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RESEARCH

INVASIVENESS OF CUT-LEAF GROUND-CHERRY (*Physalis angulata* L.) POPULATIONS AND IMPACT OF SOIL WATER AND NUTRIENT AVAILABILITY

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Biological invasions are a major threat to natural ecosystems and agroecosystems, while weed flora is noticeably changing globally. In this study we evaluated the potential of cut-leaf ground-cherry (*Physalis angulata* L.), a species native to America, to invade the semi-arid regions of Greece. Greenhouse and laboratory experiments were conducted to evaluate the effects of different environmental resources (nutrient and water availability) on seedling growth, biomass production, fecundity, and seed germination of four populations of cut-leaf ground-cherry. Our results suggest that cut-leaf ground-cherry does not tolerate extreme drought during the first growth stages, while it can survive and produce adequate and rapidly germinated seed (> 85%) under low soil moisture conditions. Moreover, high water and nutrient availability results in high growth and biomass production and ensures high seed production, reaching more than 4000 seeds plant^{-1}. We suggest that soil water content and nutrient availability are the two critical factors affecting the invasive potential of cut-leaf ground-cherry in semi-arid environments. Understanding the plant's ecological features through a study conducted at an early stage rather than a late stage of invasion will help us to take appropriate control measures for this species, which should primarily target frequently fertilized fields after precipitation events.

Key words: *Physalis angulata*, invasion, Greece, water stress.

Invasive species infestation and spread have been recognized as major threats after the loss of habitat facing native plant and animal species across the world, especially in arid and semi-arid environments (Reichard and White, 2001). Invasive (exotic) plants are often intentionally introduced as food, for ornamental, medicinal, and other purposes. Free from the complex array of natural enemies present in their native environments, exotic plants in new lands can experience rapid and unrestricted growth (Zhou *et al*., 2006). Once established, these plants have the potential to become troublesome weeds and pose long-term problems for agriculture and natural environments (Westbrooks, 1991). The occurrence of invasive and alien species in new habitats depends on habitat conditions and available environmental resources where resource-poor environments often support natives better than aliens (Daehler, 2003). In particular, soil moisture is the main ecological factor in many arid and semi-arid environments, while nutrients also play an important role (Reynolds *et al*., 2004; Rahlao *et al*., 2010).

Prevention of invasion into natural habitats is constrained by a lack of knowledge about the requirements of invasive species for recruitment, growth, reproduction, and survival (Rahlao *et al*., 2010). Moreover, understanding and identifying environmental resources that promote or restrict the success of invasive, alien species during the critical life stages can be used to focus on how to manage them (Ward *et al*., 2006; Speziale and Ezcurra, 2011).

During the last few years, there have been complaints from several regions of Greece for reduced efficacy of herbicides or increased competitiveness of many alien or recently problematic species (Travlos *et al*., 2009; Travlos and Chachalis, 2010). A species which belongs to the Solanaceae family was found in 2009 during our weed surveys and field experiments conducted (Travlos *et al*., 2010; 2011) in summer crops (corn, cotton, and soybean) in Greece. This species was *Physalis angulata* L., a xenophyte of American origin, previously unknown in crop fields in Greece but already identified as an invader in several countries (Reddy *et al*., 1999; Travlos *et al*., 2010). The only record for this species in Greece was in a ruderal site in the Ilia prefecture, Peloponnese (Greuter and Raus, 2001). Although *P. angulata* has a new record for the weed flora of summer crops in Greece, it was found to be a highly distributed invader in corn fields (Travlos, unpublished data).

The objective of this study was to experimentally assess growth and biomass production of cut-leaf ground-cherry under different environmental resources. In particular,

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seedling growth of several populations under a different nutrient and water status was assessed. Moreover, the effects of drought and nutrient stress on seed production and germination of several weed populations were also studied in order to further evaluate the invasive potential of this species.

MATERIALS AND METHODS

Experimental details

The prefectures of Etoloakarnania, Preveza, and Arta were selected to collect cut-leaf ground-cherry seeds since they were already known to have a history of invasion by this species; this was reported in previous surveys (Travlos *et al*., 2010). Samplings were conducted in corn (*Zea mays* L.) fields during a 4-d period at the beginning of crop maturity from 23 to 26 July 2009. Berries and seeds were collected from 50 individual plants in each field and transferred to the Laboratory of Agronomy, Agricultural University of Athens after the *in situ* determination of species according to morphological characters (Travlos *et al*., 2010). Seeds were separated, air-dried, and stored in paper bags at room temperature until used. Table 1 shows four *P. angulata* accessions included in each regional study.

Two pot experiments were conducted in a greenhouse of the Agricultural University of Athens (37°59'12'' N; 23°42'96'' E; 29 m a.s.l.) during the summers of 2010 (2 May to 20 August) and 2011 (8 May to 21 August). Average minimum/maximum air temperature and relative humidity in the glasshouse during the experiments in both years were 20/40 °C and 40/60%, respectively, and plants were subjected to natural day length of 13-15 h with a mean PAR value of approximately 995 μmol m^{-2} s^{-1}.

Seeds were germinated in soil trays (after tetrazolium seed viability testing); germinated seedlings were transplanted in 1.4-L plastic pots and maintained at room temperature. Afterwards, a total of 240 seedlings were translocated into 3.2-L pots containing two soil types with a similar mechanical classification and different nutrient availability (Table 2). Seedlings were randomly assigned to two different treatments in a factorial design with three alternatives of soil water content ($n = 3 \times 80$), two soil-type alternatives ($n = 2 \times 120$), and four weed populations ($n = 4 \times 60$).

At the beginning, and until 5 d after sowing (DAS) in the big pots, plants were irrigated with abundant distilled water (40% water-holding capacity) to promote plant emergence and first growth. Then, by withholding irrigation for 5 d, soil water content of all the pots fell to 25% water-holding capacity; the differentiation of the water treatments started at 10 DAS. To estimate the soil-moisture effects on several plant growth parameters, watering treatments were divided into high-water plants (HWT) receiving 200 mL three times a week, low-water plants (LWT) receiving 200 mL once a week, and minimum-water plants (MWT) receiving only 200 mL 15 DAS. These treatments were selected to simulate rainfall patterns within the full range of regions that have been or could be potentially invaded by cut-leaf ground-cherry; this is a common approach followed in similar studies (Rahlao *et al*., 2010). The driest treatment simulates a prolonged drought following seedling establishment. Both soils were selected as representative of sites where cut-leaf ground-cherry already occurs in crop fields. Plant height was measured every 10 d, while plants were harvested and the number of leaves was counted at 90 DAS in both growing seasons. The number of seeds per plant was also determined after seeds were collected and cleaned, while harvested plants were oven-dried for 48 h at 60 °C and weighed to estimate total (root and shoot) biomass.

In addition, a germination experiment was carried out with a completely randomized design in an incubator (Conviron T 38/Lb/AP) at a constant temperature (25 °C) and total darkness. Freshly harvested seeds were directly obtained by crushing individual berries and thoroughly rinsing the seeds with running water. The experiment was set up according to a 3 × 2 factorial design with eight replicates (Petri dishes) that consisted of seeds from plants grown under three water treatments (HWT, LWT, and MWT) and in two soils (rich and poor). Twenty seeds were placed between two Whatman N° 1 paper filter disks (Whatman Ltd., Maidstone, England) in each 9-cm Petri dish and allowed to germinate for 10 d. Distilled water (5 mL) was added to keep filter papers moist. Seed germination was expressed as a percentage of the total number of tested seeds (germination percentage, GP). Seeds were considered germinated when the healthy white radicle had emerged through the integument and reached a length of more than 1 mm (Bewley and Black, 1978).

Table 1. Prefecture, site, and geographical position of *Physalis angulata* populations included in the present study.

Prefecture	Site	Positions (latitude, longitude)
Etoloakarnania	Monastiraki	38°51'41'' N, 20°52'26'' E
Etoloakarnania	Vonitsa	38°53'46'' N, 20°54'31'' E
Preveza	Louros	39°06'05'' N, 20°44'09'' E
Arta	Kostakioi	39°07'13'' N, 20°56'37'' E

Table 2. Properties of two soil types used to grow *Physalis angulata* seedlings in greenhouse experiments.

Soil properties	Rich	Poor
Soil pH (in H_2O)	7.6	7.4
N total, %	3.8	0.8
P, mg kg^{-1}	7400	54
K, mg kg^{-1}	2300	340
Na, mg kg^{-1}	120	130
CEC, mmol kg^{-1}	4360	2670
Organic matter, %	2.93	2.16
Sand, %	37.8	36.1
Clay, %	32.6	33.3
Silt, %	29.6	31.6
Mechanical classification	Clay loam	Clay loam

CEC: cation-exchange capacity.

Statistical analysis

Data from greenhouse experiments were analyzed together and treatment values for all features were expressed as means between the 2 yr since there was a similar response in both years. Statistical analysis of the results was performed by ANOVA, while mean comparison was performed by Fisher's least significant difference (LSD) test at $p < 0.05$ with the Statistica 9.0 software package (StatSoft, Tulsa, Oklahoma, USA). All data were tested for normality and variance before further analyses. Seed germination percentages were subjected to angular transformation followed by ANOVA.

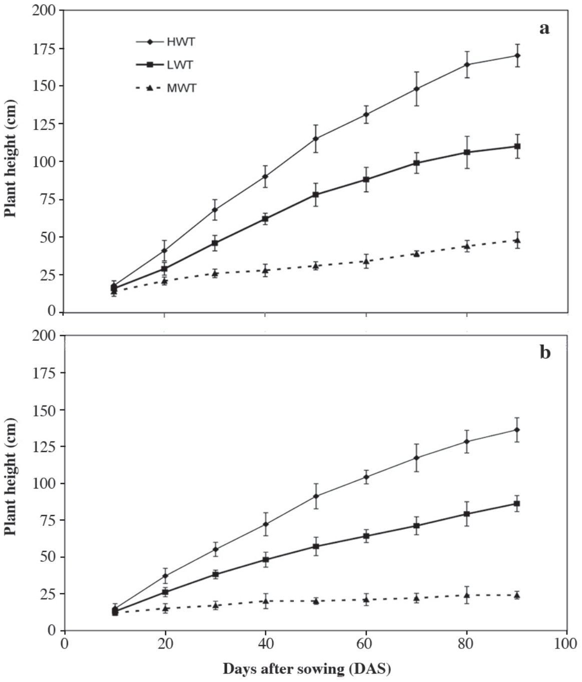
RESULTS

Since ANOVA indicated no significant effect of year or treatment × year interaction, means were averaged over the 2 yr; accordingly, 2-yr means will be presented in the data that follow.

Water availability appeared to clearly promote vegetative growth of *P. angulata* plants (Figure 1). The time course of plant height exhibited significant differences ($P < 0.05$) among water treatments (already starting at 30 DAS). Plant height was consistently the highest in HWT plants and reached a value of 170 cm at the end of the experimental period. Nutrient availability also has a significant effect on plant height since rich soil results in significantly higher cut-leaf ground-cherry plants ($P < 0.05$), especially in the case of low water availability.

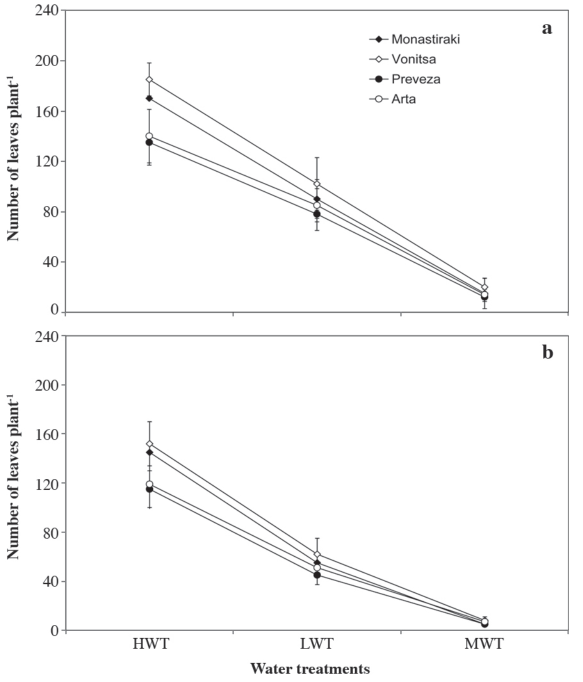
The mean rate of stem elongation for the first 50 DAS was relatively high for both HWT and LWT plants and ranged from 1.14 to 2.3 cm d^{-1}. For the rest of the experimental period, rates were significantly reduced, especially for the more water-stressed plants grown in poor soil. Significant differences detected between the three water treatments indicate the beneficial effect of water supply on plant growth (Figure 1).

The effects of several treatments on the number of leaves and dry biomass production are given in Figures 2 and 3, respectively. High water treatment significantly increased ($P < 0.05$) the number of leaves of *P. angulata* from 39-47% to 89-91% as compared to LWT and MWT plants, respectively. The corresponding differences were even higher in the case of low nutrient availability because of prolonged leaf senescence (Figure 2b). Dry biomass was also significantly higher ($P < 0.05$) in HWT plants with differences ranging from 43-50% to 88-91% (depending on weed population) as compared to LWT and MWT plants, respectively. Nutrient availability also seems to play a crucial role since the dry biomass of *P. angulata* grown in rich soils was 28- 33% higher than in poor soils (depending on weed population). These differences are higher in the case of high water availability since in the



HWT: high-water plants received 200 mL three times a week; LWT: low-water plants received 200 mL once a week; MWT: minimum-water plants received 200 mL 15 d after sowing.

Figure 1. Time course of cut-leaf ground-cherry height for three watering treatments (*n* = 80 for each treatment) in (a) rich and (b) poor soil (*n* = 120 for each soil type). Each point represents the mean of all four populations. Vertical bars indicate standard error of the means.



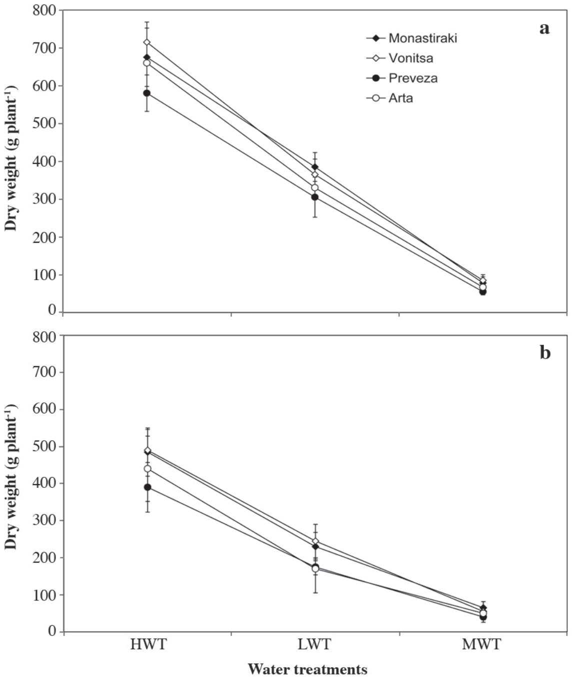
HWT: high-water plants received 200 mL three times a week; LWT: low-water plants received 200 mL once a week; MWT: minimum-water plants received 200 mL 15 d after sowing.

Figure 2. Number of leaves per plant of cut-leaf ground-cherry for three watering treatments (*n* = 80 for each treatment) and four weed origins (*n* = 60 for each population) in (a) rich and (b) poor soil (*n* = 120 for each soil type). Vertical bars indicate standard error of the means.

opposite case, dry matter production is already restricted. There were noticeable differences among the several cut-leaf ground-cherry populations and Vonitsa was the most productive (Figure 3).

The Monastiraki population of *P. angulata* had a very large seed production with up to 4100 seeds plant^{-1}. Fecundity was significantly higher ($P < 0.05$) in HWT plants with differences up to 77% as compared to LWT plants (Figure 4). Moreover, even in the case of intense drought stress (MWT), further spread of the species is ensured since each plant produces 65 to 240 seeds depending on nutrient level and weed population.

Seed germination data are shown in Table 3. High soil moisture and nutrient availability significantly increased ($P < 0.05$) *P. angulata* seed GP from 86% to 96% as compared with seeds from MWT plants grown in poor soils. The rest of the treatments resulted in intermediate germination values that were still very high.



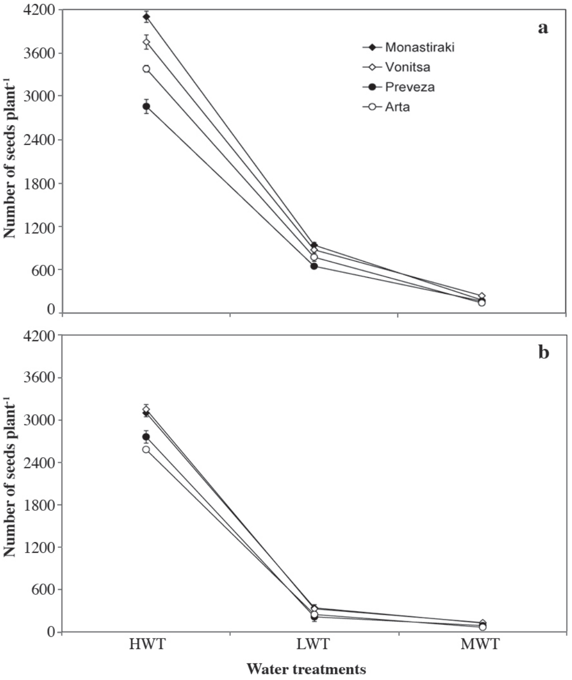
HWT: high-water plants received 200 mL three times a week; LWT: low-water plants received 200 mL once a week; MWT: minimum-water plants received 200 mL 15 d after sowing.

Figure 3. Dry matter production per plant of cut-leaf ground-cherry for three watering treatments (*n* = 80 for each treatment) and four weed origins (*n* = 60 for each population) in (a) rich and (b) poor soil (*n* = 120 for each soil type). Vertical bars indicate standard error of the means.

Table 3. Effects of water and nutrient availability on *Physalis angulata* seed germinability (means and standard deviations).

Watering treatment	Soil type Rich	 Poor
HWT	96 ± 9.6a	91 ± 7.2ab
LWT	90 ± 4.6ab	87 ± 2.3ab
MWT	88 ± 6.5ab	86 ± 4.1b

Values followed by different letters in the columns are significantly different ($P < 0.05$) according to Fisher's LSD test.
HWT: high-water plants received 200 mL three times a week; LWT: low-water plants received 200 mL once a week; MWT: minimum-water plants received 200 mL 15 d after sowing.



HWT: high-water plants received 200 mL three times a week; LWT: low-water plants received 200 mL once a week; MWT: minimum-water plants received 200 mL 15 d after sowing.

Figure 4. Number of seeds per plant of cut-leaf ground-cherry for three watering treatments (*n* = 80 for each treatment) and four weed origins (*n* = 60 for each population) in (a) rich and (b) poor soil (*n* = 120 for each soil type). Vertical bars indicate standard error of the means.

DISCUSSION

The high decrease in vegetative growth rate, stem elongation, and leaf appearance in water-stressed plants is common among several invasive species of arid and semi-arid environments and can be plausibly ascribed to induced loss of turgor, which affects cell expansion rate and ultimately cell size (Acosta-Gallegos and Adams, 1991; Natale *et al*., 2010; Rahlao *et al*., 2010). In the case of *P. angulata*, water-stressed plants had a low stem elongation rate, while water availability had a significantly positive effect. Moreover, well-watered plants produced significantly more leaves in comparison with all other plants, probably because of more profuse branching. This significantly higher vegetative growth of well-watered cut-leaf ground-cherry plants is consistent with the concept found in many other plants of arid environments (including drought-tolerant species) where vegetative growth is significantly enhanced by the supply of adequate soil moisture (Sangakkara *et al*., 2001; Rahlao *et al*., 2010).

The results of the present study revealed that *P. angulata* plants responded positively to N, P, and K levels, while this invasive species could also survive, grow, and reproduce in poor soils. This positive reaction of growth, biomass, and seed number to increased nutrient availability has been recently reported in related species such as *P. peruviana* L. (El-Tohamy *et al*., 2009). It is also suggested that nutrient availability is a critical factor affecting the successful establishment of several invasive plants in arid environments (Rahlao *et al*., 2010), while the invasive potential of a species such as *P. angulata*, which withstands low-resource availability, is even higher.

Furthermore, there was a novel and surprising finding regarding the observed differences among the four populations as to their growth and seed production. Indeed, cut-leaf ground-cherry populations originating from the Monastiraki and Vonitsa regions had a significantly higher growth and seed production than the others, while there was a noticeable phenotypic variation among plants belonging to these populations (data not shown). This high variability observed among morphological characters of these populations is probably due to an earlier introduction of the species in these particular regions; it is common not only in *P. angulata* (Menzel, 1951; Reddy *et al*., 1999) but also among several weeds and other invasive plants (Travlos and Giannopolitis, 2010). Phenotypic plasticity and better local adaptability allow many alien, invasive species to be highly invasive under variable environmental conditions (Richards *et al*., 2006).

Our results revealed an outstanding *P. angulata* seed production (up to 4200 seeds plant^{-1}) under high water and nutrient availability. Recent evidence suggests that exotic plants can be invasive because they can better exploit disturbed habitats or have better dispersion features than native species (Didham *et al*., 2005); this also appears to be true for cut-leaf ground-cherry. Moreover, even in the case of intense drought stress (MWT), each plant managed to produce 65 to 240 seeds depending on nutrient level and weed population. This feature, combined with high density, which was recently observed (Travlos *et al*., 2010), further promotes the invasiveness of this species.

Seed germination of invasive or other alien species is one of the main factors that defines their spread and invasion potential, and it is therefore extensively studied (Travlos *et al*., 2007; Pucheta *et al*., 2011). Seed germination aspects of *P. angulata* have already been studied, and it has been reported that cut-leaf ground-cherry seeds were less sensitive than seeds of other species to simulated moisture stress (Thomson and Witt, 1987). The present study is the first report on *P. angulata* seed germination related to environmental conditions under which mother plants were grown. The surprisingly high germination ability of seeds even after water or nutrient stress combined with early anthesis and an extended flowering period ensure the further spread of this invader in arid and semi-arid environments.

CONCLUSIONS

Results of 2-yr experiments revealed that environmental resource availability (i.e., water and nutrients) improves growth and fecundity of an invasive species. In ideal conditions, *P. angulata* shows high seed production, which clearly promotes its invasiveness. Furthermore, seed germinability is exceptionally high even in arid and semi-arid regions with limited water and nutrient availability, especially for specific populations. Based on our findings, it is suggested that *P. angulata* should be carefully managed, especially after precipitation events and in areas subjected to frequent nutrient enrichment where cut-leaf ground-cherry vigorously grows and spreads under unfavorable conditions.

Potencial invasor de poblaciones de tomatillos de Brihuega (*Physalis angulata* L.) e impacto del contenido de agua y disponibilidad de nutrientes del suelo. Las invasiones biológicas son una amenaza importante para los ecosistemas naturales y agroecosistemas, mientras que, globalmente, la flora de malezas parece cambiar notablemente. En este estudio se evaluó el potencial de una especie nativa de América, tomatillos de Brihuega (*Physalis angulata* L.), para invadir las regiones semiáridas de Grecia. Se realizaron experimentos de invernadero y laboratorio para evaluar los efectos de diferentes recursos ambientales (disponibilidad de nutrientes y agua), crecimiento de las plántulas, producción de biomasa, fecundidad y germinación de las semillas de cuatro poblaciones de tomatillos de Brihuega. Nuestros resultados sugieren que *P. angulata* no tolera una extrema sequía durante las primeras etapas de crecimiento, pero puede sobrevivir y sus semillas germinar adecuada y rápidamente (> 85%) incluso en condiciones de baja humedad del suelo. Además, con alta humedad y disponibilidad de nutrientes genera un alto crecimiento y producción de biomasa y asegura una alta producción de semillas, llegando a más de 4000 semillas por planta. Sugerimos que la alta humedad del suelo y en segundo lugar la disponibilidad de nutrientes son los factores críticos que afectan el potencial invasor de *P. angulata* en ambientes semiáridos. Comprender las características ecológicas de las plantas mediante un estudio realizado en una fase de invasión temprana en lugar de tardía, permitirá adoptar medidas de control apropiadas para esta especie, las cuales deben dirigirse primeramente a campos fertilizados con frecuencia después de eventos de precipitación.

Palabras clave: *Physalis angulata*, invasión, Grecia, estrés hídrico.

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