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Annual *Datura* accessions as source of alkaloids, oil and protein under Mediterranean conditions

J.T. Tsialtas[a,*], E. Kostoglou[a], D. Lazari[b], I.G. Eleftherohorinos[a]

[a] Aristotle University of Thessaloniki, Faculty of Agriculture, Laboratory of Agronomy, 541 24 Thessaloniki, Greece
[b] Aristotle University of Thessaloniki, School of Pharmacy, Laboratory of Pharmacognosy, 54 124 Thessaloniki, Greece

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ABSTRACT

Potentially, *Datura* species can turn to a multipotent crop providing alkaloids for pharmaceuticals, oil for non-edible uses and protein for livestock feed. In a two-year (2012–2013) field experiment, five *Datura* accessions (one *D. stramonium* f. *stramonium*, three *D. stramonium* f. *tatula*, and one *D. ferox*) were tested for alkaloid (atropine, scopolamine) concentration in aerial plant parts and seed oil (Oil) and protein concentration (Prot) and yield. Above-ground biomass was sampled 105 days after seeding (DAS) and in parallel leaf physiological traits were determined. Alkaloids were measured in stems, leaves, flowers, fruits and the alkaloid yield (the sum of the products of plant part weights with the respective alkaloid concentrations) were calculated. Leaves, consisting about 30% of the dry biomass, were the most enriched in both alkaloids, followed by flowers; in contrast, stems were depleted with some accessions having very low to nil concentrations. In general, *D. ferox* had the lowest concentrations. Accessions did not differ in scopolamine yield but *D. stramonium* accessions outstripped *D. ferox* in atropine yield; no significant differences in atropine yield were found among *D. stramonium* accessions. Growing season affected significantly alkaloid concentrations and yields; wet and cool 2013 decreased them detrimentally. About 150 DAS, harvest took place to estimate seed yield (SY), 1000-seed weight, Oil and Prot. Seed yield, Prot and protein yield (PY) were favored by wet and cool conditions in 2013; in contrast, Oil and oil yield (OY) were plummeted. With the exception of CO_2 assimilation rate and stomatal conductance, leaf physiological traits were affected by growing season but only carbon isotope discrimination (Δ) and leaf N concentration differed between accessions. High-yielding accessions had higher Δ indicating that SY were controlled by water uptake and transpiration. Accessions of f. *tatula* had the highest Oil ($>$ 12%) but no genotypic differences were found for Prot; the large-seeded *D. ferox* had the highest SY and PY. Accessions of f. *tatula* were larger-seeded than f. *stramonium*. Concluding, growing season conditions controlled *Datura* qualitative traits and the respective yields. Variation among accessions can be exploitable.

1. Introduction

The genus *Datura*, family Solanaceae, is consisted of 13 species originating from the New World (Bye and Sosa, 2013), and thus *Datura* species found in Greece are invasive (Arianoutsou et al., 2010). *Datura stramonium* f. *stramonium* (green shoot and white flowers) is the most common variant and is found as spring weed in fields, roadsides, and dumps usually coexisting with the recently reported in Greece *D. stramonium* f. *tatula* (red shoot and purple flowers). Fierce thornapple (*Datura ferox*) is the dominant species in some sites in northern Greece where it shares habitat with *D. stramonium* (Tsialtas et al., 2013, 2014).

Tissues of *Datura* species contain a variety of tropane alkaloids with hyoscyamine (atropine) and scopolamine to be the most abundant (Miraldi et al., 2001; Berkov et al., 2006; El Bazaoui et al., 2011). These alkaloids have been evolved as a defense mechanism against herbivory (Shonle and Bergelson, 2000; Castillo et al., 2014) and exhibit hallucinating, toxic (for both humans and animals) and putative pharmaceutical actions (Steenkamp et al., 2004; Cortinovis and Caloni, 2015). The therapeutic effects of *Datura* tissue intake are known since antiquity and are still part of ethnopharmacology (Dafni and Yaniv, 1994; Soni et al., 2012). Moreover, the anticholinergic actions and control on nerve system by hyoscyamine and scopolamine are being exploited by modern pharmacopeia and these two substances are found in proprietary products (Henig, 2012; King et al., 2014; Ullrich et al., 2017). Thus, among other species, *Daturas* can be a source of these active substances for modern medication.

Alkaloid content and pattern and consequently alkaloid yield in *Daturas* were found to be influenced by genotypic and abiotic factors.

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* Corresponding author.
E-mail address: tsialtai@agro.auth.gr (J.T. Tsialtas).

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Previous works have revealed that alkaloid pattern and content differed between *Datura* species as well as between species accessions of different origin (Berkov et al., 2006; Jakabová et al., 2012). As regards abiotic factors, increases in soil pH (from 5.0 to 7.0), nitrogen (N) and mineral levels resulted in increased alkaloid content (Dethier et al., 1993; Demeyer and Dejaegere, 1995; Al-Humaid, 2004). Moreover, increased air temperature did not affect scopolamine concentration but increased the concentration and amounts of atropine (hyoscyamine) per plant in *D. stramonium* (Ziska et al., 2005). In this line, increased root-zone temperature altered the root/shoot distribution of alkaloids and increased their concentration in leaves in the Solanaceae species *Nicotiana tabacum*, the cultivated tobacco (Malik et al., 2013).

Datura species can be characterized as multipotent plants since, apart from the tropane alkaloids contained in their tissues, seeds are oleiferous and have high protein content. It was reported that seeds of *Datura stramonium* had oil content as high as 21.4% (Wang et al., 2012) and even higher (22.9%) was reported for *D. candida* (Ruan et al., 2012). Though non-edible, this oil could be a feedstock for biodiesel production with *Datura* species exploiting arid, degraded and unproductive lands (Banković-Ilić et al., 2012; Ruan et al., 2012; Luna et al., 2014). In addition, seeds of *D. metel* were found to contain crude protein as high as 20.73% (Rai et al., 2013). The protein by-product, after oil extraction from the seeds, could be used to feed livestock as it was proposed for seeds of other Solanaceae species like tobacco (Rossi et al., 2013).

While much effort has been put on estimating the useful constituents (alkaloids, oil, protein) in plant parts of *Datura* species collected in the wild or grown under controlled conditions (e.g. in pots), there is a lack of works on studying *Datura* response as a putative crop. An exception is the work by Bhagat (1981) who studied, in the field, agronomic traits, the biomass partitioning into plant parts and the relationship of 1000-seed weight with seed yield of populations and their crosses in *D. stramonium*.

More emphatically, works are missing on leaf physiological differentiation of *Datura* genotypes and the effect on biomass and metabolites (alkaloid, lipid, and protein) production and partitioning. To produce energy-costly constituents like alkaloids and lipids (Seigler, 1998), plants have to sustain active, highly-functioning photosynthetic machinery. Prerequisite for this is the ample N and water uptake by roots and their translocation to the photosynthetic sites. However, the situation is intricate since conditions favorable (e.g. high temperatures) for the accumulation of metabolites like alkaloids may down-regulate leaf physiological responses.

Leaf gas exchange physiology can be assessed by both instantaneous and long-term measurements. Parameters like CO_2 assimilation rate (A), transpiration rate (E), stomatal conductance (g_s), and consequently the intrinsic and instantaneous water use efficiency (A/g_s and A/E, respectively) can be assessed instrumentally mirroring the response of the photosynthetic mechanism to current environmental conditions. However, these measurements can easily be biased by fluctuations of abiotic conditions and cannot display the tissue behavior for a long time past; stable isotopes of carbon (C) and N come to fill in the gap. Carbon isotope discrimination (Δ, a measure of the $^{13}C/^{12}C$ in plant tissues compared with the air) was found to relate with the ratio of the intercellular to ambient CO_2 concentrations (c_i/c_a) and is inversely associated to A/g_s in C_3 species (Farquhar and Richards, 1984). Its great advantage is that it imprints the "history" of CO_2 assimilation all along the life-span of the plant tissue being a long-term assessment of the water use efficiency (Farquhar et al., 1989). Moreover, Δ was related with yield in many C_3 species (Turner, 1996). On the other hand, N isotope ratio ($\delta^{15}N$) in plant tissues is used as a useful tool to get information about the N transformations in the soil and how these are reflected on plant tissues explaining possible differences in N concentrations (Craine et al., 2015). Supportive to stable isotope use, non-destructive chlorophyll assessment by SPAD-502 (SPAD) can provide information about how water and N availability affect leaf chlorophyll content and thus leaf photosynthetic machinery (Hawking et al., 2009).

The aim of the present work was to test five *Datura* accessions (one *D. stramonium* f. *stramonium*, three *D. stramonium* f. *tatula*, and one *D. ferox*) in the field as potential sources of alkaloids (atropine and scopolamine), oil, and protein and to find out differences in biomass allocation and leaf physiological traits using instantaneous [CO_2 assimilation rate (A), transpiration rate (E), intracellular CO_2 concentration (c_i), stomatal conductance (g_s), leaf-to-air temperature difference ($\Delta T = T_{leaf} - T_{air}$), intrinsic water use efficiency (A/gs), and instantaneous water use efficiency (A/E)] and long-term assessments [chlorophyll content as assessed by SPAD-502 (SPAD), carbon isotope discrimination (Δ), N isotope ratio ($\delta^{15}N$), and leaf N concentration]. Also, the significant correlations between physiological parameters and yield or quality traits were established.

2. Materials and methods

2.1. Datura accessions and experimental set up

Five *Datura* accessions [one *D. stramonium* f. *stramonium* (hereafter called G), three *D. stramonium* f. *tatula* (hereafter called R), and one *D. ferox* (heareafter called F)] were tested for two growing seasons in a field experiment established in the farm (40°32′N, 22°59′E, 5 m a.s.l.) of Aristotle University of Thessaloniki (AUTh), Thermi, Greece. The soil was a Typic Xerorthent, left in fallow for two years before the establishment of the experiments. Some of the soil characteristics are given in Table 1.

Mature seeds of R and G accessions were collected in October 2009 from Larissa, central Greece (R1: 39°35′18N, 22°35′67E, 62 m; R2 and G: 39°32′62N, 22°26′61E, 108 m; R3: 39°31′46N, 22°24′15E, 126 m) while F accession was picked up from Serres, northern Greece (40°50′47N, 23°49′25E, 15 m) in October 2011. Intact seeds of the accessions were kept in a common fridge at 4 °C.

Experiments were hand-seeded on 26 April 2012 and 24 April 2013 according to a Randomized Complete Block (RCB) design with three replications. Each plot was consisted of five 5 m-long rows at 0.50 m separation (an area of 12.5 m^2). On the row, five seeds per hill were placed at 0.02 m depth and 0.20 m apart. To minimize edge effects, a 1 m-wide buffer zone separated plots within the block while the respective separation between blocks was 2.5 m. At the two-leaf stage, hand-thinning left one plant per hill. Weeds were suppressed by hand-

Table 1
Soil characteristics at 0–30 cm depth before the establishment of the experiments. Where: EC, electrical conductivity.

Sand (%)[a]	14.0
Silt (%)[a]	48.0
Clay (%)[a]	38.0
Texture	silty clay loam (SCL)
pH (1:1 in H_2O)[b]	8.0
Organic matter (%)[c]	1.5
NO_3-N (mg/kg)[d]	40
P (mg/kg)[e]	5
K (mg/kg)[f]	190
Cu (mg/kg)[g]	2.2
Zn (mg/kg)[g]	0.5
Fe (mg/kg)[g]	9.0
Mn (mg/kg)[g]	10.0
EC (μS/cm)[h]	800

[a] Hydrometer method.
[b] By pHmeter.
[c] Wet oxidation method.
[d] Extraction with 2 M KCl.
[e] Olsen method.
[f] Extraction with 1 N CH_3COONH_4.
[g] DTPA extraction.
[h] In the saturation extract by conductance meter.

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