

REVIEWS

Datura stramonium L.: alkaloids and allelopathy

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Summary

Datura stramonium (common thorn-apple) is distributed worldwide and is a significant weed in the family Solanaceae. Alkaloids are the characteristic secondary chemical compounds of the family. Although long used in pharmacy and known to be toxic to many organisms, their involvement in allelopathy has been little explored. The weed status of *D. stramonium* is reviewed. Recent additions to the literature suggest that the alkaloids of the species are important allelochemicals in some Australian agricultural systems.

Introduction

Datura stramonium L. (common thorn-apple) has been associated with mankind for over twenty centuries (Schultes, 1969), and with Australian agriculture since at least the 1950s (Haegi, 1976). Its life cycle has been studied far more extensively than that of many other species considered to be major weeds on a worldwide basis (Holm *et al.*, 1977). Research has, however, been so directed that the characteristic which makes *D. stramonium* different from most other broad-leaved weeds – its high concentrations of physiologically active alkaloids – has remained imperfectly understood with respect to interactions between the weed and other plants.

This paper reviews the weed status of *D. stramonium* with particular reference to the potential for allelopathy to contribute to interference between the weed and crop plants.

Life cycle

D. stramonium is a summer-growing annual (Hooker, 1885) which reproduces by seeds. Germination commences in late spring, stimulated by preceding rainfall or irrigation of at least 1 cm (Miguel and Soriano, 1974; Stoller and Wax, 1974), and continues through mid-summer. Controlled-environment studies in Illinois, U.S.A., indicate that germination is most rapid under a 30°C day/24°C night temperature regime, with seedlings emerging 3 days after the onset of imbibition. Germination will occur with temperatures of 18°C day/12°C night but seedlings do not emerge for 10 days or more (Frazee and Stoller, 1974). Seedlings grow rapidly provided the temperature remains high (Parsons, 1973), with growth rates approaching 2.0 cm day⁻¹ in height at 30°C day/24°C night (Frazee and Stoller, 1974).

D. stramonium seedlings exhibit only moderate tolerance to moisture stress, germination being reduced by 60% and radicle growth by 50% as soil moisture tension increases from 0 to 6 bars (Hoveland and Buchanan, 1973). As is characteristic of many annual weeds, flowering commences when plants are 2–3 weeks old, minimizing the possibility of adverse environmental conditions killing the seedlings prior to maturity (Parsons, 1973). Mature *D. stramonium* plants may reach 2 m in height, although 0.5–1.5 m is more usual. Flowering and fruiting occur throughout the summer and up to 23 000 seeds can be produced by each large plant in one season. The plants are frost-susceptible and die rapidly in autumn, particularly in temperate regions (Rydberg, 1932; Moore, 1972; Parsons, 1973).

Seed dormancy

The seeds of *D. stramonium* are dormant at maturity, requiring 5–11 months after-ripening before being able to germinate (Monaghan and Felton, 1979). Dormancy is caused principally by a chemical inhibitor in the seed coat which must be oxidized or removed by diffusion before germination (Soriano *et al.*, 1964; Gugliada *et al.*, 1967). The rate of breakdown or removal of the inhibitor is influenced by moisture levels in the soil (Miguel and Soriano, 1974), depth of seed burial and soil temperature (Soriano, *et al.*, 1970). If the environmental conditions for the breaking of dormancy are not met seeds can remain viable in the soil for over 20 years at 20 cm, and for 4 years at 2.5 cm below the soil surface (Toole and Brown, 1946; Stoller and Wax, 1974).

Geographic distribution

D. stramonium has a worldwide distribution, characteristically in waste areas, disturbed and cultivated ground and in irrigation areas in temperate and subtropical regions (Parsons, 1973). It is common throughout much of the United States (Anon., 1970), the tropics and the subtropics (Holm *et al.*, 1979) but its origin is now uncertain (Rydberg, 1932; Parsons, 1973; Everist, 1981). It is presently the most widespread of all the *Datura* species (Haegi, 1976).

The genus *Datura* in Australia

One native and five naturalized species of *Datura* presently occur in Australia: *D. leichhardtii* F.Muell. ex Benth. (native thorn-apple); *D. ferox* L. (fierce

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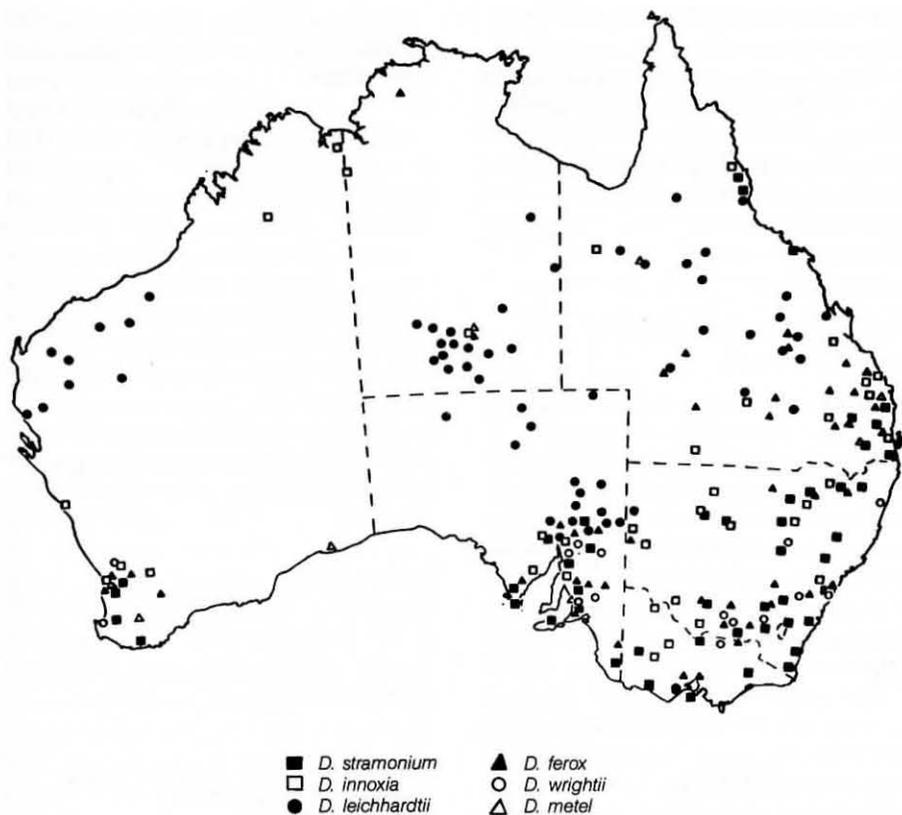


Figure 1 Distribution of *Datura* species on mainland Australia. The points plotted are based on herbarium specimens seen. (After Haegi, 1976.)

thorn-apple); *D. metel* L; *D. innoxia* Miller (downy thorn-apple); *D. wrightii* Regel (hairy thorn-apple); and *D. stramonium* (common thorn-apple) (Purdie, Symon and Haegi, 1982). The species are found throughout Australia with *D. stramonium* occurring in all States (Figure 1). *D. stramonium* was first recorded in Australia by Mueller in Victoria in 1853 (Haegi, 1976).

Weed status

Of the numerous weeds in the family Solanaceae, members of the genus *Datura* are among the most widely distributed in Australia and the rest of the world (Everist, 1957). Although susceptible in early growth stages to herbicides, for example 2,4-D (Parsons, 1973), infestations in Australia remain widespread in a variety of situations. *D. stramonium* is a major weed in many summer crops including sorghum, maize, soy beans (Felton, 1979), peanuts, cotton (Parsons, 1973) and vegetables (Fricke, 1977). It also invades waste land, disturbed sites, railway stock yards, river banks, irrigated pastures and, in some instances, native pastures in lower rainfall areas (Haegi, 1976).

Five species of *Datura* have been classified as noxious weeds by the State Departments of Agriculture: *D. stramonium* and *D. ferox* in New South

Wales, Victoria and Queensland; *D. innoxia* in Victoria and Queensland; and *D. metel* and *D. leichhardtii* in South Australia and Western Australia (Fricke, 1977).

D. stramonium is a serious weed for many reasons. Its life cycle ensures long-term persistence in the field, with high seed production (Parsons, 1973) and dormancy (Toole and Brown, 1946) resulting in dense populations of seedlings for many years following an initial infestation. It is an efficient competitor for light, moisture and nutrients (Parsons, 1973) and can cause significant yield reductions in many crops. For example, field trials in north west New South Wales showed that infestations of *D. stramonium* reduced the yield of sorghum by 6%, of maize by 19%, of soy beans by 36%, of sunflower by 38% and of mung beans by 90% compared with weed-free controls (Felton, 1979). Germination may continue for 2-3 months after crop emergence and this complicates control (Stoller and Wax, 1974). *D. stramonium* is generally unpalatable to stock and large infestations in pastures reduce the amount of usable dry matter (Lamp and Collet, 1976). Since it is also highly toxic (Tampion, 1977) contaminated hay is unfit for consumption by stock (Everist, 1957). A maximum of six *D. stramonium* seeds are allowed per kilogram of grain for stock feed in

Australia, while export regulations limit the amount in grain sorghum to 1.5 seeds per kilogram (Everist, 1981).

The toxic principals of *D. stramonium* are alkaloids (Mothes, 1955), secondary chemical compounds which are characteristic of the Solanaceae and which have been the subject of research since their use as narcotics in classical times (Schultes, 1969). Humans and other animals (McKillop, 1970), microorganisms (Rice, 1974) and insects (Rothschild, 1972) are all affected by these compounds, several of which appear to fulfil a defensive role for the plants which produce them.

Alkaloids of the Solanaceae

At least 27 of a total of 90 genera in the Solanaceae are known to contain one or more of over 150 named alkaloids, 27 of which have also been isolated from species in other angiosperm families (Raffauf, 1970). Of over 2400 species in the Solanaceae, approximately 100 have been investigated for the presence of alkaloids, which occur in 84 of them (Willaman and Schubert, 1955). Alkaloids occur in the crop (food and drug) as well as in the weed species of this family (Lindley, 1853).

The majority of the solanaceous alkaloids belong to one of the three groups pyridine, steroid and tropane. The latter group is well known for its dramatic pharmacological effects on humans and other animals (McKillop, 1970), and it is members of this group which are most common in the Solanaceae and which are found in *Datura* spp. (Miller, 1957). Atropine is apparently unique to the Solanaceae, whilst hyoscyamine is found in some members of the Agavaceae and scopolamine occurs in the Lentibulariaceae (Raffauf, 1970).

The occurrence of the major tropane alkaloids of the Solanaceae is shown in Table 1.

Distribution of alkaloids within the plant

In the initial stages of plant growth alkaloids are evenly distributed amongst the various organs, but with increasing age become localized in fewer sites (Manske, 1950). Concentrations of alkaloids are normally high in the active tissues of growing fruits, the epidermis, the piliferous layer, and the layers just below, adjoining and penetrating the vascular tissue (James, 1953).

Alkaloids may only occur in certain organs. Examples include the fruits of

Table 1 Major tropane alkaloids of the Solanaceae (modified from Gibbs, 1974).

Alkaloid name	Genus or species
atropine	<i>Datura</i> (thorn-apples)
	<i>Atropa</i> (nightshades)
	<i>Scopolia</i>
	<i>Duboisia</i> (corkwoods)
	<i>Hyoscyamus</i> (henbanes)
	<i>Solanum</i>
	<i>Mandragora</i> (mandrakes)
	<i>Solandra</i>
l-hyoscyamine	<i>Datura</i>
	<i>Scopolia</i>
	<i>Mandragora</i>
	<i>Hyoscyamus</i>
	<i>Anthocoris</i> (tailflowers)
	<i>Atropa</i>
	<i>Duboisia</i>
<i>Solandra</i>	
(-) scopolamine	<i>Datura</i>
	<i>Duboisia</i>
	<i>Scopolia</i>
	<i>Atropa belladonna</i> L. (deadly nightshade)
	<i>Hyoscyamus</i>
	<i>Mandragora vernalis</i> Bertol. (mandrake)
	<i>Psychoclaina praealta</i> (Walp.) Hook.f.

Solanum species (McBarron, 1976), the leaves of *Duboisia hopwoodii* F.Muell. which contain nicotine and nor-nicotine (Everist, 1974) and the green parts of the potato which contain the glycoalkaloid solanine (Francis and Southcott, 1968). Bellaridine is found in the roots of *Atropa belladonna*, four species of *Datura* and several other genera (Haga, 1954). In contrast the tropane alkaloids atropine, scopolamine and hyoscyamine are found in the leaves, seeds, nectar and roots of many species of *Datura* (Francis and Southcott, 1968; Everist, 1974).

When a particular alkaloid is found in several organs of the same plant its concentration usually varies between organs (Roddick, 1977). Fully-expanded flowers have the highest

concentration of tomatine in tomato, whilst young green fruits are also rich in this alkaloid, which is absent from ripe fruits (Roddick and Butcher, 1972). Alkaloid concentrations in *Datura metel* and *Hyoscyamus niger* L. is shown in Table 2 to illustrate differences both between plant species and plant organs.

Factors affecting alkaloid concentrations

Solanaceous drug plants have an optimum time of harvest which is seldom, if ever, when the plant is senescent (Robinson, 1974). Plant factors which can affect alkaloid concentration in a given species include the age of the plant, its health and whether the plant is haploid or diploid. Environmental factors include daylength, altitude, weather and nutrition (Everist, 1974).

The period of maximum alkaloid output often coincides with early flowering (Manske, 1950) through to peak maturity (Cromwell, 1944). Stress caused by mechanical damage increases glycoalkaloid production in potato (Osman *et al.*, 1979). Ploidy level influences the alkaloid concentration in *D. metel* seeds, with haploid plants containing 0.15% alkaloid, diploid 0.33% and tetraploid 0.42% (Karnick and Saxena, 1970).

McNair (1942) showed that as soil pH decreases so does alkaloid production, with plants producing their greatest amount of alkaloid when the concentration of electrolytes in their sap is at a maximum. This is associated with the nitrogen status of the plant: as much of the active nitrogen in alkaloids is in the amino form, the presence of ammonium nitrogen tends to increase alkaloid production more than the presence of nitrate nitrogen. The rate of nitrate and ammonium utilization by the plant is in turn influenced by soil pH. Manske (1950) postulated competitive formation of protein and alkaloids during growth, the calcium favouring the diversion of nitrogen for alkaloid production and potassium favouring the synthesis of proteins.

Work by Karnick and Saxena (1970) showed that some factor associated with altitude affects alkaloid production in *D. metel*. The alkaloid concentration of *D. metel* flowers is 0.69% in plants grown at sea level compared with 0.99% in plants found growing at 2000 m.

Many alkaloids are synthesized in roots. Cromwell (1944) found that the leaves of *Atropa* grown in full sunlight generally contained more alkaloid than those grown in shade, and suggested that the greater transpiration occurring in sunshine tends to draw more alkaloid up from the root system. Ultra-violet light is more effective than infra-red or visible wavelengths in stimulating solanine formation in potato tubers (Conner, 1937). Long days favour alkaloid production in *D. metel* (Robinson, 1974), *D. stramonium* (Lovett *et al.*, 1981) and *Nicotiana tabacum* L. (Tso *et al.*, 1970).

Alkaloid production in *Datura stramonium*

The processes of alkaloid biosynthesis, translocation and accumulation in the Solanaceae are still being elucidated. Many alkaloids have specific sites of synthesis and may or may not be translocated after their formation to be concentrated and stored in other parts of the plant.

Clautriau (1906) found that shortly after fertilization in *D. stramonium* the embryo and endosperm are enclosed in a well-developed perisperm containing abundant quantities of alkaloid. Starch and protein are also present in significant quantities. As the endosperm grows this layer loses its starch and protein but the alkaloids remain without loss. The cells finally dry up and are crushed against the integument by the continuing growth of endosperm and embryo, so that at maturity they form a thin membrane from whose dead cells the alkaloids are readily leached.

James (1946) showed that roots of *D. stramonium* seedlings 1–2 mm long contain no alkaloid, roots 3 mm long show trace amounts, and longer roots contain large quantities of alkaloid. The alkaloids appear to originate from the meristem just behind the root cap. The shoots give a strong positive reaction for alkaloids at first appearance but the hypocotyl and cotyledons do not contain alkaloids at any time (James, 1953).

Mothes (1955) described the later stages of alkaloid ontogenesis in *D. stramonium*. Not until the sixth day of germination when the cotyledons

Table 2 Distribution of the alkaloid scopolamine in *Datura metel* and *Hyoscyamus niger* (after Schultes and Hofmann, 1973).

Plant organ	Percentage alkaloid by weight	
	<i>Datura metel</i>	<i>Hyoscyamus niger</i>
fruit	0.12	—
leaves	0.20–0.50	0.04–0.08
roots	0.10–0.20	0.16
seeds	0.20–0.50	0.06–0.10

turn green are alkaloids detected in the peripheral tissues of the root, thereafter continuing to spread to the epidermis. In the course of 1 month they reach the pith, cork and phelloderm. During senescence the alkaloid concentration of the root decreases, with only the central cylinder giving a positive test. Alkaloid appears in the stem about the tenth day of germination, first in the parenchyma of the bark and later in the cork and pith. In the leaves, alkaloids are first found in the epidermis, and in the flower a trace in the corolla.

The accumulation of alkaloids in the large vacuoles of storage tissue occurs as a later development in the plant (James, 1946).

Allelopathy and *Datura stramonium*

Alkaloids are associated with toxicity towards a variety of organisms, and it would seem axiomatic that they could be linked with allelopathy. Curiously, the majority of biologically active alkaloids have not been implicated in this way (Muller and Chou, 1972), although the majority have not even been tested for such activity (Mandava, 1979). In most cases where growth retardation of plants by members of the Solanaceae has been documented, the chemicals responsible have not been identified and their primary mode of action has not been specified.

The effects of different concentrations of aqueous leachates of seeds and leaves of *D. stramonium* on the germination and radicle elongation of linseed were examined by Lovett *et al.* (1981). The presence of both scopolamine and hyoscyamine in the plant washings was confirmed by gas chromatography/mass spectrometry. Concentrations were higher in seed washings than in foliage washings and both the germination and radicle elongation of linseed were significantly reduced by *D. stramonium* washings.

Seeds of *D. stramonium* on and in the ground represent a substantial reservoir of alkaloid-containing material from which the toxic principals may readily be leached (Lovett and Levitt, 1982). The fact that *D. stramonium* is reported as being a significant weed in areas of irrigated summer cropping (Felton, 1979) suggests that allelopathy may occur in the field as a consequence of rainfall and/or pre-irrigation releasing alkaloids from the weed seeds into the soil. Experiments were conducted to examine the influence of time, moisture relation and soil type on the effect of *D. stramonium* allelochemicals on the germination of sunflower seeds

under laboratory and field conditions using different agricultural soils. Under laboratory conditions it was found that inhibition of sunflower radicle elongation was more pronounced in a lateritic podzolic than in a black earth soil (Table 3).

Under controlled conditions the phytotoxicity of *D. stramonium* alkaloids persisted for 20 weeks in lateritic podzolic soil. It has been postulated (Levitt and Lovett, 1984) that the most important soil characteristic contributing to this difference was the clay fraction. Since alkaloids in soil behave as cations, clays with a higher capacity for cation adsorption (as found in black earth) are likely to reduce the amount of alkaloid free in the soil and thereby reduce its phytotoxicity.

The field significance of these phenomena was demonstrated through studies of a black earth soil collected at Moree in north-western New South Wales. This soil had a history of heavy infestation of *D. stramonium* and difficulties in crop establishment. In controlled experiments it was shown that the field-collected soil inhibited radicle elongation of sunflower (Table 4).

The tropane alkaloids scopolamine and hyoscyamine were recovered from the soil and appeared to be present in approximately equal concentrations. Seedling populations of *D. stramonium* in the field were 10 000–50 000 seed-

lings per square metre, comparable to heavy infestations in irrigation areas of north-western New South Wales (Felton, W. L., personal communication).

Whilst the identification of allelochemicals in the literature is comparatively rare (Lovett, 1982), studies in which named chemicals of plant origin have been positively identified in soil and with which allelopathic activity has then been demonstrated are extremely uncommon in the literature.

These data strongly suggest that allelopathy should be recognized as contributing to the weed status of *D. stramonium*. The widespread occurrence of alkaloids in solanaceous species at large further suggests that similar phenomena will be of significance in other species within the family.

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Table 3 Effect of *D. stramonium* seeds and seed washings on radicle growth of sunflower in black earth and lateritic podzolic soils after 72 hours (modified from Levitt and Lovett, 1984).

Treatment	<i>H. annuus</i> radicle length (mm)		Lateritic podzolic % black earth
	Black earth	Lateritic podzolic	
Sterile water	60.7	55.8	91.9
<i>D. stramonium</i> seeds	51.0	32.0	62.7
<i>D. stramonium</i> seed washings	42.8	22.5	52.6

(0.1% LSD = 6.80)

Table 4 Effect of *D. stramonium* infestation on radicle length of sunflower seedlings in black earth soil (after Levitt and Lovett, 1984).

Sample	Radicle length (mm) (means of 80)		Percentage reduction	Probability
	Control	Infested		
1	40.5 ^d	15.9 ^{ab}	60	<0.001
2	35.3 ^{cd}	20.2 ^b	42	<0.001
3	33.7 ^{cd}	16.8 ^{ab}	50	<0.001
4	29.9 ^c	13.7 ^a	54	<0.001

Means followed by the same letter are not significantly different at the 5% level using the Studentized Range Test.

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