

The Effects of June Precipitation on *Alliaria petiolata* (Garlic Mustard) Growth, Density and Survival

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ABSTRACT. The factors that determine population dynamics of invasive plant species are not well studied. *Alliaria petiolata* (garlic mustard), an invasive biennial, exhibits annual fluctuation in rosette and adult density. June precipitation has been found to correlate with rosette *A. petiolata* density in October and adult density the following May. Since ability to predict density would facilitate management of this invasive species, we experimentally tested the impact of precipitation on *A. petiolata* rosette growth and survival. Rain was excluded in June 2005 from thirty-six 0.8 x 0.8 m plots in a second-growth woodlot in southwest Ohio. Plots were lined to a depth of 20 cm, and randomly assigned to receive a dry (1 cm), average (10 cm) or wet (20 cm) water treatment. In the central 0.25 m² of each plot we assessed soil moisture, rosette root depth, root and shoot biomass, and survival. Soil moisture content, measured with a time domain reflectometer, was significantly affected by treatment. However, rosette biomass, root length, fruit production and survival did not differ among treatments. Assessment of soil water availability between treatments indicated dry treatments may not have dried the soil as much as occurs in drought years. While the hypothesis that heavier June precipitation enables rosettes to survive summer drought was not supported, it cannot be rejected based on our experiment. June precipitation is probably not a reliable predictor of *A. petiolata* rosette survival in years with above average precipitation; however the effect of spring drought on *A. petiolata* requires further investigation.

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INTRODUCTION

Due to the impacts of invasive species on natural communities (Vitousek and others 1996; Wilcove 1998; Parker and others 1999; Mack 2000) and economic costs of control (Pimentel and others 2005), ecologists, conservationists and land managers are concerned about factors that influence population densities of introduced species (D'Antonio and Kark 2002; Mack 2005). The role of abiotic environmental stress (e.g. extremes in temperature, moisture and light) in determining potential invasibility (Burns 2004) as well as distribution (Beerling 1993) and density fluctuations (Winterer and others 2005) in established invasive populations has important implications for invasive management (Alpert and others 2000). If spatial or temporal fluctuations in an abiotic factor affect demographic rates, and hence population size of an invasive species, this abiotic factor may have predictive power for decisions regarding management and control of the species (Slaughter and others 2007).

A native of western Eurasia, *Alliaria petiolata* (M. Bieb.) Cavara and Grande (garlic mustard, Brassicaceae) is an invasive understory herb established throughout the northeastern United States and adjacent Canada (Nuzzo 1993). A biennial, seeds germinate in February or March, and the rosettes (juveniles) live through the summer and often remain evergreen throughout the winter. In the spring of the second year, adults flower, senesce, and set seed (Cavers and others 1979). Some seeds germinate the following spring, while others remain viable in the soil. This seed bank persists about five years (Baskin and Baskin 1992; Byers and Quinn 1998). Most commonly found in shaded riparian, wooded, and roadside areas in the east (Nuzzo 1993; Shuster and others 2005), *A. petiolata* populations exhibit higher survivorship and germination in floodplains than in upland forests with generally drier soils, greater light penetration, and absence of disturbance from floods (Byers and Quinn 1998; Meekins and McCarthy 2001).

From March to July both first-year rosettes and second-year adults are present, and population densities fluctuate from year to year (Baskin and Baskin 1992; Carlson and Gorchov 2004;

Winterer and others 2005; Slaughter and others 2007). Slaughter and others 2007 found that both survival of rosettes from May to October and adult density the following May correlated positively with June precipitation over a 5-year period. For example, in a second-growth stand, rosette survival was lowest (2.5%) following the driest June (6.98 cm) and very high (26.9%) following the wettest June (13.63 cm). They hypothesized moist soil promotes survival of rosettes through the summer, with greater reproduction of *A. petiolata* following wetter years.

While comparisons across years are useful for detecting relationships between weather and population dynamics, establishing cause-and-effect requires controlled studies. In the case of *A. petiolata*, interannual variation in rosette demography could also be due to variation in temperature or rosette competition with adult *A. petiolata*, which may co-vary with precipitation. Rain enclosures have been employed in a variety of ecosystems and habitats to manipulate precipitation duration, intensity, and timing in otherwise natural settings (Foale and others 1986; Owens 2003). Long-term ecosystem studies using permanent rain enclosures have been based in temperate mesic grassland (Harrington 1991; Fay and others 2000), rangeland (Svejcar and others 1999) semi-desert grassland (English and others 2005), and deciduous forest (Bredemeier 1995; Hanson and others 1995; Hanson and others 1998). Small-scale, temporary rain enclosures (Frampton and others 2000; Flemmer 2003) however, reduce costs and enhance flexibility for short-term ecological studies (Owens 2003). Implementing subcanopy rain shelters in forest stands with considerable shrub growth pose additional logistical problems as shelters either need to be small enough to fit between shrubs, be large enough to cover shrubs, and/or need to preclude rainfall in and around shrub and tree trunks (Jacoby and others 1988). Multiple small-scale enclosures avoid pseudoreplication in experimental design, an issue of large-scale enclosure designs due to cost constraints (see Hanson and others 1998).

Our objective in this study was to assess the impact of June precipitation on *A. petiolata* populations in a temperate deciduous forest understory. Specifically, we tested the hypothesis that heavier June precipitation promoted more extensive root growth enabling rosettes to survive summer drought (Slaughter and others 2007). To eliminate confounding effects of temperature and competition

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with adult *A. petiolata*, we tested rosette growth and survival over a single season through a rain manipulation experiment at a site lacking an adult cohort.

Testing of this hypothesis is compelling because the ability to predict density would facilitate management of this invasive species. Fall season herbicide spraying of rosettes is an effective control method of adult *A. petiolata* (Carlson and Gorchov 2004; Slaughter and others 2007). Support of this hypothesis would suggest that control of this invasive by fall herbicide application would be most important and cost effective in years when June precipitation was high (Slaughter and others 2007).

MATERIALS AND METHODS

Study Site

This study was conducted in an approximately 90-year, 4 ha woodlot (Vankat and Snyder 1991) 2.5 km NNE of Oxford, Ohio, at the Miami University Ecology Research Center (ERC), Butler Co. (39°30' N, 84°44' W). Long-term (20-year) mean annual precipitation is 92.4 cm and mean annual temperature is 11.4°C. Forest soils are moderately eroded Russell-Miamian silt loams with 2-6% slopes over limestone bedrock (Lerch and others 1980; Vankat and Snyder 1991) with a mean bulk density of 1.077 g cm⁻³ (Hochstedler 2006). The site was chosen because of its uniform slope, consistent soil type, and protection from the public. Second-growth *Acer saccharum* and *Ulmus rubra* were the major canopy dominants, with a dense shrub layer of *Lonicera maackii* (Amur honeysuckle). Species common in the understory included *Parthenocissus quinquefolia*, *Stellaria media*, *Sanicula canadense*, *Pilea pumila*, *Hackelia virginiana*, *Polygonum cespitosum*, *Impatiens* spp. and *Viola* spp. (nomenclature follows Gleason and Cronquist 1991).

Field Experiment

Thirty-six 50 cm x 50 cm plots were established in areas of rosette density > 15 per 0.25 m² with plot centers > 2.5 m from each other and > 1 m from trees and stems of large *Lonicera maackii*. Around each plot a fixed-location rain shelter was constructed and covered with a clear polyethylene roof (Harrington 1991; Fay and others 2000; Hanson and others 2003; Owens 2003) with open ends to maximize ventilation. Hanson and others (1998), Harrington (1991), and English and others (2005) found the effects of polyethylene covers on understory microclimate to be insignificant. Each shelter was constructed of ½ inch PVC, measured 175 x 175 cm, was 100 cm tall at the peak, was oriented north-south, and anchored with landscaping staples at each corner. Each shelter covered a central 80 x 80 cm experimental plot containing a 50 x 50 cm sampling area (Fig. 1). Lateral movement of surface and ground water was restricted by a 20 cm deep subsurface barrier of aluminum sheeting installed around the plot (Harrington 1991; Fay and others 2000; Flemmer 2003; Owens 2003). Trailing vegetation and roots were clipped at the plot edge in order to install the aluminum sheeting and minimize disturbance to the plot interior.

Plots were randomly assigned to dry (1cm/month), average (10 cm/month), or wet (20 cm/month) June water treatment to simulate drought, average, and high rainfall for the month of June in southwest Ohio. Treatments were based on historic state climatology records (Rogers 1993) and June precipitation over the past 20 years at the ERC (Ohio Agricultural Research and Development Center, The Ohio State University; mean = 9.7 cm). Treatments did not differ in rosette density at the onset of the experiment (Hochstedler 2006).

Shelters were installed over plots May 23, 2005; rainfall in May prior to this date was below average. Beginning in June, one-eighth of the assigned water treatment was applied eight times during the month (twice per week) using a low-pressure backpack sprayer and watering can. Water used in the experiment was collected at the ERC from a barn roof. Due to lack of precipitation during the early part of the month, water from a rainwater supply pond was substituted when rains were not frequent. Nutrient concentration in these water sources was low (Hochstedler 2006). The polyethylene plastic covering the shelters was wiped every other day to clear the surface of fallen leaves, debris and dust, and checked for holes from fallen branches after each storm.

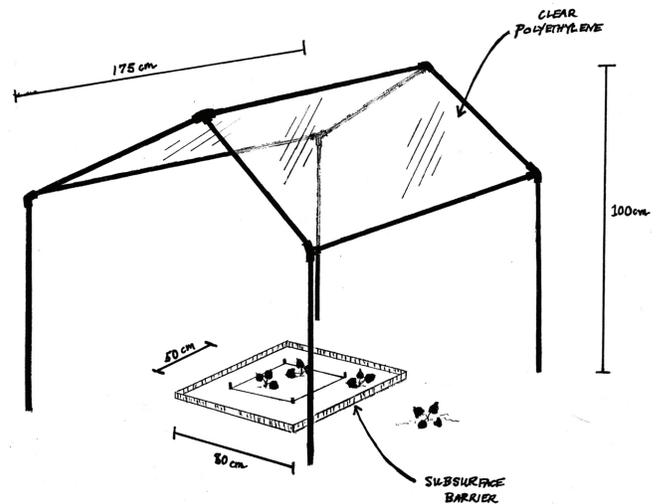


FIGURE 1. Fixed-location rain shelter with sample plot (50 x 50 cm) and subsurface moisture barrier (80 x 80 cm).

To monitor soil moisture-precipitation relationships in each treatment, soil water content in each plot was measured weekly with a time domain reflectometer (TDR, Moisture Point, Environmental Sensors, Inc.) (Jackson and others 2000) with 20 cm probes following the procedure of Topp and Davis (1985). Simultaneous sampling of soil water content by destructive gravimetric and TDR methods was conducted at the study site in September 2005 to verify TDR readings; soil cores for gravimetric measurements were collected to a depth of 20 cm and dried at 105°C to a constant weight of <0.01% change. The linear relationship between TDR readings and gravimetric measurements indicated consistent readings from the TDR (Fig. 2).

In order to gauge plant and soil responses to water treatments in rain manipulation experiments, soil water content was assessed in relation to soil water potential as an indicator of water availability (Klute 1986a; Carter 1993; Hillel 1998). Pressure plates were used to determine soil water potential as they allow for the equilibration of soil water in a sample at known pressure which can be subsequently weighed to determine soil water content. This method is advantageous as correlations of soil characteristics are more reliable when measured simultaneously (Phene and others 1992). Pressure plates accommodate measurement of undisturbed soil samples; undisturbed soil samples are more representative of field conditions because soil structure and pore-size distribution influences soil water holding capacities (Klute 1986b).

Undisturbed soil samples (rings: 2.95 cm h x 5.35 cm d) were collected from between 1 – 7 cm below ground level using a soil core sampler. Soil water potential was measured using 5 and 15 bar pressure plate extractors following Klute (1986b) and Carter (1993). After saturation with distilled water, water was removed

from samples at 6 pressure levels (0.33–15.0 bars) and water content by mass assessed after equilibration at each level of pressure. A soil moisture retention curve was constructed following the procedure of Bruce and Luxmoore (1986) and Carter (1993). The retention curve is reported here as an assessment of plant available water in soils (soil matric potential) over the range of soil water contents observed in the three treatments (see Hanson and others 1998; English and others 2005).

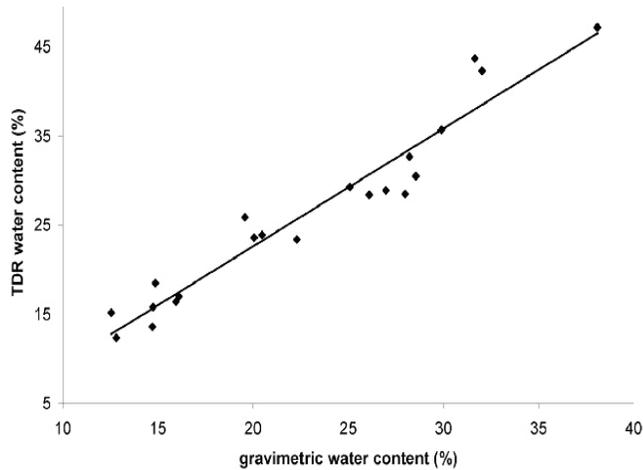


FIGURE 2. Calibration of percent soil water content as measured by a time domain reflectometer (TDR, %, volume/volume) with gravimetric soil water content (% mass/mass) ($y = 1.3197x - 3.7548, R^2 = 0.9334$).

To assess the reduction of photosynthetic active radiation (PAR) by the polyethylene plastic we measured PAR above and below the plastic in full sunlight using a LI-COR quantum line and point sensor. To assess the effect of shelters on microclimate, we measured the following parameters at 12 non-sheltered sites within the study area: PAR during an overcast day (Gendron and others 1998), soil temperature with a soil thermometer at depths of 5 cm and 10 cm, and soil water content.

At the end of June, rosette density was recorded for each plot, and two rosettes per plot (closest to two predetermined points outside the sampling area) were excavated with a hand trowel to assess root length and root and shoot biomass. Rosettes were rinsed to remove soil particles, root lengths were measured, and roots and shoots were dried in a drying oven to a constant weight. Polyethylene roofs were removed from the shelters at this time, however PVC frames were left in place for the remainder of the study to deter deer access to the plots. In October 2005 and May 2006, density was again recorded. In May 2006 fruits of all sizes were counted in each plot; immature fruits with any brown coloration were not included.

Data Analysis

The effects of water treatment on soil moisture, rosette growth, survival, and number of fruits, and on shelter microclimate were determined using one-way ANOVAs ($\alpha = 0.05$) with SAS version 9.1.3 for Microsoft® Windows (SAS Institute, Inc. 2001). We also used one-way ANOVAs to assess whether June precipitation affects rosette density on June 30, 2005 (“June”), October 27, 2005 (“October”), and May 31, 2006 (“May 2006”), as well as percent survival from June 1 to each of these three dates. To meet ANOVA assumptions of homoscedasticity, densities were $\log(x+1)$ transformed, October and May 2006 survival were arcsine transformed, and root biomass was square root transformed. One

outlier was removed from each of the following analyses: root length, root biomass, and shoot biomass.

RESULTS

Precipitation and Soil Moisture

Precipitation during the month of June was 9.2 cm, 0.8 cm less than the water added to the average treatment (Fig. 3). After one outlier was removed from the first week’s measurements, soil in the dry treatment was drier than that in the average treatment during each of the 4 weeks in June, but soil moisture did not differ between average and wet plots in any of these weeks (Fig. 4, see Hochstedler 2006 for ANOVA statistics). Soil water potential was asymptotically related to soil water content (Fig. 5).

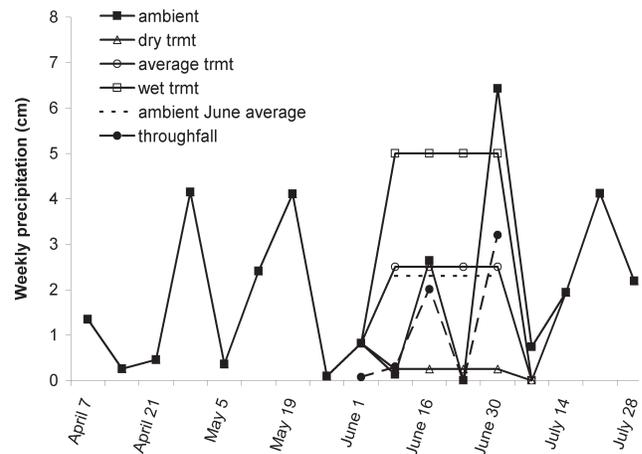


FIGURE 3. Weekly ambient precipitation at the ERC from April 1 thru July 28, 2005, throughfall for June 2005, average ambient precipitation for the month of June, and the amount of water applied to each treatment (dry, average, and wet).

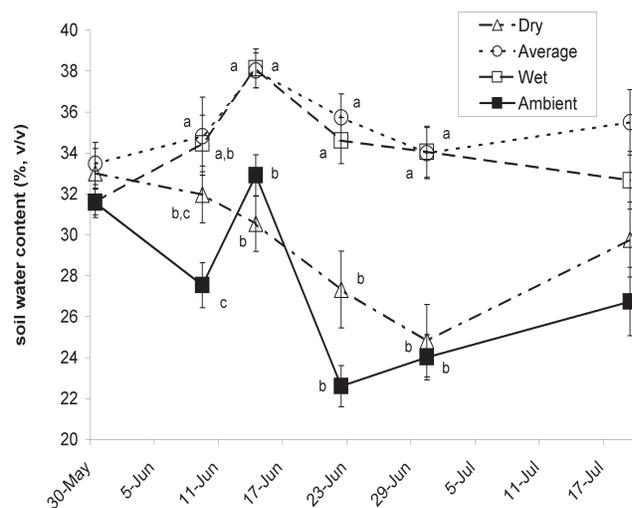


FIGURE 4. Weekly soil water content (means \pm SE) from May 30 – July 19, 2005 in treatment and ambient plots. For each date, treatments sharing a letter (a, b, or c) did not have different soil water content levels as determined by Bonferroni (Dunn) t -test (Hochstedler 2006). One-way ANOVAs revealed that treatment significantly affected soil water content each week (all ANOVAs $df = 3$ and $p < .0001$; week 1: $F = 11.01$, week 2: $F = 13.05$, week 3: $F = 19.10$, and week 4: $F = 16.54$).

Rosette Response

Treatments did not differ in density of rosettes on June 30, in October, or in May 2006 (Table 1). Neither did treatments differ in percent survival through June, October, or May 2006 (Fig. 6). Treatment did not affect rosette root length, root biomass, or shoot biomass (Table 1). Diseased spots were noted on many rosettes in the plots by mid-June, however these were noted across all treatments with equal prevalence. Treatments did not differ in number of fruits per adult in May 2006 (Table 1), and no differences were noted in relative stage of fruit maturity.

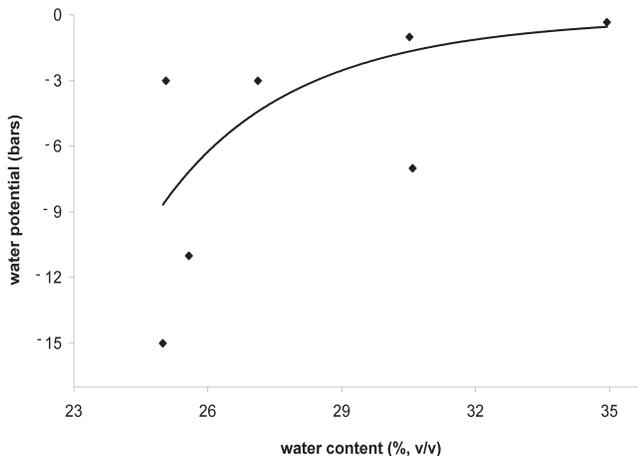


FIGURE 5. Soil moisture release curve for Russell-Miamian silt loam soils at study site. Line was fit with a power function, $y = -3E+12x^{-8.2596}$, $R^2 = 0.6074$.

Shelter and Microclimate

Rain shelters were effective at excluding naturally occurring rainfall from sample plots, as evidenced by the decline in soil moisture in the dry plots during and after the rains in the second week of June (Fig. 3 and Fig. 4) and by the rain shadow seen outside the plots immediately after a rain event. Light was reduced to $89.48\% + 0.26$ (mean \pm SE, $n = 32$) under the polyethylene sheeting on the shelters (Hochstedler 2006), and by potentially more between periods when fallen leaves, debris and dust were cleared from the

surface. PAR reaching plots did not differ among treatment plots and non-sheltered ambient sites ($df = 3$, $F = 1.91$, $p = 0.14$). Soil temperatures did not differ among treatment plots and ambient sites (at 5 cm: $df = 3$, $F = 2.01$, $p = 0.13$; at 10 cm: $df = 3$, $F = 1.57$, $p = 0.2105$) (Hochstedler 2006).

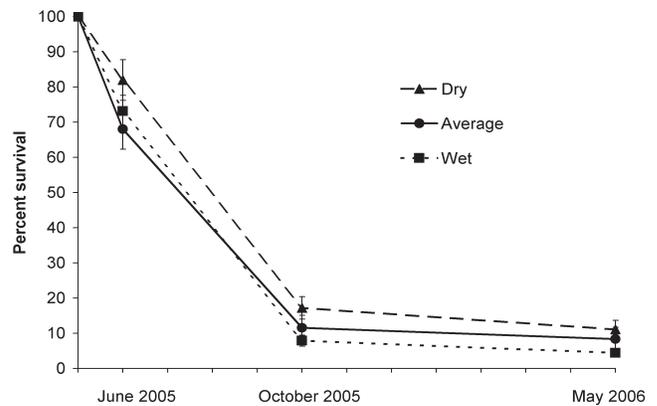


FIGURE 6. Effect of June water treatments on mean rosette survival (mean \pm 1 SE, $n = 12$ per treatment). One-way ANOVA indicated no difference in survival between treatments (June: $df = 2$, $F = 1.74$, $p = 0.19$; October: $df = 2$, $F = 2.83$, $p = 0.07$; and May 2006: $df = 2$, $F = 1.64$, $p = 0.21$).

DISCUSSION

June precipitation treatments had no effect on *A. petiolata* growth, survival or number of fruits, however lack of treatment differences was not because soil moisture was unaffected. The dry treatment was drier than the average and wet treatments, although the latter two did not differ. This suggests that the average treatment supplied water sufficient to saturate the soil. Byers & Quinn (1998) found that rosettes experience greatest mortality during dry summer months, however our soil moisture manipulations in June did not affect root length or biomass, which we hypothesized would influence survivorship during later months of moisture stress.

The dry moisture regime may not have been dry enough to avoid low water availability characteristic of a year with a dry June. Soil water content of dry treatments averaged 29.6% in the first 3

TABLE 1

Mean and 95% confidence intervals of *A. petiolata* response variables in dry, average and wet treatments, and one-way ANOVA statistics. There was no significant effect of water treatment on any of these variables (all variables, $df = 2$).

	Dry	Average	Wet	F	p
Rosette density, June 2005	130.1 \pm 33.2	143.3 \pm 40.1	145.0 \pm 39.8	0.13	0.88
Rosette density, October 2005	31.3 \pm 15.4	21.6 \pm 12.6	20.0 \pm 11.2	1.01	0.38
Rosette density, May 2006	19.5 \pm 10.2	13.1 \pm 8.9	11.7 \pm 8.7	0.92	0.41
Root length (cm)	9.8 \pm 1.1	9.4 \pm 1.0	8.8 \pm 0.8	1.35	0.27
Root biomass (mg)	17.9 \pm 6.7	17.7 \pm 10.8	16.2 \pm 6.7	0.57	0.57
Shoot biomass (mg)	78.1 \pm 21.7	60.6 \pm 38.1	64.9 \pm 26.1	2.07	0.14
Fruits per individual	15.4 \pm 5.0	19.0 \pm 9.4	18.4 \pm 9.6	0.21	0.82

weeks; at these levels soil water availability was about -2 bars, not much lower than the water availability in the average treatment (water content of 35.9%) (Fig. 5). Similar results were noted in a forested rain manipulation study by Hanson and others (1998) where deep soils were significantly different in soil water content, but not in soil water potential.

There are reasons to believe that soil water content and water availability in our 'dry' treatment were not as low as those that occur in years when June precipitation is low. Throughout June, soil water content in the dry treatment was similar to that at non-sheltered ambient sites, although ambient precipitation was 9 times that of the dry treatment and close to long-term average. This was likely due to the fact that throughfall is less than precipitation, due to interception and stemflow; growing-season throughfall was 76.3% of above-canopy rainfall in a broad-leaved deciduous forest in Japan (Deguchi and others 2006). Throughfall at our site during June 2005, as measured at a single HOBO weather station (Onset Computer Corp), was 5.54 cm (J.P. Costanzo, pers. comm.), 60.2% of precipitation the same month (Fig. 3). Since our water addition treatments were based on above-canopy precipitation, rather than throughfall, soils were presumably less dry than they would be in a year when June precipitation equaled 1 cm. Furthermore, relative humidity during droughts may be lower than that achieved in our dry treatment, and this may suppress *A. petiolata* growth.

Because the dry treatment did not simulate drought conditions, the hypothesis that heavier June precipitation enables *A. petiolata* rosettes to survive summer drought cannot be rejected based on our experiment. Low June precipitation may reduce rosette survival, but in years when June precipitation is above average it is probably not a reliable predictor of rosette survival. Instead of replicating drought rainfall amounts, withholding water until symptoms of wilting indicate drought-stress may be more effective in inducing extreme conditions (Baruch and others 2000).

Other studies have looked at the impacts of varied precipitation regimes and water availability on invasive population dynamics (Alpert and others 2000). Compensation and plasticity in invasive populations (Claridge and Franklin 2002) may aid establishment in new habitats and spread of existing populations (Kolar and Lodge 2001). *A. petiolata* populations seem to compensate for lower survival rates (decreased density) by allocating increased proportions of biomass to reproduction and thus yielding greater seed banks (Byers and Quinn 1998; Meekins and McCarthy 2000). Management practices that reduce survival may not be an effective control method if population-level seed production is not greatly influenced by reduced survival. Year-to-year variation in moisture may, however, affect reproduction, and future studies should determine more specifically how precipitation patterns and soil moisture availability influence reproduction.

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