E. alatus plants to be at least in the hundreds of thousands and more likely in the millions. In Connecticut alone, sales of just the cultivar Compactus represent $5 million annually (Heffernan, 2005).

Unfortunately, many of the same characteristics that make E. alatus a successful ornamental in challenging planting locations also makes it potentially aggressive in natural environments. Although E. alatus is grown primarily for its dependable red fall foliage, its orange aril fruits are considered another important ornamental feature. Mature E. alatus plants can produce thousands of seeds annually that may be dispersed by birds, small mammals, and surface water runoff. Seeds may establish feral populations in areas located a considerable distance from the original plantings. E. alatus is currently considered invasive in many states in the eastern United States (Ding et al., 2006; Mehrhoff et al., 2003). Concern over the detrimental ecological effects of E. alatus has prompted many states to consider banning the sale of this species. Both Massachusetts (Anonymous, 2005) and New Hampshire (Anonymous, 2004) have passed legislation banning the sale of all E. alatus. Two counties in Long Island, NY, have legislation in place that will ban E. alatus in 2016 (Anonymous, 2009a, 2009b).

For several woody plants, including Acer, Berberis, Buddleja, and Rhododendron, studies have revealed that certain cultivars may produce significantly fewer seeds than the species or other cultivars (Anisko and Im, 2001; Conklin and Sellmer, 2009; Lehrer et al., 2006; Wheeler and Starrett, 2001). These low-fruiting genotypes are often considered to represent a smaller environmental threat than the more prolific genotypes of the same species (Knight et al., 2011). In Connecticut, 25 cultivars of Japanese barberry that produce high seed yields were voluntarily banned by the Connecticut Nursery and Landscape Association and only lower fruiting cultivars may be sold after 2013 (Connecticut Nursery and Landscape Association, 2010). In Oregon, where there is a ban on Buddleja davidii, cultivars that produce less than 2% viable seeds are exempt from the ban (Oregon Department of Agriculture, 2010).

Because E. alatus is a popular commercial species, there is considerable pressure to avoid a complete ban of the species and allow the sale of “safe” genotypes that are less prolific seed producers (Knight et al., 2011). Preliminary research suggests that substantial differences in seed production may exist between E. alatus cultivars. Ranney et al. (2007) found that 'Odom' Little Moses produced only 3% of the fruit set observed on 'Compactus', the most important commercial cultivar. Finesseth et al. (2009) found that 'Rudy Haag' produced extremely low amounts of seeds in comparison with 'Compactus'. Both studies suggest that use of the low seed-producing cultivars may reduce the risk of invasion.

Nineteen E. alatus cultivars are known (Dirr, 2009), e12 of which are available in commerce in the United States and are prominent in the nursery and landscape arena. This study was conducted to broadly examine E. alatus cultivars to determine if any may be promoted as non-invasive. We studied cultivar seed production as well as germination, establishment, and survival in a deciduous woodland. In a separate study we investigated which types of natural environments were most conducive to E. alatus seedling establishment. Because most trees and shrubs are both heterozygous and cross-pollinated (Hartmann et al., 2011), our experimental design included significant opportunity for cross-pollination by many genotypes. Previous studies on E. alatus fruiting potential may have produced low fruit set results as a result of inadequate cross-pollination or immaturity of experimental plants.

Materials and Methods

Cultivar seed production. Nine winged euonymus cultivars were evaluated: 'Compactus', 'Groove Compact', 'Monstrosus', 'Nordine Strain', 'Odom' Little Moses', 'Pippaz' Pip squeak·, 'Rudy Haag', 'Select' Fire Ball', and 'Timber Creek Chicago Fire'. Plants were obtained from eight nurseries. All plants were maintained at the University of Connecticut, Department of Plant Science Research Farm, Storrs, CT (lat. 41.794415°; long. -72.227320°) in USDA hardiness zone 5, in Paxton and Montauk fine sandy loam,
with full sun exposure. The corridor between New York, NY, and Boston, MA, has been heavily invaded by *E. alatus*, so the study location in Storrs, CT, is ideally situated in an area where *E. alatus* grows well (Mehrhoff et al., 2003). Plants were installed in the field in May 2004 with three replications of each cultivar. Cultivars were arranged in a completely random design. At the time of field establishment, plants were 3 years old from rooted cuttings. Spacing within rows was 3 m on center and spacing between rows was 4.5 m on center. Clean cultivation was maintained within rows using hand-weeding and early summer application of glyphosate herbicide. Grass alleyways were mowed between rows.

Plants were allowed to establish in the field for three growing seasons and were 6 years old when first evaluated for seed production. Seed data were collected in Oct. 2006 and 2007 when capsules ripened and orange–red arils were visible. Plants were harvested completely with all fruits present removed by hand. Each capsule produces a single aril/seed, so fruit counts are equivalent to seed counts. Data were subjected to analysis of variance (PROC MIXED) and mean separation using Fisher’s least significant difference (PROC LSMEANS) in SAS for Windows Version 9.2 (SAS Institute Inc., Cary, NC).

Germination and establishment of *E. alatus* ‘Compactus’ were studied in five environments. The dry woods site was the full sun meadow, edge of woods, dry deciduous woods, moist deciduous woods, and pine woods. We selected these environments, which differed in sunlight exposure, soil moisture, nutrient content, and vegetation (Table 1), because they represent a broad range of environments found in southern New England. All five environments were located on unmanaged University of Connecticut properties in northeastern Connecticut. The first round of this study was initiated in 2003 and a second round was initiated in 2004. On cloudless days in April and July of 2004, sunlight (μmol·m⁻²·s⁻¹) was measured at all five environments with a LI-191 line quantum sensor connected to a LI-189 quantum meter (LI-COR Inc., Lincoln, NE). Readings were taken between 1200 and 1300 HR.

We considered the light measurement at the full sun meadow site to represent 100% sunlight and the sunlight level for the four other environments was determined relative to the full sun environment. In Nov. 2003, four soil samples (15-cm cores) were extracted from each site. The samples were homogenized into one composite sample for each site and a subsample was removed from each composite sample for soil moisture analysis. Subsamples were weighed, dried overnight at 25 °C, re-weighed, and the percent soil moisture calculated. The remaining composite samples were sent to the University of Connecticut Soil Nutrient Analysis Laboratory, Storrs, CT, for analysis of: 1) nutrients, using a Modified Morgan Extractable test; 2) organic matter, as determined by loss on ignition; and 3) soil texture.

*E. alatus* ‘Compactus’ seeds were collected from a cultivated planting located on the University of Connecticut campus in Storrs, CT. Seeds were sown in 1 m × 1-m plots at each of the five environments. One hundred seeds, with their orange aril coverings left intact, were sown per plot and there were four replicates per environment. Seeds were broadcast over the plot surfaces by hand in early November and all existing leaf litter, twigs, and vegetation were left in place. A 3-ft tall, 5-cm grid wire mesh fence was installed around the perimeter of the plots to deter disturbance by wild turkeys.

Experimental plots were evaluated for 3 years to satisfy the complex dormancy of *E. alatus* seeds and allow sufficient time for germination and establishment. Germination and survival data were taken in June of each year. Surviving plants were harvested in Sept. 2006 for the first replication of the study and in Sept. 2007 for the second replication of the study. At harvest, the number of branches, total branch length (summed for the entire plant), and dry weight were recorded for each plant. Analysis of variance was conducted using the PROC MIXED procedure of SAS for Windows Version 9.2 (SAS Institute Inc.).

Germination, survival, and growth of seeds from *E. alatus* cultivars in deciduous woods. Seeds from nine *E. alatus* cultivars were evaluated for their ability to germinate, survive, and grow in the previously described dry deciduous woods site. The goal was to observe any differences in the ability of seeds from different cultivars to establish in the same natural environment. The dry woods site was chosen because the study measuring *E. alatus*

Table 1. Descriptions of the five natural environments.

| Site            | Full sunlight (%) | Primary vegetation                                      |
|-----------------|-------------------|--------------------------------------------------------|
|                 | April  | June |                 |                     |
| Dry woods       | 51    | 1    | Maple (Acer sp.), oak (Quercus sp.), ash (Fraxinus sp.), birch (Betula sp.), white pine (Pinus strobus), hemlock (Tsuga canadensis) |
| Edge of woods   | 74    | 39   | Hickory (Carya sp.), oak (Quercus sp.), poison ivy (Toxicodendron radicans), oriental bittersweet (Celastrus orbiculatus), multiflora rose (Rosa multiflora), bramble (Rubus sp.) |
| Full sun meadow | 100   | 100  | Orchard grass (Dactylis glomerata), timothy (Phleum pratense), red clover (Trifolium pratense) |
| Moist woods     | 55    | 1    | Maple (Acer sp.), oak (Quercus sp.), american hornbeam (Carpinus caroliniana), spicebush (Lindera benzoin), interrupted fern (Osmunda claytoniana), jewel weed (Impatiens capensis), skunk cabbage (Symplocarpus foetidus) |
| Pine woods      | 50    | 4    | White pine (Pinus strobus); scattered individuals of American hornbeam (Carpinus caroliniana), maple (Acer sp.), and oak (Quercus sp.) |

| Site            | Sand | Silt | Clay | Soil classification | Organic matter content (%) | Organic matter classification | Soil moisture (%) |
|-----------------|------|------|------|---------------------|---------------------------|-----------------------------|------------------|
| Dry woods       | 52.9 | 34.6 | 12.5 | Sandy loam          | 7.3                       | Medium                      | 35               |
| Edge of woods   | 53.9 | 37.4 | 8.7  | Sandy loam          | 9.0                       | High                        | 63               |
| Full sun meadow | 65.4 | 32.0 | 2.6  | Sandy loam          | 6.5                       | Medium                      | 35               |
| Moist woods     | 47.0 | 37.6 | 15.4 | Loam                | 13.4                      | High                        | 75               |
| Pine woods      | 59.2 | 30.0 | 10.8 | Sandy loam          | 9.6                       | High                        | 35               |

| Site            | Soil pH | Calcium (lbs/acre) | Magnesium (lbs/acre) | Phosphorus (lbs/acre) | Potassium (lbs/acre) |
|-----------------|---------|--------------------|----------------------|----------------------|----------------------|
| Dry woods       | 5.3     | 545 (low)          | 82 (low)             | 1 (very low)         | 183 (medium)         |
| Edge of woods   | 5.2     | 1370 (medium)      | 186 (medium high)    | 1 (very low)         | 285 (medium high)    |
| Full sun meadow | 5.7     | 1118 (medium)      | 216 (medium high)    | 1 (very low)         | 358 (medium high)    |
| Moist woods     | 5.6     | 3057 (high)        | 311 (high)           | 1 (very low)         | 155 (low)            |
| Pine woods      | 4.4     | 85 (very low)      | 12 (very low)        | 1 (very low)         | 78 (very low)        |
'Compactus' seed growth in five environments showed that the dry deciduous woods was the most favorable for establishment. The study was conducted twice with one-time replication beginning in 2006 and the second beginning in 2007.

Seeds used in this study were collected fresh each year from the replicated cultivar planting at the University of Connecticut, Department of Plant Science Research Farm, Storrs, CT. Seeds of each cultivar were sown in early November into 30 cm × 60-cm wooden frames that were 8 cm tall. The wooden frames were recessed halfway into the soil and all forest floor litter was left in place. Forty seeds were sown per frame by hand-broadcasting over the plot surfaces. The brown aril coverings were left intact on seeds used in this study. There were five replications of each cultivar treatment arranged in a randomized complete block design. After seed sowing, frames were covered with hardware cloth with 6-mm mesh openings to protect the seeds from disturbance by birds and small mammals. Experimental plots were harvested in early September, 3 years after the seeds were sown. The number of seedlings present was counted and all seedlings were harvested at the soil line and dry weights were determined. Data were subjected to analysis of variance (PROC MIXED) and mean separation using Fisher’s least significant difference \((P \leq 0.05)\) using SAS for Windows Version 9.2 (SAS Institute Inc.).

**Results and Discussion**

*Cultivar seed production.* All cultivars of *E. alatus* produced seeds with no cultivar yielding consistently low production (Table 2). Two cultivars, *Compactus* and Nordine Strain, produced over 8000 seeds per plant. ‘Monstrosus’ had the lowest 2-year average seed production (981) but was not statistically different from the other cultivars except ‘Compactus’. Seven of nine cultivars produced more seeds in 2007 than in 2006, suggesting that larger plant size and maturity may be important considerations when evaluating the potential seed production of *E. alatus* cultivars.

Ranney et al. (2007) found that 3- to 4-ft tall by 2- to 3-ft wide plants of ‘Odom’ Little Moses™ produced only seven fruits per plant, whereas plants of ‘Compactus’ produced 270 fruits per plant. They suggest that the lower fruit set on ‘Odom’ Little Moses™ may have been the result of denser foliage and branching of this cultivar in comparison with ‘Compactus’, which reduced pollinator access. Hand pollinations produced similar fruit set on ‘Odom’ Little Moses™ and ‘Compactus’, which was provided as further evidence in support of reduced pollinator access. In 2007, we found that ‘Odom’ Little Moses™ produced 1786 seeds per plant and ‘Compactus’ plants produced 8086 seeds (Table 2). The significantly higher seed production we observed for both cultivars may be attributed to larger, longer established plants with wide cross-pollination by nine genotypes rather than just two. With *E. alatus*, like with many woody species, it is important that studies evaluating cultivar seed productivity use plants that are old enough and sufficiently established to fully express their reproductive potential. Ample opportunity for cross-pollination with many other unrelated genotypes may also be important to accurately assess seed set potential in a manner that is representative of typical landscape settings.

Another study in Kentucky examined seed production by ‘Compactus’ and ‘Rudy Haag’ (Finneseth et al., 2009). Over a 3-year evaluation period, ‘Compactus’ produced on average 1238 seeds per plant, whereas ‘Rudy Haag’ produced only 12 seeds per plant. This seed production again falls well below what we observed for ‘Compactus’ and ‘Rudy Haag’ (Table 2). Both the Ranney et al. research (North Carolina) and the Finneseth et al. work were conducted in locations much further south than Connecticut and it is possible that *E. alatus* sets seed better in cooler regions, although there is no published evidence to support this theory.

**Germination and establishment of *E. alatus* ‘Compactus’ seeds in five environments.** No seeds of *E. alatus* ‘Compactus’ germinated in any environment in the first spring after fall sowing (Table 3). Substantial germination was observed, however, in the second spring with a small amount of additional seed germination occurring in the third spring. This germination pattern suggests that *E. alatus* seeds have a complex dormancy that requires one or more cycles of warm stratification followed by cold stratification to stimulate germination. Our results contradict most references, which state that *E. alatus* seed dormancy can be relieved by 90 d of cold stratification and not warm stratification (Dirr and Heuser, 1987; USDA,

### Table 2. Seed production per plant for *Euonymus alatus* cultivars for 2 consecutive years.

| Cultivar            | Seeds/plant |
|---------------------|-------------|
|                     | 2006        | 2007        | Combined 2-year avg |
| Compactus           | 4094 a      | 8086 a      | 6990 a              |
| Grove Compact       | 487 b       | 1928 b      | 1208 c              |
| Monstrosus          | 1597 b      | 365 b       | 981 c               |
| Nordine Strain      | 857 b       | 8362 a      | 4609 ab             |
| Odom Little Moses   | 308 b       | 1786 b      | 1047 c              |
| Pipzam Pipsqueak    | 850 b       | 3532 ab     | 2191 bc             |
| Rudy Haag           | 986 b       | 2186 b      | 1586 bc             |
| Select Fire Ball    | 275 b       | 2020 b      | 1148 c              |
| Timber Creek        | 3596 a      | 2660 b      | 3128 abc            |
| Average for all     | 1450        | 3436        |                     |

*Mean separation of cultivars within columns by Fisher’s least significant difference test at \(P \leq 0.05\).*

### Table 3. Germination, survival and growth of *Euonymus alatus* ‘Compactus’ seeds in five natural environments.

**Time replication 1**

| Environment       | First year germination (%) | Second year cumulative germination (%) | Third year cumulative germination (%) | Seeding survival (%) | Seedling dry wt (g) | No. of branches per plant | Total branch length (cm) |
|-------------------|---------------------------|---------------------------------------|--------------------------------------|---------------------|---------------------|--------------------------|--------------------------|
| Dry woods         | 0 a^2                     | 34.8 a                                | 37.8 a                               | 80.7 b              | 0.13 a              | 1.1 a                    | 6.8 a                    |
| Edge of woods     | 0 a                       | 0.3 b                                 | 1.0 b                                | 100.0 a             | 0.05 b              | 1.0 a                    | 4.6 a                    |
| Full sun meadow   | 0 a                       | 0 b                                   | 0 b                                  | N/A                 | N/A                 | N/A                      | N/A                      |
| Moist woods       | 0 a                       | 0.3 b                                 | 0.3 b                                | 100.0 a             | 0.03 b              | 0.3 b                    | 1.5 b                    |
| Pine woods        | 0 a                       | 28.5 a                                | 32.3 a                               | 55.2 c              | 0.15 a              | 1.2 a                    | 7.3 a                    |

**Time replication 2**

| Environment       | First year germination (%) | Second year cumulative germination (%) | Third year cumulative germination (%) | Seeding survival (%) | Seedling dry wt (g) | No. of branches per plant | Total branch length (cm) |
|-------------------|---------------------------|---------------------------------------|--------------------------------------|---------------------|---------------------|--------------------------|--------------------------|
| Dry woods         | 0 a^2                     | 31.0 a                                | 31.8 a                               | 77.1 a              | 0.13 a              | 1.2 a                    | 8.7 a                    |
| Edge of woods     | 0 a                       | 0 b                                   | 0 c                                  | N/A                 | N/A                 | N/A                      | N/A                      |
| Full sun meadow   | 0 a                       | 0 b                                   | 0 c                                  | N/A                 | N/A                 | N/A                      | N/A                      |
| Moist seeds       | 0 a                       | 0 b                                   | 0 c                                  | N/A                 | N/A                 | N/A                      | N/A                      |
| Pine woods        | 0 a                       | 9.5 b                                 | 13.0 b                               | 83.3 a              | 0.13 a              | 1.1 a                    | 8.4 a                    |

^Within time replication mean separation in columns by Fisher’s least significant difference test \(P \leq 0.05\). Data were subjected to arcsine transformation before analysis. Untransformed data are presented.

^Survival after 16 months for seedlings, which germinated in the second year. N/A = not applicable.
The dry deciduous woods and pine woods were the only two environments that supported significant germination. A maximum cumulative germination of 37.8% occurred in the dry deciduous woods. In time replication 1, the pine woods produced a statistically similar germination percentage to the dry deciduous woods, but in time replication 2, the pine woods produced only one-third the germination observed for the dry deciduous woods. No seeds germinated in the full sun meadow environment in either time replication. The moist deciduous woods and the edge of woods environments produced less than 1% germination in the first time replication with no seeds germinating in the second time replication.

Lubell and Brand (2011) found that Japanese barberry, another invasive woody shrub, also germinated well in a dry deciduous woods environment. Unlike E. alatus ‘Compactus’, however, barberry also germinated well in a full sun meadow environment and failed to germinate in pine woods. Because barberry seeds require only a single winter stratification period to break dormancy and germinate, seeds that land on top of the thick layer of needle duff typically found in pine woods are very vulnerable to desiccation when they germinate in the first spring after fall sowing or natural deposition (Lubell and Brand, 2011). E. alatus ‘Compactus’ seeds that land on the thick layer of needles, however, do not germinate until the second spring as a result of a complex dormancy requiring alternating warm moist and cold moist stratification. This time delay allows the euonymus seeds to be sheltered with two annual layers of cast needles, which provide a more uniformly moist environment than that experienced by the quick germinating barberry seeds. Ellis and Manley (2003) documented an 8-acre E. alatus invasion in mid-Coast Maine found beneath an Eastern white pine canopy. Feral establishment of E. alatus in a natural pine woods setting supports our findings about establishment in coniferous areas.

The failure of E. alatus ‘Compactus’ seeds to germinate in the moist deciduous woods site is understandable, because E. alatus is considered to be intolerant of water-logged soils. It is less clear why E. alatus ‘Compactus’ seeds failed to germinate in the edge of woods or full sun meadow environments because E. alatus incursions are documented in these types of environments (Mehrhoff et al., 2003). Perhaps in the full sun meadow there was too much competition from the very dense grass vegetation, which rapidly developed in the spring and would have shaded and smothered small seedlings developing at the soil surface. Finnseth et al. (2009) reported no germination of E. alatus ‘Compactus’ in a simulated understory seed bank study, although the conditions of the simulated understory environment were not provided. Finnseth et al. (2009) also reported limited persistence (only 2%) of E. alatus seeds in the soil after 12 months, which is in contrast to our study in which germination did not occur for 2 years and then reached as high as 37.8%.

Survival of E. alatus ‘Compactus’ seedlings in environments that supported germination (dry deciduous woods, pine woods) was generally high, reaching up to 80.7% (Table 3). Seedling dry weights were between 1 and 1.5 g and plants were mostly unbranched with a total stem length of as much as 8.7 cm. Overall, E. alatus seedling survival in these two sites was much higher than the 18.1% survival rate attained by Berberis thunbergii in a dry deciduous woods site (Lubell and Brand, 2011). E. alatus seedlings appear to be significantly more resilient than B. thunbergii seedlings when they germinate in favorable environments and their persistence seems to be more probable.

Germination, survival, and growth of seeds from E. alatus cultivars in dry deciduous woods. Overall, cultivar seedling establishment was higher in the 2007 to 2010 time replication than the 2006 to 2009 time replication (Table 4). In the 2006 to 2009 replication, seedling establishment rates ranged from a low of 6.5% for ‘Odom’ Little Moses™ to a high of 42.5% for ‘Monstrosus’. In the 2007 to 2010 replication, all cultivars exceeded 30% seedling establishment with the majority establishing at levels exceeding 40%. Seedling dry weights for cultivars were higher in the 2007 to 2010 time replication than in the 2006 to 2009 time replication (Table 4). Seedlings of most cultivars had an average dry weight of ρ 1 g.

The level of seedling establishment for E. alatus cultivars is dramatically higher than the seedling establishment rate of 3% to 5% reported for Japanese barberry, a comparable invasive ornamental shrub (Lubell and Brand, 2011). In addition, euonymus seedling dry weights are roughly double those reported for Japanese barberry seedlings of the same age (Lubell and Brand, 2011). Winged euonymus may be a more aggressive invader than Japanese barberry because euonymus cultivars produce at least as much seed as barberry cultivars and have greater ability to establish in natural areas and then grow vigorously.

By combining the highest seed set value with the best establishment rate for each cultivar, it is possible to estimate the potential number of seedlings that a medium-to-large sized specimen could contribute each year to a natural environment (Table 5). Using this estimate, large individual plants of cultivars such as ‘Compactus’ and ‘Nordine Strain’ could contribute over 3500 seedlings annually. 'Compactus' is the primary E. alatus cultivar sold for landscaping and millions of these plants have been planted across the United States.
horticultural characteristics, they should be plants prove to be sterile and possess desirable Euonymus alatus should be considered a minimal invasive risk. Cultivars evaluated are non-invasive or should be able to survive in at least some natural environments. Because they can germinate and survive in natural environments, we found that some cultivars produce significantly fewer seeds than others, our data suggest that all cultivars have the potential to produce large amounts of seed if the plants are allowed to mature and are exposed to cross-pollination with different genotypes. Seeds of all Euonymus alatus cultivars we studied also display the ability to use of specific genotypes that appear to set insights into the risks associated with continued invasive plants would provide additional in- formation about their growth rates (Knight et al., 2011). It is likely that even low levels of seed production on Euonymus alatus cultivars will produce positive pop-ulation growth. Further research on how pollen movement, pollen availability, and pollen genetic source influence seed set in invasive plants would provide additional in-sight into the risks associated with continued use of specific genotypes that appear to set limited numbers of seeds.

After considering long-term reproductive potential, we do not believe that any of the cultivars evaluated are non-invasive or should be considered a minimal invasive risk. Cultivar exemptions for these genotypes in areas where Euonymus alatus has been banned cannot be recommended. Recently, triploid Euonymus alatus plants have been produced from seed endosperm tissue (Thammina et al., 2011). If these plants prove to be sterile and possess desirable horticultural characteristics, they should be recommended as the safe alternatives of choice to replace older, seed-producing cultivars.

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