buds occurred haphazardly on the ramet surface within ca. 10 cm of the ramet base (the point at which it attached to another ramet or root) and were *not* associated with leaf axils (Figure 5). Based on the sample of 3 randomly chosen ramets per plant, 82% of the 2005 ramets arose directly from basal buds on the 2004 ramets at Bellamy. Values for Brown, Pease, and Peverly were 81%, 76%, and 48%, respectively (Table 2). The location where 2005 ramets derived from was site dependent (χ^2 test of independence, χ^2 = 17.46, d.f. = 3, P < 0.001). I also analyzed the data from plants at all four sites that were not missing any tags from 2004 (n = 32 plants). On these plants, an average of 83% of the 2005 ramets originated from 2004 ramets.

Basal
Ramet

Figure 5. Basal ramet produced near the base of a 2004
Lythrum salicaria stem in 2005.

Table 2. Origin of *Lythrum salicaria* ramets produced in 2005 at four southeastern New Hampshire sites.

	Number of living plants	Number of ramets	% 2005 ramets arising from a 2004 ramet (st. dev.)	% 2005 ramets arising from a 2005 ramet (st.dev.)	% 2005 ramets arising from root tissue (st. dev.)	% 2005 ramets arising from old ramet (2+ year) (st.dev.)	% 2005 ramets arising from an untagged ramet (st.dev.)	% 2005 ramet origin undetermed (st. dev.)
Pease	30	84	75.6 ±30.2	0.0 ±0.0	10.0 ±23.4	5.6±12.6	7.8 ±14.3	1.1 ±6.1
Bellamy	28	77	82.2 ±27.9	0.0 ±0.0	1.2 ±6.3	1.8 ±9.5	13.7 ±21.8	1.2 ±6.3
Peverly	14	34	47.6 ±38.0	2.4 ±8.9	22.6 ±36.8	2.4 ±8.9	25.0 ±31.2	0.0 ±0.0
Brown	21	53	81.0 ±34.7	0.0 ±0.0	1.6 ±7.1	1.6 ±7.1	9.5 ±18.4	6.4±16.7
Plants with no missing tags	32	66	83.3 ±29.0	0.0 ±0.0	5.7 ±20.1	0.0 ±0.0	8.9 ±18.0	2.0±11.8

Some 2005 ramets originated from ramets estimated to be 2 years old (Figure 6). This was clearly the case when both a marked 2004 *and* a marked 2005 ramet originated from the same ramet. At the Pease site, on average, 5.6% of the 2005 ramets originated from ramets produced in years prior to 2004. Corresponding values for Brown, Peverly, and Bellamy were 1.6%, 2.4%, and 1.8%, respectively. In the reduced sample of plants that were not missing any tags from 2004 (n = 32), *none* of the 2005 ramets were produced on ramets that were 2 or more years old.
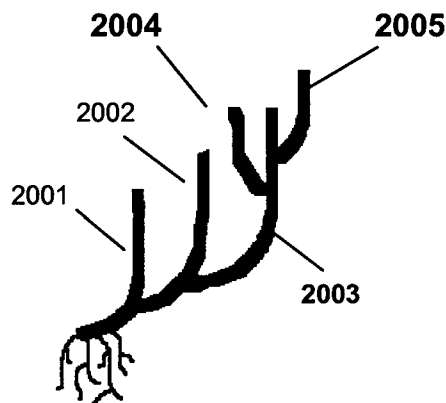
Figure 6. Stems of *Lythrum salicaria* depicting a 2005 ramet that originated from a ramet estimated to be 2 years old.

Some 2005 ramets were found to originate directly from root tissue (Figure 7). Origin from the roots occurred at Bellamy on 1.2% of the ramets. At Pease 10.0%, and at Brown 1.6% of the 2005 ramets had at least one 2005 ramet that originated directly from the rootstock. At Peverly, a very high 22.6% of the 2005 ramets originated from root tissue. Of the plants not missing any tags from 2004

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(n = 32), only 5.73% of the 2004 ramets produced ramets in 2005 that originated from root tissue.
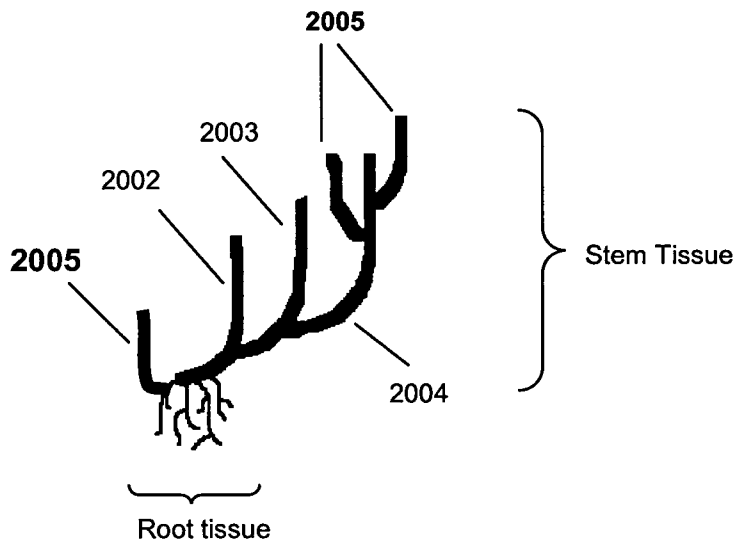
Figure 7. *Lythrum salicaria* stem depicting 2005 ramets originating from root tissue.

Finally, I examined the possibility that some 2005 ramets arose from another 2005 ramet (Figure 3b). As shown above, when a 2004 ramet produced multiple ramets in 2005, each 2005 ramet was usually produced directly from basal buds on the 2004 ramet; thus, the 2005 ramets were denoted as all having the same "rank". Only in one instance, at Peverly, did a 2005 ramet arise from the base of *another* 2005 ramet (Figure 8). The result was that a 2004 ramet produced *two ranks* of new ramets in 2005. In this particular case, it appeared that the plant exhibited injury, possibly herbivory, to the upper part of the initial 2005 ramet at some point during the 2005 season.

2004 Ramet

Ramets
produced
in 2005

Figure 8. *Lythrum salicaria* stem depicting a 2005 ramet
producing an additional ramet in 2005 (different rank).

Clearly, some 2005 ramets originated from untagged ramets. These 2005

ramets may have arisen from 2004 ramets that were missed (i.e., not tagged)

during the initial sampling procedure or from ramets that lost their tags during the

winter. Others may have arisen on ramets originating in years prior to 2004. At

all sites, between 8 – 25% of the 2005 ramets were produced on these 'untagged

ramets'. When I eliminated from the data all plants that lost tags on 2004 ramets

and then combined data from all four sites (n = 32), only 8.85% of the 2005

ramets were produced from ramets other than those flagged in 2004.

The origin of a small number of 2005 ramets could not be determined. In some of these cases, factors such as decomposition and breakage inhibited my ability to determine ramet origin. In other cases, the 2005 ramet originated too close to the base of the older ramet making it difficult to differentiate between ramet and root tissue. At the Pease, Brown, and Bellamy sites, the origin of the 2005 ramet could not be determined in 1- 7% of the ramets. The origin of all ramets could be determined at Peverly. I also analyzed the data from plants at all four sites that were not missing any tags from 2004. The origin of each the 2005 ramets in this reduced sample was unaccounted for in 2.08% of the ramets.

B.   *Estimation of Age*

Mean Age

The age of each plant was estimated by counting backwards, rank by rank, from the 2005 ramet to the plant's oldest available or original ramet. Aging required complete removal of peat and debris from the ramets and root system. While dissecting the plants, it became apparent that some plants tagged as one were actually comprised of 2 or more plants that could be identified as separate individuals. These plants were counted as separate individuals when estimating age.

Some plants included the original ramet while others could only be traced back to a point where the ramet was broken or decomposed. In the latter case the plant's age could have been much greater than estimated. On plants that had multiple branches, each branch was individually aged back to the original ramet or, in the case of broken plants, the oldest available ramet. In some branched plants, there was disagreement among the branches in estimated age. Inconsistent aging was caused by ramets that did not give rise to a new ramet in the next year, ramets that produced a ramet in the same year it originated (different rank), or when a ramet greater than one year in age produced a new ramet. In these cases, the age from the branch that could most clearly be aged was used. Often this was the youngest age.

Based on this analysis, the estimated age of plants at Pease ranged from 2-14 years (Figure 9). The mean minimum age was 6.3. The modal age was 3. Brown plants also ranged in minimum age from 2–14 years old, but here the mean minimum age was 6.1 years, with 6 year old plants being the most common. Plants ranged from 4-14 years old at Bellamy, with a mean minimum age of 6.9. Most plants fell in the 6 year old age class. At Peverly, the plants ranged from 2-5 years with the mean minimum age being 3.4. The modal age was 3.

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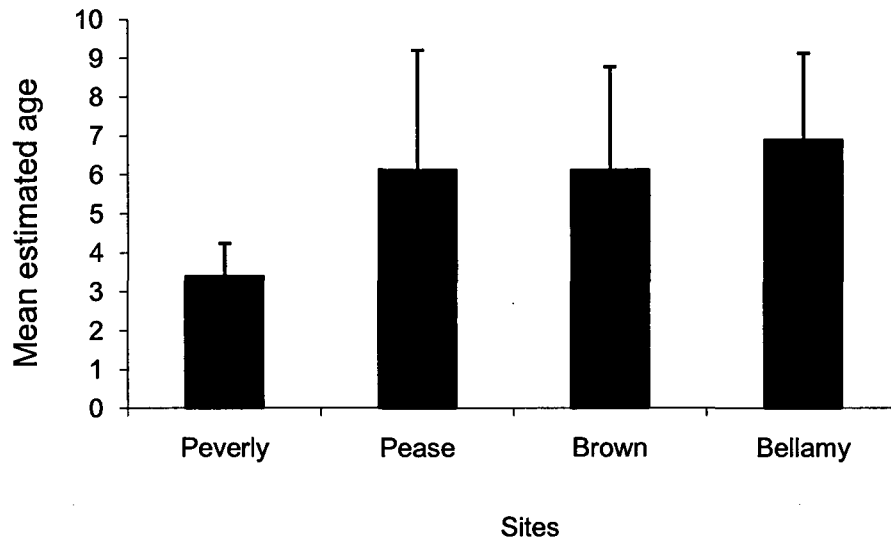
Figure 9. Comparison of mean age estimates of *Lythrum salicaria* at four sites in southeastern New Hampshire (st. dev.).

At Peverly, Pease, and Bellamy 72 – 88% of plants were complete, including what appeared to be the original ramet. The remaining plants ended in a broken ramet. Only 12% of the plants at Brown were complete. The plants at Brown were difficult to extract from the deep water (greater than 1 m in some cases) and dense peat and tussocks of *Carex stricta*.

When a plant was branched, I estimated plant age from each branch. Specifically, I counted the ranks of ramets on each branch starting with the most recent ramet and working back to the original ramet or break. For each plant, I then compared the ages to see if they were congruent. If age estimates differed among branches, I determined the difference between the maximum and minimum age estimates and called this 'deviation in years'. At all four sites,

mean deviation was less than 1 year (Table 3). The maximum deviation in years

was 3 at both Pease and Brown.

Table 3. Number of plants[1] with branches, mean plant age based on all
branches, mean minimum and mean maximum age, and deviation in branch
age (max − min) of Lythrum salicaria individuals at four southeastern New
Hampshire sites.

	Number of plants with branches	Mean age	Mean Minimum age	Mean Maximum age	Deviation in Years (max age − min age)	Maximum Deviation
Pease	34	7.8	7.4	8.1	0.8	3
Bellamy	23	7.1	6.9	7.3	0.4	2
Brown Mill	9	6.6	6.3	6.9	0.6	3
Peverly	2	3.5	3.5	3.5	0.0	0

Age structure graphs of Lythrum salicaria at the four sites show that these

populations were multi-aged (Figure 10). It appears that these populations had

continual recruitment, but because some plants were damaged and thus

impossible to age, recruitment patterns were difficult to determine. At Bellamy

and Pease, the percentage of broken plants was 11.1% and 26.7%, respectively.

At these sites, the number of broken plants seemed to increase with age. The

percentage of broken plants was 22.2% at Peverly. These plants were much

smaller in size than those at the other three sites. A larger percentage of broken

plants occurred at Brown (88%) due to the difficulties during extraction and to the

decomposition of the buried portions of these plants.

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[1] Plant number exceeds 30 at Pease as some Lythrum salicaria plants identified and tagged as
individuals were later determined to be comprised of two or more plants that could be identified
as separate individuals.
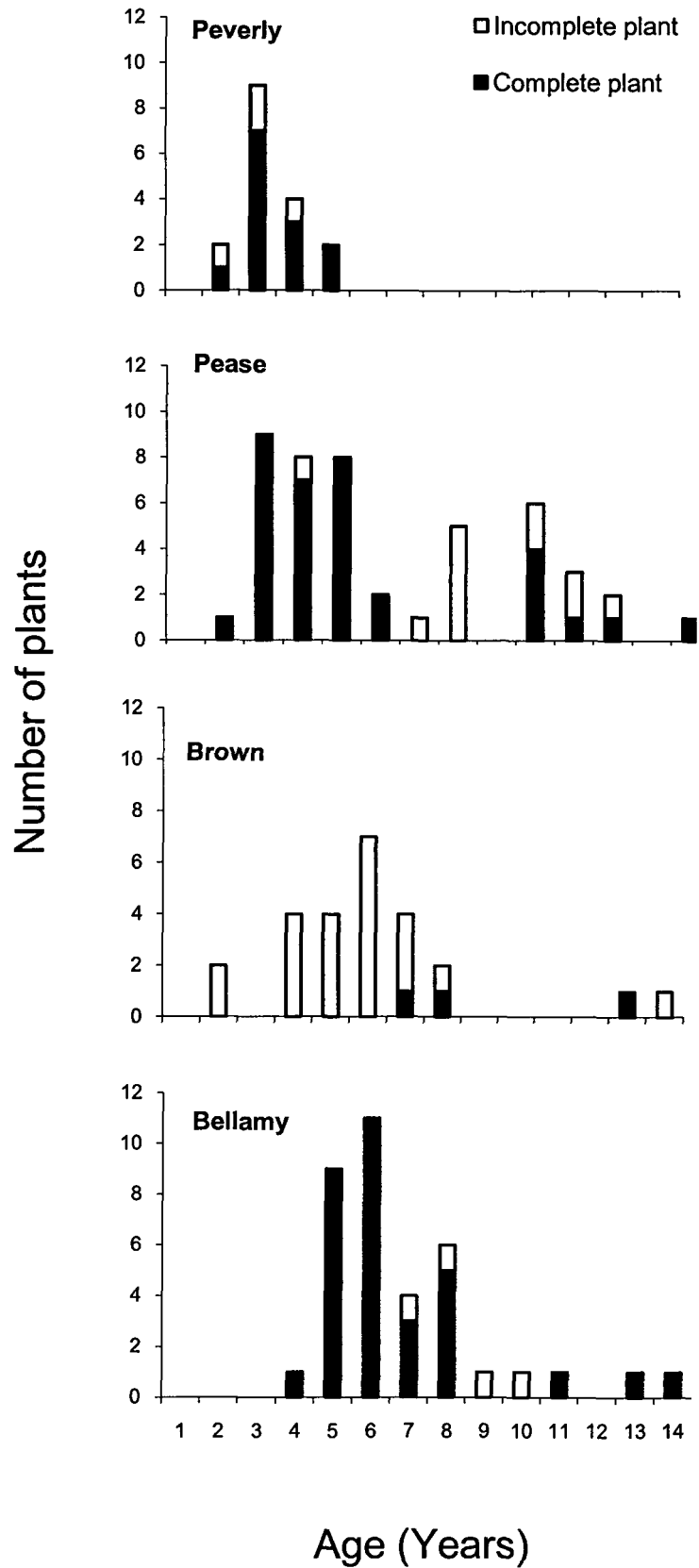
Figure 10. Age structure of *Lythrum salicaria* populations at four sites in southeastern New Hampshire. Solid columns indicate complete plants, open columns indicate incomplete plants (plants ending in broken or decomposed ramets).

C.   Effects of Clipping

Individual loosestrife ramets can produce new shoots either from buds within a few cm at the base of the ramet, or from the axils of leaves which occur from near the ramet base to the ramet tip. I refer to shoots produced from the leaf axils as 'lateral ramets' and those from basal buds as 'basal ramets'. Lateral ramets have a distinctive growth form in which they ascend from the axils of leaves and leaf scars, forming a "V" relative to the original ramet. Basal ramets have a distinguishable curvature from the point of origin on the base of the original ramet (Figure 11).

a)   b)
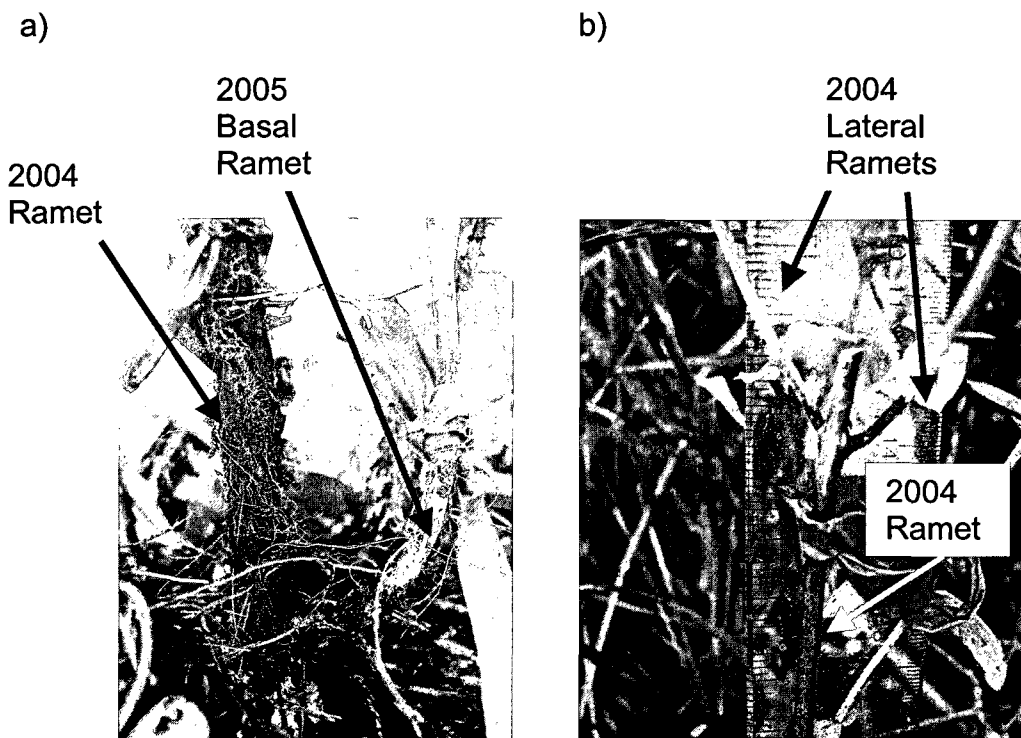
Figure 11. *Lythrum salicaria* ramet producing a) a basal ramet and b) lateral ramets on clipped ramet.

Of the ramets that were clipped at 16 cm above water level in 2004, 92.5% at Pease and 92.1% at Bellamy produced lateral ramets later that year (Table 4; note that observations were mean percent of ramets producing lateral ramets per plant). The unclipped ramets on the same plants produced lateral ramets less frequently: 11.1% of the ramets at Pease and 13.1% at Bellamy. It is important to note that clipped ramets had less stem length available for lateral ramet production than did unclipped stems. The percent of ramets producing lateral ramets varied significantly between the clipped and unclipped treatments (Kruskal-Wallis non-parametric ANOVA, for Bellamy $\chi2 = 40.3$, d.f. = 1, P < 0.001; for Pease $\chi2 = 40.2$, d.f. = 1, P < 0.001). The control plants (no clipped ramets) at these sites produced lateral ramets less frequently, however the difference was not significant (5.1% at Bellamy, 5.1% at Pease) than unclipped ramets on clipped plants (Kruskal-Wallis non-parametric ANOVA, for Bellamy $\chi2$ = 0.065, d.f. = 1, P = 0.799; for Pease $\chi2$ = 0.250, d.f. = 1, P = 0.617). At all sites and in all treatments, the ramets produced in 2004 were of the lateral form and were not produced from the bases of ramets.

Table 4. Percent of *Lythrum salicaria* ramets that produced lateral ramets in two southeastern New Hampshire sites in 2004. Observations were the mean percent of ramets producing laterals per plant.

Site	Number of Plants	Clipped Ramets (%)	Unclipped Ramets (%)	Control Ramets (%)
Pease	30	92.5	11.1	5.1
Bellamy	30	92.1	13.1	5.1

IV. DISCUSSION

A. Can we age purple loosestrife plants?

The method of aging purple loosestrife proposed by Anderson (1991) assumes that each current year ramet produces a single rank of one or more new ramets in the following year, and that each new ramet arises from basal buds on the ramet of the previous year. Anderson noted that over time the persistent woody base creates a sequential pattern of growth with multiple branches radiating from a central core. By counting the progression of ramets backwards from the current year's ramet to the original ramet or oldest ramet, a minimum age can be estimated.

My results suggest that, while Anderson's assumptions are usually met, there are some notable exceptions. Most importantly, not all new ramets emerged from the basal buds of the previous year's ramets. Some ramets arose from root tissue, some arose from the base of ramets produced earlier in the year, others arose from ramets that were more than one year old, and the origin of some was difficult to determine.

Production of new ramets from ramets more than a year old is the most serious source of error in aging loosestrife. For example, a ramet produced in 2004 may produce a ramet in 2005 and another in 2006 (Figure 12a), or a branch may not produce a new ramet in 2005, but does so in 2006 (Figure 12b). In both cases, simply counting backwards through the ranks of ramets would yield an under-estimate of age. The problem is not negligible, as between 1.6 and 5.6% of new ramets arose from ramets more than a year old in my study, numbers that compare favorably to Anderson's (1991) estimate of 4% from sites in Massachusetts. Gilbert and Lee (1980) noted that some loosestrife plants may not produce new ramets in some years. In addition, stressed plants may decrease ramet production (Rawinsky 1982).

a.   b.
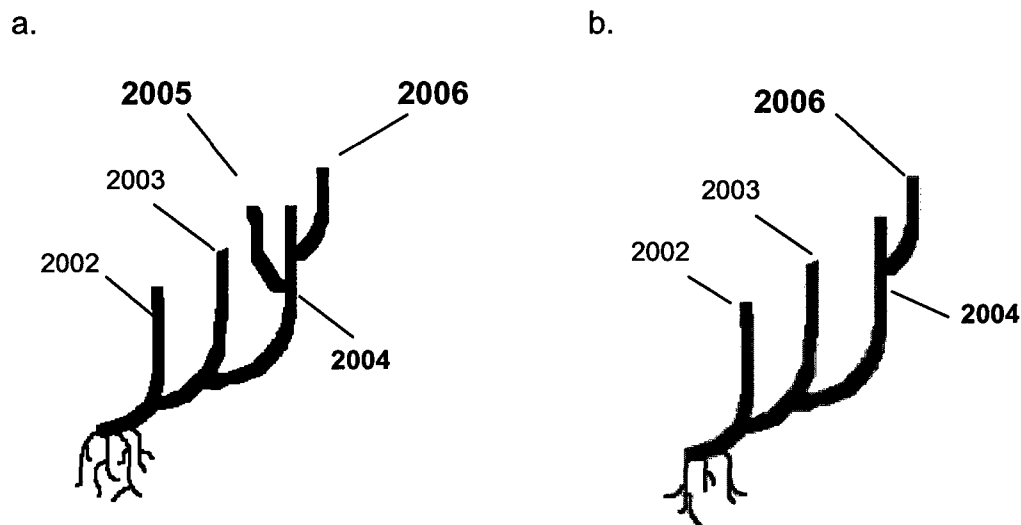
Figure 12. Stems of *Lythrum salicaria* depicting: a) a 2004 ramet producing ramets in both 2005 and 2006 and b) a 2006 ramet produced from a 2004 ramet.

Overestimation of plant age can be avoided to some extent with branched plants. Anderson (1991) was able to verify estimated plant age by comparing the ages of different branches on the same plant. Using this method, I was able to estimate a minimum mean age for most of my plants (55% of the aged plants were branched) even when ramets were not produced sequentially.

Ramets arising from root tissue do not necessarily prevent Anderson's method from being used to age loosestrife. It is usually obvious when ramets arise from roots, and as long as some ramets on the plant produce new basal ramets every year, accurate aging of the plant should be possible. Anderson (1991) found that the sequential branching pattern was hampered by compacted soils resulting in a compressed appearance where stem tissues fuse forming a woody central core.

Only in one instance (out of 248 ramets examined in my study) did I observe a 2004 ramet producing two ramets of differing rank in 2005 (i.e., the first 2005 ramet gave rise to another ramet in 2005). The initially produced 2005 ramet on this plant, which was located at Peverly, was damaged (either eaten or trampled) close to the base of the plant by white-tailed deer (*Odocoileus virginianus*). As shown by my clipping experiment, plants respond to herbivore damage on the upper portion of the ramets by producing multiple lateral ramets from axillary buds immediately below the point of damage. Consumption of

ramets close to the basal portion of the plant, however, may result in the release of buds near the stem base. These ramets may resemble the basal ramets typically produced at the start of each year.

I was not able to determine the origin of some ramets. In some cases this was due to stem breakage during extraction or decomposition of plants in deep water. Radial proliferation of stem tissue sometimes impaired the ability to clearly identify where a stem originated. This was most problematic where the stem was produced at or near the junction of shot and root tissue. Inability to determine ramet origin complicates the estimation of plant age. However, as noted above, if the plant has multiple branches, a minimum plant age can be estimated by comparing the ages and growth patterns of the different branches.

The minimum age of each purple loosestrife plant was derived by counting backwards from the youngest to the oldest available ramet. When possible this included the original ramet tissue. The original ramet tissue was not present on some plants due to stem decomposition or stem breakage during extraction. At Brown, many loosestrife plants were broken during extraction from the dense *Carex stricta* tussocks and some plants in deep water were partially decomposed. Broken loosestrife stems are capable of serving as vegetative propagules (Brown and Wickstrom 1997, Thompson et al. 1987). Given the

frequency of broken and decomposed plants at Brown, plant age was certainly underestimated.

Even when whole plants were collected, age was probably greater than estimated. Radial proliferation of stem and root tissue at the original base of the plant often covered the remnants of stems produced earlier, making it difficult to determine if the oldest observed ramet was indeed the first. Some have tried to age loosestrife by counting the annual growth rings (Dietz 2002). However, this method might not work well with loosestrife as older sections of root may die off. It was not possible to estimate how many years came prior to the oldest discernible ramet in either the whole or incomplete plants. Thus, using the aging method outlined here results in a minimum estimation of age.

I found that loosestrife plants respond to manual clipping by producing lateral ramets just below the point of damage. Similarly, Schat & Blossey (2005) observed an increased branching resulting from insect herbivory on foliage. Severe herbivory alters the branching pattern in loosestrife and may affect the ability to estimate age. Some stems at Peverly were consumed to the base of the plant by white tailed deer. The result was new stems produced close to the plant base and in some cases from root tissue. Although severe herbivory may complicate the estimation of age, a small amount herbivory and damage to the upper portion of the ramets will not affect the ability to age, as it only releases

axillary buds resulting in lateral ramets. High levels of herbivory at Peverly were not only associated with the single case of multiple basal ramets but also with whole plant mortality.

The loosestrife populations at Bellamy, Pease, and Brown were estimated to be a minimum of 14 years old and a minimum of 5 years at Peverly. As some plants were incomplete and, in whole plants, the first years were not always included in the age estimate, these populations were likely older than estimated. Even if plants could be aged accurately, these populations might be older than their oldest living plant and may have been in existence for many generations. Both Bellamy and Pease are recent impoundments formed in the 1960's; therefore, the loosestrife populations were at most ca. 50 years old when I sampled them. The loosestrife population at Peverly was as great as ca. 100 years old as Upper Peverly Pond was constructed around the 1900's. It is more difficult to determine the maximum possible age of the populations at Brown as this site has been in existence for over 200 years.

Herbaceous plants vary greatly in maximum ages. Of the loosestrife plants aged, I estimated the oldest plants to be 14 years old, while Anderson (1991) reported loosestrife plants in wetlands of northeastern Massachusetts that were at least 22 years old. Inghe & Tamm (1985) calculated the half life of *Hepatica nobilis* and estimated a range from 32 years to 320 years old. A review

of 23 herbaceous species determined life spans to range from 3.9 – 127.7 years (Garcia et al. 2008). Similarly, Harberd (1962) found that a population of *Festuca rubra* was mostly derived from clones, despite the short lived nature of the perennial. Given the pattern of stem proliferation of loosestrife described in this study, it is possible that loosestrife could grow indefinitely. In addition, loosestrife has the ability to vegetatively propagate from stem fragments (Thompson et al. 1987). Thus, it is possible that the loosestrife plants I sampled were derived from a few individuals and therefore are actually much older than estimated. Despite the potential for unlimited growth, mortality is a factor. At my sites, 22.5% of plants did not survive. Factors such as fluctuating water levels and herbivory can lead to mortality.

B.   Recruitment Patterns and Population Growth

The ability to determine the age structure of a population may be useful to characterize demography, estimate the rate of spread, and develop hypotheses about the processes and factors controlling the invasion. In some cases, the current maximum population age can be used to infer an approximate time of invasion. For instance, Frappier et al. (2003b), used population age structure of *Frangula alnus L.* to estimate that the time of invasion in a forest stand in southeastern New Hampshire.

Age structure can be used to recreate invasion pattern and elucidate the rate of expansion. Wangen and Webster (2006) were able to reconstruct the invasion pattern of non-native *Acer platanoides* on Mackinac Island in Michigan using dendrochronology. They found a lag time occurred between the introduction of species and period of rapid expansion. Others have been able to map invasion history of common buckthorn and estimated rate of expansion using estimate plant ages (Frappier et al. 2003b).

Age structure can provide insight to the life history characteristics that govern invasion. Frappier et al. (2003b) suggested that the lag phase in the invasion of *Frangula alnus* resulted from early local selection and adaptation to environment. Perkins et al. (2006) aged populations of *Potentilla recta L.*, an invasive plant in northeastern Oregon to examine the relationship between age and plant size or production of flowers. In addition, they studied whether population age was related to either environmental gradients or disturbance history. By reconstructing the invasion pattern and rate of spread, Wangen & Webster (2006) were able to infer that the key factors governing invasion for *Acer platanoides* were seed dispersal and creation of canopy gaps.

Age structures can be used to make inferences about the past and future of a population. In general, a growing population would be dominated by young individuals with numbers of individuals per age class declining with age

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(Silvertown and Charlesworth 2001). Similarly, a population with few juveniles and dominated by old individuals would be declining. A population characterized as having episodic or irregular recruitment would be described as some classes being well represented and others with few or no individuals. A population fitting this description could either be stable or be in decline depending on the rate of mortality. I suggest that the loosestrife populations at my four sites can be characterized as being dominated by older individuals with episodic recruitment.

Similar to my results, Anderson (1991) found that his Massachusetts loosestrife populations were dominated by older plants and, based on lack of representation in some age classes, appeared to have irregular recruitment. In both our populations it was difficult to know if these loosestrife populations were increasing or decreasing in number of individuals. Age specific mortality rates would provide the insight needed to determine if a population is growing or in decline. In an increasing population, the population would be dominated by young genets with few older individuals. In a declining population, the population would be dominated by older individuals. If my populations were increasing at all, expansion would be occurring slowly as recruitment seems to be occasional. The absence of 1 year old plants at my sites is an artifact based on the methods of sampling. Loosestrife plants flagged in 2004 would be at least 2 years old when extracted in 2005. The infrequent number of 2 year olds at my sites could be a result of either low recruitment, the juveniles are hard to identify, or a biased sampling procedure. It is unlikely juveniles were missed as the area was

searched closely. It is possible that older plants with a greater number of ramets were more likely to be selected. At the Bellamy, Brown, and Pease sites there are certain age classes not represented. At Bellamy age class 12, at Pease age class 9, and at Brown age classes 9-12 are not represented. Plants either did not survive or there was no recruitment in these years. Given the number of juveniles at my four sites is low it is unlikely that loosestrife will become a dominant figure at these sites. Anderson (1991) also thought it was unlikely that loosestrife would form a monoculture at his sites. However, the existing plants (genets) may expand by production of increasing numbers of new ramets, and until we know the rate of expansion it is dangerous to say the populations are in decline. However, in Table 1, the total number of ramets per plant either stays the same or is in decline.

Lower survival and obvious herbivory at Peverly suggest that constant pressure from white tailed deer prevent these plants from reaching ages from in excess of 5 years. In contrast, the other populations have plants that are at least 14 years old. Anderson (1991) reports ages of up to 22.

In North America, loosestrife invades two wetland types: recently disturbed habitats and established, undisturbed wetland. Some research has emphasized the tendency of loosestrife to form monocultures, but monocultures are typically found only on sites that have been recently and heavily disturbed

(Rawinski 1982, Thompson et al. 1987). In these cases, loosestrife colonizes open space quickly and at high densities. Neither my sites nor Anderson's showed evidence of loosestrife forming monocultures. In older, less disturbed wetland communities, loosestrife has a different population structure. As the community matures, limited access to resources due to competition reduces recruitment and the rate of expansion slows. In an established wetland, only occasional recruitment is expected.

V.   CONCLUSION

Current year ramets of purple loosestrife generally emerged from basal buds on a previous year's ramet.   While current year ramets occasionally originated on stem tissue or on older ramets, it was usually possible to estimate the age of an individual by counting the number of ranks of ramets. Some plants (34%) were broken due to decomposition and others during the process of extraction. Even though the breakage interfered with the ability to accurately age these plants, I was still able to estimate a minimum age.

Other ramets originated elsewhere on the plant (current year ramets, ramets 1 year or older, and root tissue).   Over-estimation of age would result if a current year ramet produced an additional ramet in the same year. A new ramet that was produced on a ramet greater than one year old would result in the under estimation of age. A minimum mean age can be estimated on plants that are branched by aging each branch separately. This can alleviate errors that may arise when ramets are not produced by basal buds on previous year ramets.

Using this method of aging, I was able to estimate a minimum age for four populations in the New Hampshire Seacoast region. Minimum population ages were 2 and maximum ages were 14. The mean age at Bellamy, Brown, and

Pease was 6. The mean age at Peverly was 3. Based on the age structure of loosestrife in these four wetlands, the populations were dominated by older individuals and had relatively few juveniles. Given the low number of juveniles at my sites, it is unlikely that loosestrife will become a dominant species in the future. However, as some plants were damaged and thus impossible to age accurately, actual recruitment patterns were difficult to determine.

Loosestrife ramets can produce new shoots either from buds within a few cm the base of the ramet (basal ramet), or from the axils of leaves (lateral ramet) which occur from near the ramet base to the ramet tip. I investigated whether or not mechanical damage to stems affected basal ramet production and thus the method of aging. Loosestrife plants responded to clipping by producing lateral ramets on 92% of the ramets clipped at Bellamy and Pease. At all sites and in all treatments, the ramets produced in 2004 associated with clipping were of the lateral form and were not produced from the bases of ramets. Thus, unless mechanical damage occurs close to the plant base, it is unlikely to induce the production of basal ramets that would confound the aging process.

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