EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON THE GROWTH AND DEVELOPMENT OF SILVERLEAF NIGHTSHADE (*SOLANUM ELEAGNIFOLIUM*)

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INTRODUCTION

Each of the three parts of this thesis is a separate manuscript to be submitted for publication in Weed Science, the journal of the Weed Science Society of America.

PART I

SILVERLEAF NIGHTSHADE (*SOLANUM ELEAGNIFOLIUM*): ORIGIN, DISTRIBUTION, AND RELATION TO MAN

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Abstract. Silverleaf nightshade (*Solanum eleagnifolium* Cav.) is a perennial weed that has become increasingly troublesome over the past several years. Extensive use of soil applied herbicides accompanied by a reduction in annual weed competition and reduced tillage have contributed to this species increase. Silverleaf nightshade exhibits much intraspecific variation and may be confused with horsenettle (*Solanum carolinense* L.). These two species may be distinguished by comparison of the leaf hairs and seed coat texture. Pollination of silverleaf nightshade is entomophilous. Artificial crosses have been made with horsenettle and *Solanum dimidatum* Raf., however, natural hybrids have not been reported. Indian tribes in the Southwestern United States used this plant in food preparation and tanning. The fruits offer a potential source of solamine, a chemical used in the manufacture of steroidal hormones. Silverleaf nightshade affects crops in many parts of the world through competition, harvest interference, allelopathy, and harboring insect and disease pests. Livestock have been poisoned as a result of eating this plant. An alkaloidal glucoside, solamine, is thought to be the toxic agent. Silverleaf nightshade is probably native to the Southwestern United States and Northern Mexico, but is now found in many semiarid regions of the world.

Additional index words. Synonomy, uses, alternate host, hybridization.

INTRODUCTION

Although the nightshade family is not as important to man as grasses or legumes, it nevertheless ranks near the top of any list of plant families that serve mankind (20). It includes food plants, medicinal and poisonous species, ornamentals, and several noxious weeds (20). Among the lesser known weeds in the *Solanaceae* family is *Solanum eleagnifolium* Cav. It is presumed that the genus name *Solanum* comes from the Latin word *solamen*, meaning quieting, alluding to the sedative properties of some species (20). Many members of the family produce alkaloids which have a quieting effect; in fact, sometimes a quite permanent one (20). The specific epithet, *eleagnifolium*, means with leaves of *Eleagnus*. This refers to the silvery-gray leaves which are similar to those of Russian olive (*Eleagnus* spp.). There are many vernacular names of *S. eleagnifolium* (Table 1). Presently, silverleaf nightshade is the commonly accepted vernacular name and will be used in this paper.

Prior to the last decade, this species received little attention from the scientific community. Interest has grown over the past several years as a result of two phenomena: (a) silverleaf nightshade has spread to several regions outside its native range (Table 3) and is becoming a troublesome weed in those areas (9, 26, 29, 35, 39), and (b) extensive use of soil applied herbicides over the last 10 to 15 years has reduced annual weed competition and tillage, thus creating a favorable environment for silverleaf nightshade growth (5).

The goal of this paper is to examine the relationship of silverleaf nightshade to man by bringing together the limited agronomic and botanical literature. Particular emphasis will be placed on origin, distribution, uses, and the means of which silverleaf nightshade affects man.

SILVERLEAF NIGHTSHADE

Silverleaf nightshade (Figure 1) has been described in detail in various floras (10, 22, 28, 32, 34, 38). The morphology, seedling development, and phenology in the wild have been described by Encomidou and Yannitsaros (14). Rather than a verbatim repitition of other authors, our aim is to emphasize characteristics that may be of use to weed scientists and others interested in this species. The casual observer may not be able to distinguish silverleaf nightshade from other _Solanum_ species such as _S_. _carolinense_. The large degree of intraspecific variation exhibited by silverleaf nightshade often adds to the confusion. Spines may be present or absent and leaf shapes differ widely (Figure 2). These species may be distinguished by examining the hairs on the upper leaf surface. The hairs of silverleaf nightshade are quite distinct (Figure 3), and may be seen with a hand lens. Roe (33) called these hairs short stalked (stalk not visible), porrect-stellate hairs with a short central ray. These hairs give the leaves a silvery-gray appearance and thus the name silverleaf nightshade.

Another means of distinguishing horsenettle and silverleaf nightshade is by comparing their seed coats. The seed of silverleaf nightshade have a much smoother surface. Gunn and Gaffney (17) have prepared a detailed description of silverleaf nightshade seed. They reported that the reticulum of silverleaf nightshade is only faintly visible at 30X magnification. While the coarse reticulum of horsenettle is easily seen with 10X magnification. This method is useful for identifying winter collected seed for use in weed ecology studies.

The morphological variations displayed by silverleaf nightshade might lead one to suspect hybridization with related species. Hardin et al. (18) studied the pollination ecology and floral biology of silverleaf nightshade and three other weedy _Solanum_ species in Oklahoma. No natural hybrids were observed among horsenettle, silverleaf nightshade, buffalo bur (_Solanum rostratum_ Dunal.), or _Solanum dimidatum_ Raf. (18). Pollination was entomophilous in each of the four species. Artificial crosses among silverleaf nightshade, horsenettle, and _S. dimidatum_ produced fruit, however, the ability of these seed to germinate was not substantiated (18).

SYNONOMY (10)

Solanum eleagnifolium Cav., Icon. Pl. 3:22, t.243, p.115. 1795. TYPE: Cavanilles s.n. (C,MA,P-JUSS)

Solanum leprosum Ort., Hort. Matr. Dec. 9:115. 1800. TYPE: Chile, collector unknown (MPU, ex hort. Matrit.)

Solanum obtusifolium Dun., Sol. Syn. 26. 1816. TYPE: Mexico, _Bonpland_(?P,not seen)

Solanum flavidum Torr., Ann. Lyceum New York. 2:227. 1828. TYPE: Western United States, _James_ 309 (NY)

Solanum texense Engelm. & Gray, Bost. Jour. Nat. Hist. 5:227. 1845. TYPE: Texas, Lindheimer 135 [=Drummond 200] (K,MO)

Solanum roemerianum Scheele, Linnaea 21:767. 1848. TYPE: not seen; ? = S. undatum Roemer.

Solanum eleagnifolium var. leprosum (Ort.) Dun. in DC., Prodr. 13(1):291. 1852.

Solanum eleagnifolium var. obtusifolium (Dun.)Dun. in DC. Prodr. 13(1):291. 1852. [Solanum undatum Roemer, ined., non Lam. TYPE: "ex herb. Roem." (BM)].

ORIGIN

Botanists agree that silverleaf nightshade is native to the Americas (10, 19, 28, 34). The unresolved question is whether it is indigenous to North or South America. At present, there is no indisputable evidence to indicate the geographic origin of silverleaf nightshade. Numerous gaps in the early history of this species make tracing its origin difficult at best. In the following paragraphs an attempt will be made to piece together the available information and to provide a personal hypothesis as to the geographic origin of silverleaf nightshade.

The recorded history of Solanum eleagnifolium Cav. begins in 1795 with the publication OF its name and description in Icones et Descriptiones Plantarum, a six volume work devoted to American flora (4, 23). Icones was written by Antonio Jose Cavanilles, a Spanish botanist and cleric. Cavanilles was a professor of botany at the University of Madrid and director of the Royal Botanic Gardens (23, 37). Cavanilles (4) described silverleaf nightshade's habitat as, "America caldidiore," and the phenological characteristics as, "Floret a Iulio usque ad Octob. in Regio horto Matritensi." Translation from the Latin reveals that silverleaf nightshade is from the warm regions of America, and flowers from July to October in the gardens of Madrid. Apparently, silverleaf seeds has been forwarded to Madrid and Cavanilles observed the growth and development of plants arising from these seed. It seems reasonable that knowing who sent the seed to Cavanilles would be helpful in tracing the origin of silverleaf nightshade. It is possible that Vicente Cervantes sent silverleaf nightshade seeds to cavanilles. Keefe (23) wrote that Vicente Cervantes, who was attached to the Mexico City Botanic Gardens, often sent seed of local plants to his friend Cavanilles.

In attempting to prove that a species is native to a certain region it is useful to determine if there are closely related species indigenous to that same region. Solanum hindsianum Benth. fits the above mentioned criteria. It is closely related to silverleaf nightshade and known to be native to Baja California and the Sonoran Desert (6, 34). Herbarium specimens of S. hindsianum were examined at the Missouri Botanical Garden, and the close relationship of this species to Solanum eleagnifolium confirmed by Dr. W. G. D'Arcy, a Solanaceae specialist.[1]

An examination of the collection sites of the herbarium material of silverleaf nightshade at Missouri Botanical Garden produced no clear evidence of geographic origin. Very early collections have been made in North and South America. The almost simultaneous appearance of silverleaf nightshade on both continents is of interest due to the

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[1] Personal communication, W. G. D'Arcy, Research Botanist, Missouri Botanical Garden.

considerable distance separating these regions. Thus, the very early introduction of silverleaf nightshade from North to South America, or vice versa, by Spanish or Portuguese colonists cannot be ruled out.[2]

While the data presented is by no means conclusive the meager evidence suggests that the most likely centers of geographic origin for silverleaf nightshade are the Southwestern United States and Northern Mexico.

USES

Silverleaf nightshade has a brief ethnobotanical history. The berries and seeds were used by Indian tribes native to the Southwestern part of the United States. The Pimas added the crushed berries to milk when making cheese (22). The Kiowas combined the seeds with brain tissue and used the mixture for tanning hides (40). A protein digesting enzyme similar to papain is thought to be the active ingredient in the seeds and berries (22).

Researchers in India have investigated silverleaf nightshade's potential as a source of drugs (24). Maiti and Mathew (24) report that silverleaf nightshade is rich in solasodine, a chemical used in the manufacture of steroidal hormones. The fruits of silverleaf nightshade contain about 3.2% (g/g dry weight) solasodine (24).

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[2] Personal communication, D. E. Symon, Botanist, Waite Agric. Res. Inst., Glen Osmond, S. Australia.

SILVERLEAF NIGHTSHADE IN RELATION TO MAN

Weeds manifest their influence on man in many ways. Some of the means by which weeds affect man are: (a) competition with crops, (b) exudation of plant inhibitors, (c) interference with agriculture, and (d) acting as an alternate host for phytophagous insects and plant diseases. The following section deals with silverleaf nightshade's impact in each of these areas.

Competition. In Texas and Oklahoma, the vegetative shoots of silverleaf nightshade appear in mid April and early May. Many plants have flowered by the middle of May. This rapid growth in early spring is possible due to the food reserves stored in the vegetative propagules of silverleaf nightshade. These characteristics give silverleaf nightshade a competitive advantage over many crops. Silverleaf nightshade competes with row crops, small grains, forages, and horticultural crops (1, 9, 11, 36). Under semiarid conditions, cotton yields have been reduced by 75% (1). Smith et al. (36) observed an inverse correlation between grain sorghum yields and silverleaf nightshade densities. Nine silverleaf nightshade plants per m^2 reduced Australian cereal grain yields by 12%. Table 2 lists some of the crops infested by silverleaf nightshade.

Inhibitors. A single paper has been published dealing with the allelopathic effects of silverleaf nightshade (8). Curvetto et al. (8) reported that aqueous solution of the saponins extracted from silverleaf nightshade fruits gradually reduced the root growth of cucumber (Cucumis sativa L.). Diplotaxis tenufolia (L.) DC. was similarly affected. When silverleaf nightshade fruits, from which the pericarp had been removed, were placed in petri dishes containing soil they interfered with germination and seedling development of a number of crop and weed species (8).

Interference with agriculture. Livestock have been poisoned as a consequence of eating silverleaf nightshade berries (13, 26). Cattle ingesting ripe berries equal to 0.1 to 0.3% of their body weight suffered moderate poisoning symptoms (13). At the feeding levels used by Dollahite et al. (13) sheep were more resistant than cattle, and goats were not affected. An Australian publication (26) reports the death of several sheep due to silverleaf nightshade consumption. The toxic agent in the berries is an alkaloidal glucoside, solamine (13).

Morey (27) recovered silverleaf nightshade fragments from the herbal trash of machine picked and stripper harvested cotton. Weed materials constituted as much as 35% of the cotton trash examined (27). Cotton dust arising from the micronization of herbal trash contributes to byssinosis, a respiratory disease that affects cotton textile workers (27).

Silverleaf nightshade seed and vegetative parts often contaminate seed and forage crops (2, 11, 26). Bellue (2) reported the occurrence of silverleaf nightshade seed in commercial crop seed. Davis (11) observed that livestock were reluctant to graze field infested with silverleaf nightshade. The quality of hay from infested fields is reduced by the presence of the spiny leaves and coarse stems (11).

Alternate host for insects and diseases. Several insect species that damage crops have been found in association with silverleaf nightshade (16, 41). Lygus bugs (*Lygus hesperus* Knight), an important pest in the irrigated lands of the Western states, have demonstrated a proclivity for silverleaf nightshade (41). In addition, a number of plant pathogens such as *Rhizoctonia solani* Kuehn, *Septoria lycopersici* Speg., and *Verticillium albo-atrum* Reinke & Berth. have been isolated from silverleaf nightshade (21).

DISTRIBUTION

Silverleaf nightshade is capable of propagating by means of seeds, creeping rhizomes, and root fragments (9). The seed may be dispersed by wind, water, birds, vehicles, machinery, agricultural produce, and in the feces of grazing animals (2, 26). Bellue (2) reported that dried plants, with the berries still attached, may break off and blow in the wind like tumbleweeds. The spread of silverleaf nightshade into California is thought to be a result of seed swept from contaminated railway cars (12, 31). Another common means of seed distribution is in commercial seed and feedstuffs harvested from infested fields (2). Crops such as alfalfa, grain sorghum, and cereal grains are frequent carriers of silverleaf nightshade seed (2). Feeding studies conducted in Australia have shown that 10% of the seed fed to sheep remained viable after passing through the digestive tract (26). It may be that passing through the alimentary canal enhances seed germination.

Silverleaf nightshade root fragments 1 cm long retain the ability to sprout, and sections of the taproot have remained viable for up to 15 months, if kept moist (15, 26). These data suggest that while vegetative propagation is primarily a local means of spread, there is potential for long range dispersal by root and rhizome peices. Rhizomes may extend 2 m from the original plant (26). Local distribution of vegetative propagules is generally a result of tillage operations associated with agriculture, and the creeping nature of the rhizomes.

Silverleaf nightshade has spread into many parts of the world beyond its native range (Table 2). As would be expected, the environmental conditions in these alien locations are similar to those found in silverleaf nightshade's indigenous habitat. Silverleaf nightshade seems adapted to semiarid regions (30 to 60 cm annual rainfall), and coarse textured, sandy soils (26). The means by which silverleaf nightshade arrived on other continents is not known. Australia, where it was declared a noxious weed in 1950, first recorded silverleaf nightshade in 1901 (9, 25). Australian scientists agree that multiple introductions must have occurred because silverleaf nightshade appeared almost simultaneously in several widespread locations. The introduction of silverleaf nightshade into Israel is thought to be an indirect result of politics. Silverleaf nightshade was known in Egypt prior to 1956, and was first collected in Israel in 1957 (Table 2). It has been quite logically suggested that silverleaf nightshade was introduced into Israel while the borders were open during the 1956 war. Examination of the meager literature documenting the movement of silverleaf nightshade indicates that it does not spread as rapidly as some plant species, but once established is very tenacious.

ACKNOWLEGEMENTS

I would like to thank Dr. W. G. D'Arcy, Research Botanist at the Missouri Botanical Garden, for his help in collecting information for this paper.

LITERATURE CITED

1. Abernathy, J.R. 1979. Silverleaf nightshade control in cotton with glyphosate. Proc. South. Weed Sci. Soc. 32:380.
2. Bellue, M.K. 1946. Weed Seed Handbook. Series IV. Calif. Dept. Agric. Bull. 25:15-16.
3. Boswell, T.E. 1971. Postemergence weed control in peanuts. Proc. South Weed. Sci. Soc. 24:124-127.
4. Cavanilles, A.J. 1795. _Icones et Descriptiones Plantarum_. 3:22. t. 243. 600 plates. J. Cramer-Lehre. New York.
5. Cooley, A.E. and D.T. Smith. 1973. Silverleaf nightshade (whiteweed) establishment from seed and clipped seedlings. Cons. Rep. of the T.A.E.S. Prog. Rep. No.'s 3197-3209. No. 3198. p. 6-8. Weed and Herbicide Research in West Texas.
6. Coyle, J. and N.C. Roberts. 1975. A field guide to the common and interesting plants of Baja California. Nat. Hist. Pub., La Jolla, Calif. 206 pp.
7. Crittenden, M. and D. Teller. 1975. Wildflower of the west. Celestial Arts Press. Millbrae, Calif. 199 pp.
8. Curvetto, N.R., T. Montani, S.E. Delmastra, and O.A. Fernandez. 1976. Alleopathic effects of the saponins of the fruits of _Solanum eleagnifolium_ on the germination and growth of other species. Trabajos y Resumenes, III Congreso Asociacion Latinoamericana de Malezas y su Control. 1:147-152.

9. Cuthbertson, E.G. 1976. Silverleaf nightshade-a potential threat to agriculture. Agric. Gaz. N.S.W. 87:11-13.

10. D'Arcy, W.G. 1974. Solanum and its close relatives in Florida. Ann. Mo. Bot. Gdn. 61:819-867.

11. Davis, C.H., T.J. Smith, and R.S. Hawkins. 1945. Eradication of the white horsenettle in Southern Arizona. Ariz. Agric. Expt. Stn. Bull. No. 195. 14 pp.

12. Davy, J.B. 1896. Solanum eleagnifolium in California. Erythea. 4:125.

13. Dollahite, J.W. and T.J. Allen. 1960. Silverleaf nightshade poisoning in livestock. T.A.E.S. Prog. Rep. No. 2146. 7 pp.

14. Encomidou, E. and A. Yannitsaros. 1975. Recherches sur la flore adventice de Grece. III. Morphologie, development, et phenologie du Solanum eleagnifolium. Candollea. 30:29-41.

15. Fernandez, O.A. and R.E. Brevedan. 1972. Regeneracion de Solanum eleagnifolium a partir de fragmentos de sus raices. Darwiniana. 17:434-442.

16. Goeden, R.D. 1971. Insect ecology of silverleaf nightshade. Weed Science. 19:45-51.

17. Gunn, C.R. and F.B. Gaffney. 1974. Seed characteristics of 42 economically important Solanaceae in the United States. U.S.D.A. Tech. Bull. No. 1471. 33 pp.

18. Hardin, J.W., G. Doerkson, D. Herndon, M. Hobson, and F. Thomas. 1972. Pollination and floral biology of four weedy species in Southern Oklahoma. Southwestern Naturalist. 16:403-412.

19. Hawkes, J.G. and J.M. Edmonds. 1972. Flora Europaea. 3:197-199. Cambridge Univ. Press. 370 pp.

20. Heiser, C.B. 1969. Nightshades the Paradoxical Plants. W.H. Freeman Co. 200 pp.

21. Index of Plant Dieseases in the United States. U.S.D.A. Handbook No. 165. 456 pp.

22. Kearney, R.H. 1960. Arizona Flora. Univ. of Calif. Press. Berkeley. 1085 pp.

23. Keefe, A.M. 1966. Our debt to the clerical botanists. The Biologists. 48:45-61.

24. Maiti, P.C. and R. Mathew. 1967. Rich sources of solasodine. Current Sci. 36:126.

25. Martino, A. di. 1956. Una stazione di _Solanum_ _eleagnifolium_ Cav. var. leprosum in Sicilia. Lav. Reale Ist. Bot. Palermo. 15:114-120.

26. Molnar, V.M. and D.N. McKenzie. 1976. Progress report on silver-leaf nightshade research. Pamphlet No. 61. Vermin and Noxious Weeds Destruction Board. Dept. of Crown Lands and Survey, Victoria, Australia. 12 pp.

27. Morey, P.R. 1977. Weed particles in raw cottons: a potential source of dust. Weed Science Soc. Am. Abstr. 8. p. 4.

28. Munz, P.A. 1974. Flora of Southern California, Univ. of Calif. Press. Berkeley. 1086 pp.

29. Narayan, T.R. and D. Meenakshisundaram. 1955. _S_. _eleagnifolium_- a new weed in the cultivated lands of Madras. Madras Agric. J. 42:482-484.

30. Pilar, F.M.R.C. 1937. Contribucion al estudio de Solanum eleagnifolium Cav. (meloncillo del campo). Anales. Farm. Bioquim. 8:23-44.

31. Robbins, W.W. 1940. Alien plants growing without cultivation in California. Calif. Agric. Expt. Stn. Bull. No. 637:82-83. 128 pp.

32. Robbins, W.W., W.S. Ball, and M.K. Bellue. 1970. Weeds of California. Calif. Agric. Ext. Serv. Bull. No. 437. 547 pp.

33. Roe, K.E. 1971. Terminology of hairs in the genus Solanum. Taxon. 4:501-508.

34. Shreve, F.S. and I.L. Wiggins. 1964. Vegetation and Flora of the Sonoran Desert. 3:1326-1327. Stanford Univ. Press. 1740 pp.

35. Siebert, M.W. 1975. Candidates for the biological control of Solanum eleagnifolium Cav. (Solanaceae) in South Africa. 1. Lab studies of the biology of Gratiana lutescens (Boh.) and Gratiana pallidula (Boh.) (Coleoptera:Cassididae). J. Ento. Soc. South Africa. 38:297-304.

36. Smith, D.T., A.F. Wiese, and A.W. Cooley. 1973. Crop losses from several annual and perennial weeds. Weed Sci. Soc. Am. Abstr. 21. p. 53-54.

37. Stafleu, A. 1972. Portraits of botanists. Taxon. 21:138.

38. Tackholm, V. 1956. Student's Flora of Egypt. Anglo-Egyptian Bookshop. 648 pp.

39. Tideman, A.F. 1960. Tomato weed in South Australia (Solanum eleagnifolium Cav.). J. Dept. Agric. South Australia. 63:329-331.

40. Uphof, J.C. Th. 1959. Dictionary of Economic Plants. Hafner Pub. Co. New York. 400 pp.

41. Wene, G.P. and L.W. Sheets. 1964. White horsenettle or silver-leaf nightshade; an important host of lygus bugs. J. Econ. Ento. 57:181.

Table 1. Language and geographic sites for vernacular names of *Solanum eleagnifolium* Cav.

Name	Language	Geographic Site	Reference
bullnettle	English	United States	(22)
desert nightshade	English	United States	(7)
devilbush[1]	English	South Africa	
meloncillo	Spanish	Argentina	(15)
meloncillo del campo	Spanish	Argentina	(30)
purple nightshade	English	United States	(5)
revienta caballo	Spanish	Argentina	(15)
sand brier	English	United States	(32)
satansbos	Afrikaner	South Africa	(35)
silver horsenettle	English	United States	(22)
silverleaf bitter apple	English	South Africa	(35)
silverleaf horsenettle	English	United States	(28)
silverleaf nettle	English	United States	(18)
silverleaf nightshade	English	United States	(32)
tomatillo	Spanish	Argentina	(30)
tomato weed	English	Australia	(39)
trompillo	Spanish	United States	(32)
western horsenettle	English	United States	(17)
white horsenettle	English	United States	(2)
whiteweed	English	United States	(5)

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[1] Personal Communication, H.G. Zimmerman, Weeds Laboratory, Uitenhage, South Africa.

Table 2. Crops in which silverleaf nightshade has been reported to occur.

Crop	Location	Reference
alfalfa (*Medicago sativa* L.)	U.S.A	(11)
cantaloupes (*Cucumis melo* L. var. *cantalupensis* Naud.)	U.S.A.	(11)
cotton (*Gossypium hirsutum* L.)	U.S.A.	(1)
grain sorghum (*Sorghum bicolor* L.)	U.S.A	(34)
peanuts (*Arachis hypogaea* L.)	U.S.A.	(3)
ragi (*Eleusine coracana* Gaertn.)	India	(28)
rice (*Oryza sativa* L.)	India	(25)
watermelons [*Citrullus lanatus* (Thunb.) Mansf.]	U.S.A.	(11)
wheat (*Triticum aestivum* L.)	Australia	(9)

Table 3. Movement of silverleaf nightshade into locations beyond its native range.

Geographic site	Approximate date	Reference
Australia	1901	(9)
Egypt	1956	(38)
Greece	1972	(14)
India	1955	(28)
Israel[2]	1957	
Rhodesia	1969	(Hilberg #2528,MO)
Sicily	1956	(25)
South Africa	1952	(35)
Spain	1975	(19)

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[2] Personal communication, Dr. A. Dafni, University of Haifa, Mt. Carmel, Haifa, Israel.

Figure 1. Solanum eleagnifolium Cav.

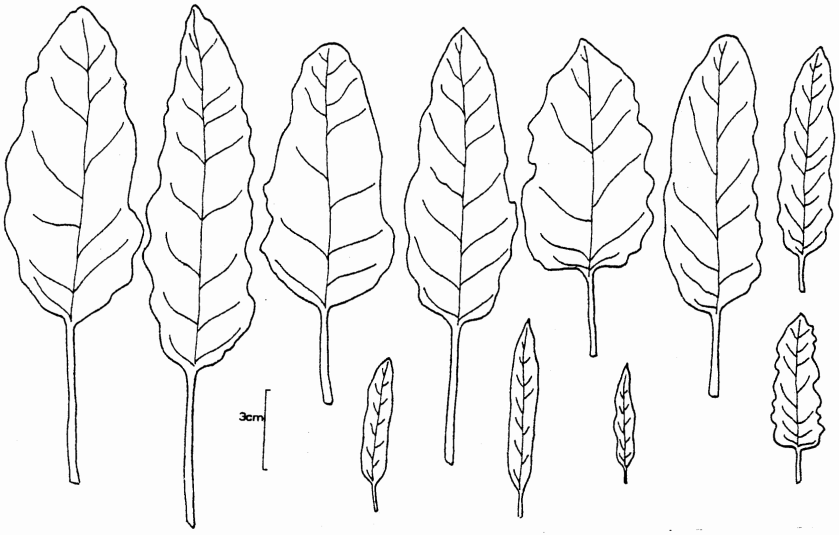

Figure 2. Leaf variation in silverleaf nightshade (12)

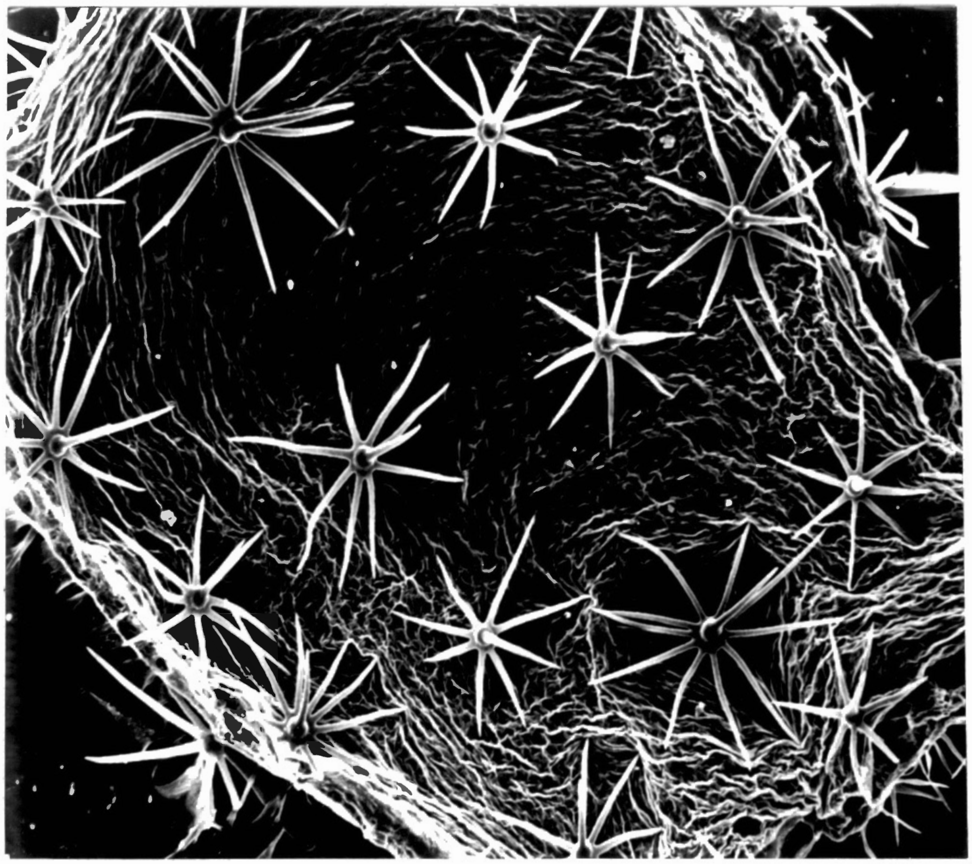

Figure 3. Hairs on the upper leaf surface of silverleaf nightshade (50X)

PART II

GROWTH AND DEVELOPMENT OF SILVERLEAF NIGHTSHADE (*SOLANUM ELEAGNIFOLIUM*)

GROWTH AND DEVELOPMENT OF SILVERLEAF NIGHTSHADE (SOLANUM ELEAGNIFOLIUM)

Abstract. Controlled environment studies were conducted to determine the influence of temperature, seed weight, pH, salinity, light and depth of planting on the germination and emergence of silverleaf nightshade (*Solanum eleagnifolium* Cav.). The effects of planting date, top removal, and root cutting length on establishment were studied in the field. Fluctuating temperatures of 20 to 30 C produced optimum germination of 57%. Seed heavier than 310 mg/100 seed did not have significantly higher germination. Maximum germination occurred between pH 6 and 7. NaCl concentrations greater than 2500 ppmw caused a significant decrease in germination. Light was not important in germination. Maximum seedling emergence was from depths of 1.0 to 2.5 cm. Collection site did not affect seedling emergence. Emergence from a sandy soil was greater than from a loam at the 2 cm depth. Delayed seeding caused a decline in dry matter and fruit production. Seed sown on or after July 1 produced no fruit. Seedlings clipped 15 days after emergence were capable of regrowth, and after 30 days 90% or more the clipped plants regrew. Shoot production, survival, height, dry matter, and fruit production increased with increased length of planted root cuttings.

Additional index words. Planting date, top removal, root length, planting depth, salinity.

INTRODUCTION

Silverleaf nightshade (Solanum eleagnifolium Cav.) is a deep rooted, perennial weed, that propagates by means of seed, creeping rhizomes, and root fragments (6). This weed infests more than 800,000 ha of crop land in Texas and Oklahoma (1). Silverleaf nightshade reduces crop yields through competition, harves interference, and quality loss (1, 5, 14).

Vegetative and sexual reproduction should be considered when developing broad based weed control programs (4). Often efforts to contorl perennial weeds are focused exclusively on vegetative phases of reproduction. Ignoring propagation of perennials by seed can result in an incomplete program, because seed are frequently the chief means of long term survival and establishment in new areas. As propagules, seed are usually more abundant, easily transported, and exhibit greater longevity than vegetative propagules. Cooley and Smith (4) reported that a dense population of silverleaf nightshade was capable of producing 250 million seed/ha. Molnar and McKenzie (12) recovered 4000 seed/m^2 from the soil of an area heavily infested with silverleaf nightshade. Silverleaf nightshade seed may be transported by wind, water, birds, vehicles, machinery, agricultural produce, and in the feces of grazing animals (2, 12) Bellue (2) reported 60% germination of silverleaf nightshade seed after 10 years of storage. These findings illustrate that the seed of silverleaf nightshade possess the previously noted advantages with seed reproduction: abundance, portability, and longevity.

Research concerned with the effect of seeding date on weed species has been minimal. Perennials have been particularly neglected in this area of investigation. Vengris (17) observed that seeding date affected height, dry matter accumulation, and seed head production of redroot pigweed (Amaranthus retroflexus L.) and yellow foxtail [Setaria lutescens (L.) Beauv.]. Johnsongrass (Sorghum halepense L.) sown at monthly intervals from June 1 to September 1 showed a decline in height, biomass, and seed production with each successively later planting date (10).

Silverleaf nightshade and other perennial weeds, including horsenettle (Solanum carolinense L.), have demonstrated a positive correlation between seedling age and regrowth after top removal (5, 9, 20). Removing the tops of silverleaf nightshade causes a loss of apical dominance resulting in multiple shoots when the plant resprouts (13). Cooley and Smith (5) clipped silverleaf nightshade tops in early August. Thirty days after clipping, root reserves had decreased 5% from the initial sampling level, while the root reserves of the unclipped plants had increased 16%.

Investigations of the factors affecting the vegetative propagation of silverleaf nightshade have been limited (3, 7, 12). Fernandez and Brevedan (7) showed that the vertical roots of silverleaf nightshade are capable of producing more new shoots than lateral roots and rhizomes. Surveying the regrowth of silverleaf nightshade in cultivated fields revealed from rhizomes (12). Cooley and Smith (3) planted root cuttings of silverleaf nightshade and three other creeping perennials: johnsongrass, woolyleaf bursage (Franseria tomentosa Gray), and Texas blueweed (Helianthus ciliaris DC.), and compared their rate of vegetative spread. They reported silverleaf nightshade to be the least aggressive of the perennials in their study.

The objectives of these experiments were to: (a) evaluate the effects of environment and seed weight on germination; (b) assess the importance of collection site, soil type, and depth of planting on seedling emergence; and (c) determine the influence of seeding date, top removal, and root cutting length on silverleaf nightshade growth in the field.

MATERIALS AND METHODS

We conducted controlled environment experiments to determine the effects of certain environmental factors on germination and subsequent establishment of silverleaf nightshade. The factors evaluated were temperature, seed weight, light, pH, salinity, and depth of emergence.

On March 17, 1978 mature silverleaf nightshade berries were collected from a cultivated field located on the Agronomy Research Station near Haskell, Oklahoma. The seed were separated from the fleshy portion of the berries by placing them in a blender of water and operating the blender at high speed for 30 sec. The blender mixture was washed through successively smaller sieves to separate the large debris from the seed. The seed were then washed for 1 h to remove most of the sticky film from the seed coat. Rutherford (13) postulated that this film may inhibit germination. Removing the mucilaginous coating also prevented the seeds from sticking together during the drying period. The seed were then cleaned with an air column seed blower which removed lightweight seed and debris from the seed lot. Approximately one-half of the original seed lot remained after the seed blower cleaning process was completed. Inspection of the discarded seed revealed that their embryos were frequently immature or lacking. Removing questionable seed allows assessment of treatment effects rather than viability. The retained seed were stored at 5 C until used. The above described seed lot will be referred to as Haskell, and unless otherwise stated was used in all experiments. Germination studies, with the exception of the specific temperature experiment, were conducted in germination cabinets operated at alternating temperatures of 20 C for 16 h, and 30 C for 8 h with light. Fifty seed were placed on 2 filter paper discs in 9 cm diameter plastic petri dishes, then covered with another filter paper disc. The filter paper substrate was moistened with 5 ml of distilled water or the appropriate solution described for the pH and salinity experiments. Additional water or solution was added in 2 ml increments to maintain optimum moisture levels during the experiments. Seed were considered to be germinated when the radicle appeared. The experimental design was randomized block with four replications. Each study was repeated at least once. Values presented are an average of two or more experiments.

Temperature. Prior to initiating germination experiments preliminary tests were conducted to establish the optimum temperature for silverleaf nightshade germination. This involved placing seed in dark germination cabinets at constant temperatures of 15, 20, and 30 C, plus alternating temperature regimes of 20 C for 16 h and 30 C for 8 h, and 15 C for 16 h and 30 C for 8 h. Temperatures used in subsequent germination studies were based on these results.

Seed weight. An experiment was initiated to determine the effect of seed weight on germination. The results of this experiment were helpful in choosing the appropriate seed weight class for use in later germination studies. An air column seed blower was used to separate the seeds into three weight classes; 310, 340, and 404 mg/100 seed. The blower setting used to obtain the 310 mg/100 group was the same as the setting used in the original seed cleaning process. The germination percentages of the three groups were compared.

pH. Buffered pH solutions were prepared according to the method of Wilson (18) using 0.1 M potassium hydrogen pthalate in combination with either 0.1 M HCL or 0.1 M NaOH to obtain solution pH levels of 3, 4, 5, and 6. A 0.025 M borax solution was used in combination with 0.1 M HCL to prepare solutions with pH levels of 7, 8, and 9. The filter paper substrate, in a petri dish containing 50 seeds, was moistened with 5 ml of the appropriate solution.

Salinity. Reagent grade NaCl was used to prepare saline solutions ranging from 500 to 20,000 parts per million by weight (ppmw) as described by Wilson (18) to study the effects of salinity on germination. Five ml of the appropriate solution was used as a substrate moistening agent.

Light. Light requirement was assessed in a germination chamber providing 8 h of flourescent light and 16 h of darkness. Seed germination in petri dishes covered with aluminum foil was compared to germination in petri dishes not covered with foil.

Depth of emergence. We investigated the effect of planting depth, collection site, and soil type on seedling emergence. To determine the effect of soil type, seed were sown 2, 4, 6, 8, and 10 cm deep in either a Teller loam (Udic Argiustolls) or a Meno sand (Arenic Haplustalfs).

The influence of collection site was evaluated using seed from a roadside near Stillwater, Oklahoma, and the previously described Haskell seed. Seed from these locations were planted 0.5, 1.0, 2.5, and 5.0 cm deep in a Meno sand. In each study 50 seed were sown in 1 L plastic pots filled with approximately 900 g of soil. Pots were subirrigated initially, then placed on a greenhouse bench at 27 C ± 3 C. Surface watering was used for the remainder of the experiment. Final emergence counts were done 35 days after planting.

Field experiments. We initiated field experiments in the spring of 1979 and 1980 to study the effect of planting date, top removal, and root cutting length on silverleaf nightshade growth and development. The experiments were located on the Agronomy Research Station near Perkins, Oklahoma. Plots, 3 rows 1 m long, were arranged in a randomized block design with four replications. Seed were sown 2 cm deep in a Teller loam. After emergence, seedlings were thinned to 10 per plot. Plots were watered regularly and kept free of weeds and phytophagous insects throughout the growing season. Because harvesting the roots of field grown silverleaf nightshade was not feasible, dry weight values represent only above ground plant parts. Values presented are an average of 2 years data and are expressed on a per plot basis.

To determine the influence of planting date, seed were sown every 15 days from May 15 to September 1. Dry matter and berry production were determined at the end of the growing season. Berries of various sizes were collected from the May 15 seeding date and the average seed per berry calculated.

The top removal experiment was seeded on May 15 of each year. Seedlings were clipped at the soil surface beginning 10 days after emergence, and then other plots were clipped at 5 day intervals for 45 days after emergence. Thus, seedlings were clipped once at ages ranging from 10 to 45 days. The height of each plant was measured 85 days after planting. Dry weight, fruit production, and percent regrowth of clipped seedlings was determined at the end of the growing season.

On June 18, 1979 and June 9, 1980 root cuttings were collected from the taproot of established silverleaf nightshade plants growing on the Agronomy Research Station, Stillwater, Oklahoma. Cuttings were taken from the portion of the taproot extending from the soil surface to a depth of 30 cm. These roots were immediately sectioned into 5, 10, 15, and 20 cm lengths, and placed in moist storage until planting the same day. Six root sections were planted 8 to 10 cm deep in each plot. Plots were watered thoroughly at planting to prevent root dessication. A shoot was defined as the appearance of a stem tip and two leaves above the soil surface. Height measurements were taken 49 days after planting. Total shoot production, and the number of shoots remaining at the end of the growing season were counted. Dry matter and fruit production were also determined at the end of the growing season.

RESULTS AND DISCUSSIONS

Temperature. An alternating temperature regime of 20 C for 16 h and 30 C for 8 h provided maximum germination of 57%. Fluctuating temperatures of 15 C for 16 h and 30 C for 8 h produced 46% germination. None of the seed germinated at constant temperatures. Our data are in agreement with the results reported by Cooley and Smith (4) who reported no germination of silverleaf nightshade at constant temperatures. Australian researchers (10, 12) report maximum germination of silverleaf nightshade with alternating temperatures of 15 to 30 C. Ecotypical variations between Australian and North American silverleaf nightshade may account for this difference.

Seed weight. In this study the percent germination of seed remaining after the initial seed cleaning process (310 mg/100 seed) was compared to heavier seed weight classes (350 and 404 mg/100 seed). Seed weighing 340 and 404 mg/100 seed did not show a higher percent germination than the seed averaging 310 mg/100 seed. Thus, subsequent germination experiments were done with seed lot whose average weight was 310 mg/100 seeds.

pH. The optimum range for germination appeared to be between pH 6 and 7 (Figure 1). Germination was 59% in this range and decreased markedly at pH levels outside this range, with only 12 and 40% germination occurring at pH 4 and 8, respectively. The rapid decline in percent germination suggests that germination of silverleaf nightshade is sensitive to pH extremes. Wilson (18) noted a similar relationship between pH and Canada thistle (*Cirsium arvense* Scop.) germination. Studying the effect of pH on germination allows inferences to be made concerning a species' potential for establishment.

Salinity. NaCl concentrations of 2500 ppmw or greater caused significant reductions in percent germination (Figure 2). Percent germination at 2500, 5000, and 10,000 ppmw was 49, 30, and 8% respectively. It should be noted that increased osmotic potential is not the only mechanism by which NaCl inhibits seed germination (16). The Na^+ and Cl^- ions exert a toxic effect on seed germination beyond the influence of increased osmotic potential. Canada thistle and honeyvine milkweed [Ampelamus albidus (Nutt.) Britt.] was reduced 48 and 88%, respectively by NaCl concentrations of 10,000 ppmw, while silverleaf nightshade germination declined 93% at the same NaCl concentration (6, 18). These data permit an estimate of silverleaf nightshade's ability to germinate in saline soils.

Light. Percent germination of silverleaf nightshade seed incubated in a light or dark environment was not different. The seed of horsenettle, another perennial Solanum, did not require light for germination (8). Earlier research by Steinbauer and Grigsby (15) indicated that the majority of the 85 weed species they tested germinated in light or dark. Thus, it appears that cultural practices excluding light from silverleaf nightshade seeds would not prevent germination.

Depth of emergence. Collection site did not influence seedling emergence (Table 1). Regardless of collection site, seeding depths greater than 1.0 cm reduced emergence. Average percent germination of seed sown 1.0 cm deep was 73% greater than seed sown 0.5 cm deep. This descrepancy was attributed to the rapid drying of the soil surface. We had hypothesized that differences in interspecific competition and fertility between the collection sites would influence seedling vigor. This was not found to be true.

Seedling emergence from a Meno sand (approximately 85% sand) was greater than from a Teller loam at the 2 cm planting depth (Table 2). At seeding depths of 6 cm or deeper, emergence ranged from 0 to 6% for both soils. Cooley and Smith (4) reported a 60% increase in seedling emergence from a sandy soil versus a loam. Our data supports the consensus that silverleaf nightshade is best adapted to coarse textured, sandy soils.

Field experiments. Each 15 day delay in seeding date caused biomass accumulation to be reduced by approximately one-half, with the exception of the June 1 and June 15 dates (Table 3). Seedlings emerged from the September 1 seeding date, but due to hot, dry weather, and blowing sand, did not produce a measureable amount of plant material. Biomass accumulation declined in the same manner for johnsongrass, redroot pigweed, and yellow foxtail sown at delayed planting dates from May through September (9, 17). Maximum berry production was obtained with the earliest planting date. Berry production decreased with each 2 week delay in seeding with no berries being produced by plants seeded on or after July 1. Because silverleaf nightshade is indeterminate in its photoperiod requirements, developmental and physiological status were thought to be the limiting factors in flower and berry production.

The May 15 date produced an average of 84 seed per berry. The range for seed per berry was from 24 to 149. Therefore, the seed production capacity of plants arising from seeds sown on May 15 is approximately 11,000 per plot. Our data substantiates the capacity of seedling silverleaf nightshade for abundant seed production.

Seedlings clipped 10 days after emergence did not regrow (Table 4). Some regrowth occurred when top removal was delayed until 15 days after seedling emergence. Further delays in top removal resulted in an increasing percentage of regrowth. When clipping was delayed 30 days or more, 90% or the plants regrew. Delayed clipping produced taller regrowth until the 30 day treatment was reached, after which there was a steady height decline. Dry matter production followed the same pattern as height response. Dry weight production increased steadily for 30 days, and then declined at 40 and 45 days. Midsummer weather and an abbreviated growing season, resulting from late summer clipping, contributed to the reduced height and dry matter values recorded for the later clipping dates. The 10, 40, and 45 day clipping dates did not bear fruit. The remaining treatments produced a minimal number of berries. The 20, 30, and 35 day clipping dates produced the most berries but none of the differences among these three treatments were significant. The 35 day date (clipped July 9) flowered 34 days after clipping. This rapid recovery is indicative of silverleaf nightshade's tenacity.

The total number of shoots arising from root cuttings taken from the taproot of silverleaf nightshade increased as the length of the cutting increased (Figure 3). The first shoots emerged 13 days after planting. Average shoot production per plot was 1, 3, 6, and 9 for the 5, 10, 15, and 20 cm long root cuttings, respectively. The number of shoots surviving the growing season also increased with longer roots, ranging from less than one for 5 cm cuttings to slightly more than 4 shoots for the 20 cm long cuttings. Fernandez and Brevedan (7) also reported that silverleaf nightshade shoot production increased with root cutting length. At 49 days after planting the plants arising from the 5 and 10 cm root sections were the same height, but the shoots produced by the 15 cm roots were twice as tall as these treatments. The 20 cm long roots produced plants significantly taller than those plants growing from the 5 and 10 cm cuttings. Similarly, Lolas and Coble (11) reported that the height of plants arising from johnsongrass rhizomes was positively correlated with rhizome length. Dry matter yield of the plants started from 20 cm root cuttings was significantly greater than that of the other treatments. The plants grown from 20 cm long root cuttings produced 70% more dry matter than the 5 cm long roots, and 85% more than the plants started from 10 cm roots. Fruit and dry weight production by the 5 cm group was greater than that of the of the plants arising from the 10 cm long root cuttings (Figure 4). The reason for this incongruity is not known. Another charasteristic of our study was that significant differences in the growth responses of adjacent treatments were rare. In most instances, a 10 to 15 cm length difference was necessary before statistically significant differences occurred. The practical implications of our results may be linked to reduced tillage. Longer roots fragments resulting from reduced tillage would: (a) have more and faster growth, (b) interfere more with crop production, and (c) make control of silverleaf nightshade increasingly difficult.

LITERATURE CITED

1. Abernathy, J.R. 1979. Silverleaf nightshade control in cotton with glyphosate. Proc. South. Weed Sci. Soc. 32:380.
2. Bellue, M.K. 1946. Weed Seed Handbook. Series IV. Calif. Dept. Agric. Bull. 25:15-16. 420 pp.
3. Cooley, A.W. and D.T. Smith. 1973. Migration of four perennial weeds. Cons. Rep. of the T.A.E.S. Prog. Rep. No.'s 3197-3209. No. 3199. p. 9-11. Weed and Herbicide Research in West Texas. 1971-1973.
4. Cooley, A.W. and D.T. Smith. 1973. Silverleaf nightshade (white-weed) establishment from seed and clipped seedlings. Cons. Rep. of the T.A.E.S. Prog. Rep. No.'s 3197-3209. No. 3198. p. 6-8. Weed and Herbicide Research in West Texas. 1971-1972.
5. Cutherbertson, E.G. 1976. Silverleaf nightshade - a potential threat to agriculture. Agric. Gaz. N.S.W. 87:11-13.
6. Evetts, L.L. and O.C. Burnside. 1972. Germination and seedling development of common milkweed and other species. Weed Sci. 20:371-378.
7. Fernandez, O.A. and R.E. Brevedan. 1972. Regeneracion de Solanum eleagnifolium Cav. a partir de fragmentos de sus raices. Darwiniana. 17:433-442.

8. Ilnicki, R.D. and S.N. Fertig. 1962. Life history studies as related to weed control in the northeast. Horsenettle. Bull. No. 368. Rhode Is. Agric. Expt. Stn. 54 pp.

9. Keeley, P.E. and R.J. Thullen. 1979. Influence of planting date on the growth of johnsongrass (*Sorghum halapense*) from seed. Weed Sci. 27:554-558.

10. Leys, A.R. and E.G. Cuthbertson. 1977. *Solanum eleagnifolium* in Australia. Proc. South Weed Sci. Soc. 30:137-141.

11. Lolas, P.C. and H.D. Coble. 1980. Johnsongrass growth characteristics as related to rhizome length. Weed Res. 20:205-210.

12. Molnar, V.M. and D.N. McKenzie. 1976. Progress report on silverleaf nightshade research. Pamphlet No. 61. Vermin and Noxious Weeds Destruction Board. Dept. of Crown Lands and Survey, Victoria Australia. 12 pp.

13. Rutherford, P.A. 1978. Effect of time of immersion in running and still water on the germination of silverleaf nightshade. Proc. of 1st Conf. of the Australian Weed Sci. Soc. 1:372-378.

14. Smith, D.T., A.F. Wiese, and A.W. Cooley. 1973. Crop losses from several annual and perennial weeds. Weed Sci. Soc. Am. Abstr. 21. p. 53-54.

15. Steinbauer, G.P. and B. Grigsby. 1957. Interaction of light, temperature, and moistening agent in the germination of weed seeds. Weeds. 5:175-183.

16. Uhvits, R. 1946. Effect of osmotic pressure on water absorption and germination of alfalfa seeds. Am. J. Bot. 33:279-285.

17. Vengris, J. 1963. The effect of time of seeding on the growth and development of rough pigweed and yellow foxtail. Weed Sci. 11:48-50.

18. Wilson, R.G. 1979. Germination and seedling development of Canada thistle. Weed Sci. 27:146-151.

Table 1. Effect of seeding depth and collection site on emergence of silverleaf nightshade.

	Collection site	
Planting depth	Cultivated field (Haskell)	Roadside (Stillwater)
(cm)	%	
0.5	16	17
1.0	67	54
2.5	39	37
5.0	35	37
LSD 0.05	21	21

Table 2. Effect of seeding depth and soil type on emergence of silverleaf nightshade.

Planting depth	Soil type Teller loam	 Meno sand
(cm)	%	
2	33	48
4	21	27
6	1	6
8	1	0
10	0	0
LSD (0.05) (soil)	9	
LSD (0.05) (depth)	10	10

Table 3. Influence of seeding date on dry weight and fruit production of silverleaf nightshade.

Planting date	Dry weight	Berries per plot
	(g)	(No.)
May 15	591	133
June 1	260	43
June 15	297	39
July 1	113	0
July 15	55	0
August 1	23	0
August 15	9	0
September 1	0	0
LSD 0.05	147	51

Table 4. Influence of top removal at various intervals after emergence on regrowth of silverleaf nightshade.

Time from emergence to top removal	Plants regrowing	Height	Dry weight	Berries per plot
(days)	(%)	(cm)	(g)	(No.)
10	0	0	0	0
15	14	2	13	< 1
20	60	30	177	13
25	51	23	150	4
30	94	36	205	12
35	96	28	205	7
40	90	17	123	0
45	99	14	179	0
LSD 0.05	33	7	118	11

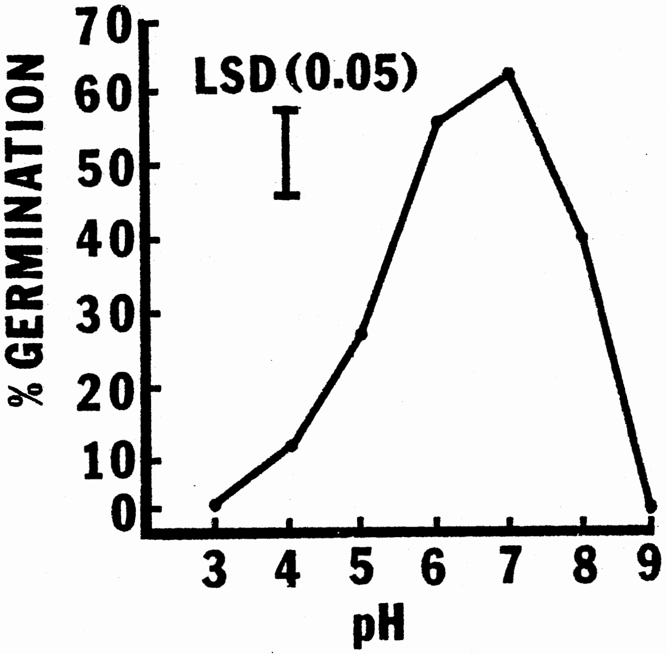

Figure 1. Effect of pH on silverleaf nightshade germination.

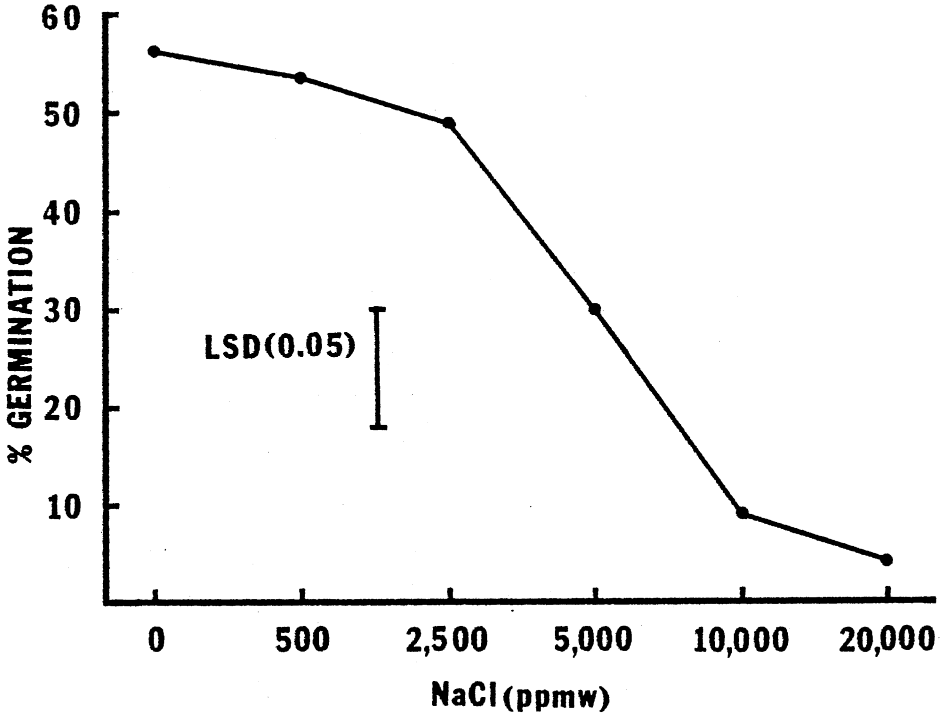

Figure 2. Effect of salinity on silverleaf nightshade germination.

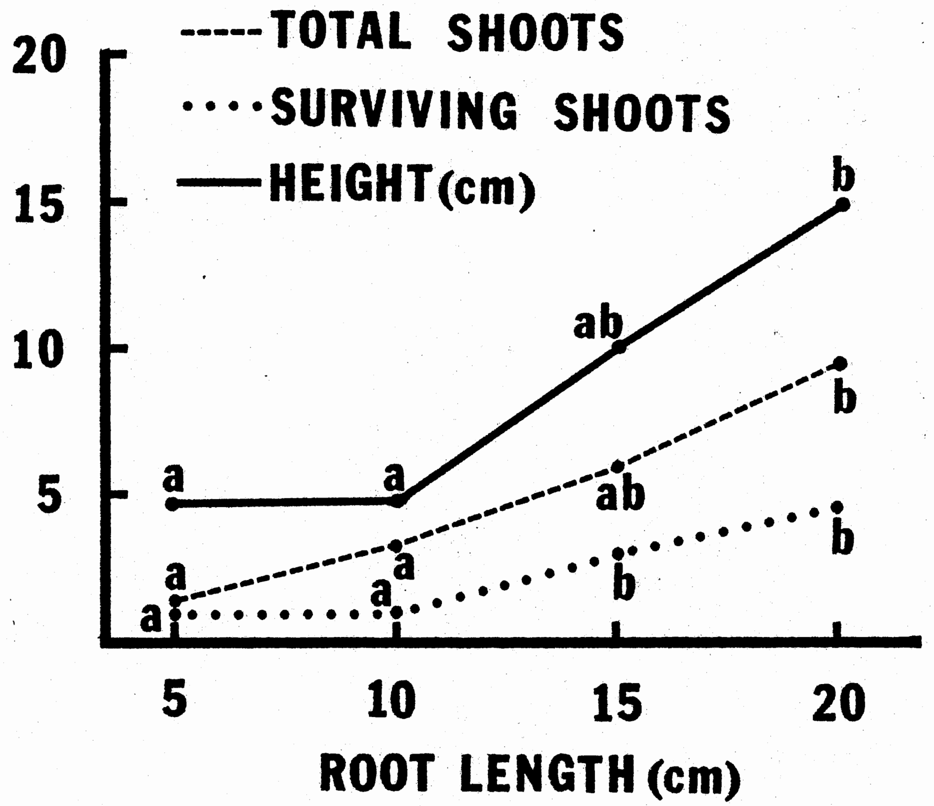

Figure 3. Effect of root cutting length on shoot production, survival, and height. Values sharing the same letter within a line are not significantly different at the 0.05 level.

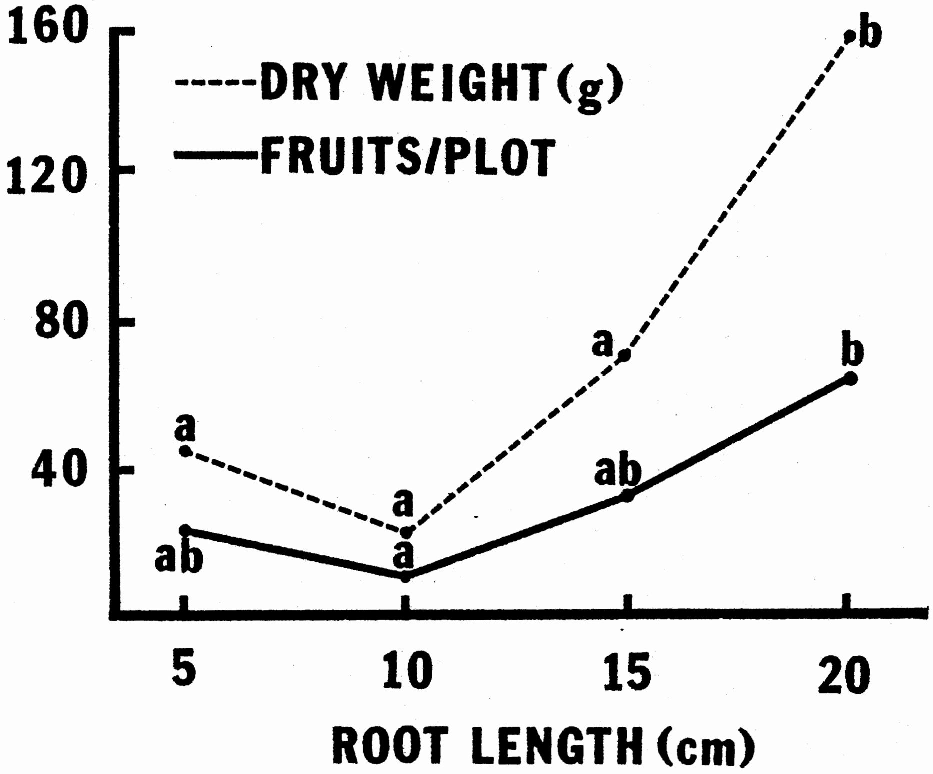

Figure 4. Effect of root cutting length on dry matter and fruit production of silverleaf nightshade. Values sharing the same letter within a line are not significantly different at the 0.05 level.

PART III

EFFECTS OF SHADE ON SILVERLEAF NIGHTSHADE

(*SOLANUM* *ELEAGNIFOLIUM*)

EFFECTS OF SHADE ON SILVERLEAF NIGHTSHADE
(SOLANUM ELEAGNIFOLIUM)

Abstract. Seedling and established silverleaf nightshade plants (*Solanum eleagnifolium* Cav.) were grown in the field under shade levels of 0, 47, 63, and 92% to determine vegetative, reproductive, and physiological responses to shade. Dry matter production declined markedly with increasing shade levels with both seedling and established plants. Established plants grown in full sun yielded seven times more dry matter than plants grown under 92% shade. Established plants did not bear fruit under 92% shade, while 63% shade prevented fruit production by seedlings. Taproots of plants grown in full sunlight contained 16% more total nonstructural carbohydrates (TNC) per g dry weight than plants grown under 92% shade. Leaves of established plants growing under shade had significantly more chlorophyll per unit leaf fresh weight than plants grown under full sun, however, plants under heavy shade (92%) had 35% less chlorophyll per unit leaf area than the unshaded plants. Chlorophyll *a/b* ratio of the 92% shade plants was significantly less than other treatments. Specific leaf area increased with increasing shade; however, leaf weight per unit area decreased due to thinner leaves. Infrared gas analysis showed that photosynthetic rates of recently expanded leaves fully exposed to ambient irradiance were 10.4, 4.6, 3.3, and 0.9 mg $CO_2 dm^{-2} h^{1-}$ for the 0, 47, 63, and 92% shade treatments, respectively.

Additional index words. carbohydrates, chlorophyll content, seedlings, perennials, photosynthetic rate.

INTRODUCTION

Silverleaf nightshade (Solanum eleagnifolium Cav.) is a deep rooted perennial that propagates by seed, creeping rhizomes, and root fragments (10). This species is thought to be native to the Southwestern United States and Northern Mexico (11). Silverleaf nightshade is a troublesome weed throughout its native range and other semiarid regions of the world (1, 10, 12, 14, 24). Domestically, it has been declared a noxious weed in 21 states (14).

Silverleaf nightshade reduces cotton (Gossypium hirsutum L.), grain sorghum (Sorghum bicolor L.), alfalfa (Medicago sativa L.), and cereal grain yields through competition and harvest interference (1, 10, 12, 24). Under semiarid conditions, cotton yields have been reduced by 75% (1). Smith et al. (24) observed an inverse correlation between grain sorghum yields and silverleaf nightshade densities. Nine silverleaf nightshade plants per m^2 reduced Australian cereal grain yields by 12% (10).

The potential of shade for suppressing weed growth has been demonstrated by several researchers (3, 15, 17, 21, 22). In 1945, Davis (12) suggested that cultivation and the shade provided by grain sorghum were instrumental in controlling silverleaf nightshade after 3 years. The effects of shade on many aspects of plant growth have been examined and shade definitely inhibits the growth of many perennial weeds (3, 17, 22). Plant height, dry matter accumulation, and reproduction are usually diminished by shade (3, 7, 15, 17, 21, 22). Relative and total pigment content, and leaf anatomy may also be altered by shade (2, 4, 5, 8, 9). As would be expected, reducing light intensity brings about a decline in relative photosynthetic rates (5, 9, 20). Shade may also impair the regrowth potential of perennial weeds by depleting the carbohydrates stored in their vegetative reproductive structures (3, 17). This has been attributed to plants growing under reduced light intensities using carbohydrate reserves to maintain growth during periods of declining photosynthate production (18).

Related research, measuring the amount of light intercepted by crops, provides an estimate of the shading potential of some agronomic crops. Knake (16) collected data during August in Illinois and reported that corn (*Zea mays* L.) provide 92 to 97% shade at the soil surface. Keeley and Thullen (15) reported shade levels of 80 to 90% in cotton and grain sorghum furrows. Their work is of particular relevance because silverleaf nightshade is a problem in cotton and grain sorghum.

The evidence demonstrating that shade suppresses weed growth, and that crop canopies provide dense shade led us to initiate our investigations. The objectives of our experiments were to evaluate the growth and development of seedling and perennial silverleaf nightshade under shade levels simulating those created by the canopies of agronomic crops.

MATERIALS AND METHODS

Experiments were conducted in the field during 1979 and 1980 near Perkins, Oklahoma in a Teller loam (Udic Argiustolls). Silverleaf nightshade seeds were planted 2 cm deep on May 15 of each year. The 1 m^2 plots were arranged in a randomized block design with 4 replications. LUMITE[1] black saran shade cloth canopies, 2 m^2, were centered over the plots, leaving a 0.5 m border separating the plot boundary from the canopy edge. The canopies were attached to four supports so that they could be raised as the silverleaf nightshade grew. Plots were watered regularly to insure seedling emergence and survival. After emergence, the plant population in each plot was reduced to 10 plants. Grain sorghum was planted in the 4.5 m corridor separating the canopy margins to prevent light from entering the sides. Treatments used were full sunlight, 47, 63, and 92% shade. The manufacturer's specified shade levels (47, 63 and 92%) were verified with a LICOR[2] quantum sensor. The percent reduction in uE(microeinsteins)$m^{-2}s^{-1}$ photosynthetic photon flux density (PPFD) under each canopy was compared to full sunlight (considered to be a maximum of 2000 $uEm^{-2}s^{-1}$ PPFD at solar noon on a clear day) and found to be in agreement with the densities specified. Pallas et al. (19) reported that the spectral quality of light in the 400 to 800 nm waveband was not altered by passing through black saran shade cloth. Unfortunately, the uniform reduction of PPFD cannot be construed as simulating the shade of a foliar canopy. Taylorson and Borthwick (26) demonstrated that leaf filtered light was richer in far red due to the absorption of incident red energy by chlorophyll.

Vegetative and reproductive growth. In 1979, the shade canopies were put into place immediately after planting the seed. In 1980, the canopies were put into position approximately 14 days after the seed-

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[1] Chicopee Mfg., Cornelia, GA.

[2] Lambda Instruments Corp., Lincoln, NE.

lings emerged. The mean number of leaves per plant was determined 56 and 66 days after the 1979 planting, and 42 and 54 days after the 1980 planting. Height and internode length measurements were taken 56, 66, and 87 days after the 1979 planting. The 1979 plants were harvested for fruit and dry weight determinations 180 days after planting. Dry weights of above groud plant parts were determined on a per plot basis. The plant material was placed in a forage drier for 7 days at 50 C.

Silverleaf nightshade arising from the roots of plants established from seed during May 1979 were allowed to grow until June 4, 1980, and were then clipped at the soil surface. The vegetative shoots were 40 to 50 cm tall when clipped. Immediately after clipping, the shade canopies were put into place. Height measurements were taken 20, 33, and 48 days after clipping. At 138 days after clipping 5 plants were collected from each plot for determination of fruit and dry matter production.

Physiological responses. Physiological data collected from the established plants included: chlorophyll content of the leaves, specific leaf area (SLA), photosynthetic rate, and total nonstructural carbohydrate (INC) content of the roots. The chlorophyll, SLA, and photosynthetic rate determinations were done using recently expanded leaves fully exposed to ambient irradiance. Chlorophyll extractions were done by homogenizing 1 g of fresh leaf tissue in 20 ml of cold, 95% ethanol. The resulting homogenate was filtered through Whatman No. 1 filter paper and brought up to a 100 ml volume. The absorbance of this solution was read at 649, 654, and 665 nm with a Bausch and Lomb Spectronic 21. Chlorophyll content (mg/g fresh weight and mg/dm^2 leaf area) were calculated using the formula of Wintermans and deMots (27). Leaf samples for chlorophyll analysis were collected at 50 and 56 days after clipping and using the results averaged. SLA calculations (dm^2/g fresh weight) were done with a LICOR[3] protable leaf area meter 70 days after clipping. Photosynthetic rates (mg CO_2 $dm^{-2}h^{-1}$) were measured 83 and 91 days after clipping using the technique described by Huber.[4] The amount of CO_2 fixed was measured with an infrared gas analyzer. The portion of the taproot extending from the soil surface to 20 cm deep was used for analysis of the TNC content of the roots. Roots were collected from the 1980 seedling plants 157 days after planting. Root samples were taken from the established plants 138 days after clipping. Sample preparation was done in accordance with Smith (23), and percent TNC was determined by the method of Spiro (25).

RESULTS AND DISCUSSION

Vegetative and reproductive growth. No seedlings emerged from plots receiving 92% shade, in 1979, thus 0 values are presented for that treatment (Table 1). In 1980, shade canopy placement was delayed until the seedling emerged. Plants grew for a short time under the 92% shade, but did not survive. Early season height and leaf production data were obtained from the 92% shade plots.

For both years seedlings height generally declined with each increase in shade density (Table 1). Plant height under 0 and 47% shade,

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[3] Lambda Instruments Corp., Lincoln, NE.

[4] Huber, A.G. 1978. Apparatus and techniques to measure photosynthesis and observed differences among cultivars. M.S. Thesis. Okla. State Univ. 50 pp.

66 days after the 1979 planting. Plant heights under 63 and 92% shade showed the same trend with the exception of the 92% group in 1979 for which no data was collected. Thus, significant differences in plant height occurred most often at the treatment extremes. During the 1980 growing season, high temperatures accompanied by drought contributed to the generally poor growth of the 1980 seedlings. It is generally held that when plants of the same species are grown under increasing shade levels height will increase until photosynthate production becomes limiting (18, 21). In our experiments, moderate shade (47%) did not cause a height increase. Our findings are in agreement with those of Cooper (7) who reported the height of seedling alfalfa and birdsfoot trefoil (Lotus corniculatus L.) to decrease with increasing shade density.

Shade had much less effect on the regrowth of established plants than on growth of plants from seed (Table 2). The only significant height difference occurred 20 days after clipping. Forty-eight days after clipping silverleaf nightshade, grown under 47% shade, were an average of 12 cm taller than full sun plants. This difference is not statistically significant at the 0.05 level, but is consistent with previous reports (18, 21) that plants grown under moderate shade will tend to be taller than plants grown under high irradiance. Thus, in our experiments regrowth from established plants followed this trend but seedlings did not. The mature root systems and stored food reserves of the established plants may have been responsible for the differential effect of shade on plant height.

No differences were observed in the internode lengths of seedling plants during 1979 (Table 1). The height differences among treatments resulted from the number of internodes per plant rather than internode length. As expected, internode length increased as the plants grew taller, but remained constant among the different shade levels. These data were collected because plants grown under high irradiance usually have shorter internodes than plants of the same species grown under reduced light intensities (9, 18). Giant foxtail (Setaria faberii Herrm.) grown in shade had longer internodes than plants grown in full sun (16). Thus, the effect of shade on internode length of various species seems to be quite variable.

Because the internode length of silverleaf nightshade did not vary with shade during 1979 these data were not collected during 1980.

In 1979, seedlings grown in full sunlight had more leaves per plant than plants grown under the three shade levels (Table 1). Seedlings grown in full sunlight produced almost two new leaves per day between July 10 and July 20, while those under 63% shade averaged less than one leaf per day for the same period. Due to the severe growing conditions during 1980, significant variations in leaves per seedling did not occur. In the seedling and perennial studies, differences in leaves per plant were least obvious between contiguous treatments. In a similar study, Knake (16) reported shade plants to have the highest number of leaves per plant, but attributed this difference to wind damage to the unprotected controls.

The 1979 seedlings produced significantly less dry matter at each increasing shade level (Figure 1). Seedlings grown in full sunlight produced more than twice the biomass of plants under 47% shade. In 1980, the seedlings in full sunlight yielded seven times the dry weight of the 47% shade group, but the 47 and 63% shade treatments were not significantly different. Cooper (7) showed the dry matter production of seedling alfalfa and birdsfoot trefoil to decrease with increasing shade levels of 0, 51, 76, and 92%.

Established plants showed a nearly linear decrease in dry matter accumulation as shade densities increased (Figure 1). Established plants in full sun produced more than seven times the dry weight of the 92% shade plants. Baake and Gaessler (3) reported increasing shade levels to have a similar effect on the dry matter production of field bindweed (Convolvulus arvensis L.). Dry weight yield of perennials far exceeded that of seedlings (Figure 1). Perennials under 63% shade produced nearly five times the dry weight of seedlings grown under the same shade level. Stored TNC content of the established plants had much to do with response to shading. The relative shade tolerance of both seedling and established plants has important implications for the use of crop shade as a means of control. The most obvious being that once silverleaf nightshade attains perennial status, greater shade densities will be needed to cause significant growth reductions.

Fruit yield of unshaded seedlings was at least 90% higher than that of plants grown under 47% shade (Figure 2). No fruits were produced by seedlings under 63% shade. This would indicate that a shade level between 47 and 63% would be necessary to prevent seed production of seedling silverleaf nightshade. Field studies with giant foxtail and yellow nutsedge (Cyperus esculentus L.) have shown the fruit production of these species to be reduced by shade (15, 16).

Established plants under 0 and 47% shade regrew and bloomed 41 days after being clipped at the soil surface, demonstrating their potential for rapid vegetative and reproductive growth. There were several blooms on plants grown under 0 and 47% shade levels 48 days after clipping. (Table 2). On this date, blooms had not yet appeared under the 63 and 92% shade densities. Our data is in agreement with the generally accepted hypothesis that each species has a minimum irradiance below which no blooming occurs, and at light intensities only slightly higher than the minimum, flowering is sparse (18).

Established plants growing under 63% shade produced 85% fewer berries than the unshaded control (Figure 2). Perennials subjected to 92% shade did not produce berries, thus a shade level between 63 and 92% is required to prevent seed production. Shade substantially reduced fruit production of perennials, but their overall fruit yield was much higher than seedlings. Perennials in full sunlight produced five times more berries than unshaded seedlings. Our data show that perennial silverleaf nightshade can: (a) produce more berries than seedlings; and (b) produce berries under lower light intensities than seedlings.

Physiological responses. Leaves from plants growing under shade had significantly more total chlorophyll (a+b), on a fresh weight basis (mg/g), than plants grown in full sunlight (Table 3). Plants grown under 63% shade had 16% more total chlorophyll than the plants grown in full sunlight. When chlorophyll content was calculated on a per unit leaf area basis (mg/dm^2), the leaves of plants grown under 92% shade contained significantly less total chlorophyll. Plants under the heaviest shade leaves had 35% less chlorophyll per unit leaf area than plants grown in full sun. The tendency for shade plants to have more chlorophyll per unit weight, and less total chlorophyll per unit leaf area has been reported by others (4, 5, 8). However, the increased chlorophyll per unit weight cannot compensate for reduced light intensities because it is more than offset by the reduction in chlorophyll per unit leaf area (5).

The chlorophyll *b* (mg/g fresh weight) content of leaves fully exposed to ambient light intensities increased with each successive increase in shade density (Table 3). Plants grown under 92% shade contained 28% more chlorophyll *b* than plants grown in full sunlight. Chlorophyll *a* showed no consistent response to shade levels. The increase in chlorophyll *b* caused a significant decline in the chlorophyll *a*/*b* ratio of 92% shade treatment (Table 3). Decreasing chlorophyll *a*/*b* ratios in response to shade have been previously documented (3, 4, 13). The increase in the relative proportion of chlorophyll *b* may be an adaptation of the photosynthetic apparatus to shade. Because chlorophyll *b* is a major component of photosystem II an increased proportion of chlorophyll *b* would facilitate harvest of the available photon flux.

The chlorophyll *a*/*b* ratios presented in Table 3 are about one-half the approximately 2.75:1 ratio reported by other researchers (2, 4). There are no published reports of *a*/*b* ratios for silverleaf nightshade, thus comparisons are impossible. The reason for this discrepancy is not known.

Specific leaf area (SLA), on a dm^2/g fresh weight basis, increased significantly at each shade level (Table 3). SLA ranged from 3.88 dm^2/g for the plants grown under full sunlight to 6.75 dm^2/g for plants grown under the heaviest shade. These values are well within the range of 1.85 to 7.93 dm^2/g reported for *Solanum dulcamara* L. (6). Differences in the SLA of silverleaf nightshade grown under various light intensities reflects changes in the thickness and structure of leaves. Thinner leaves represent an adaptation to shade because a smaller amount of the limited photosynthetic available is invested per unit leaf area. However, it is generally stated that thinner leaves due to shade have less developed palisade and spongy mesophyll regions, thus resulting in reduced volume per unit leaf area (8, 9). Others report the capacity for CO_2 fixation per unit volume of leaf is affected little by light intensity during growth, thus it may be reasoned that the greater CO_2 fixation capacity of leaves produced under high irradiance is directly related to their thickness and thus greater volume per unit leaf area (5, 9). However, our data demonstrate a decline in photosynthetic rate per unit leaf weight as shade density increased (Table 3).

Photosynthetic rates of established plants were significantly reduced by each increase in shade density (Table 3). The values ranged from 10.4 mg $CO_2 dm^{-2} h^{-1}$ for the plants in full sunlight to 0.9 mg $CO_2 dm^{-2} h^{-1}$ for the plants grown under 92% shade. Photosynthetic rates of single, fully exposed leaves appear to be a reliable indicator of overall growth because a decline in dry matter and fruit production paralleled the decrease in photosynthetic rates. The CO_2 fixation rates of silverleaf nightshade, while slightly lower, were near the range of 4.4 to 17.9 mg $CO_2 dm^{-2} h^{-1}$ reported for <u>Solanum</u> <u>dulcamara</u> (6). Variations in species and techniques may account for the observed differences.

It is difficult to determine the primary cause of altered photosynthetic rates because many factors are altered when plants are grown under various light intensities (5). It has been suggested that there is an integrated adjustment of the processes involved in CO_2 fixation to match the available quantum flux. Our data demonstrate that shade from a crop canopy would reduce the photosynthetic rate of silverleaf nightshade, thus making it a potentially less vigorous competitor.

The upper 20 cm of taproot of seedlings grown under 63% shade had significantly less TNC than plants in full sunlight (Figure 3). The 63% shade level reduced TNC by 17% as compared to unshaded plants. As anticipated, a higher shade density was required to cause a significant reduction of the root TNC levels of established plants. (Figure 3). The 92% shade treatment caused a 16% reduction in TNC. In 1945, Baake and Gaessler (3) wrote that very little has been published concerning the effect of shade on the food reserves in the roots of perennial plants. Davis et al. (11) described the use of shade created by grain sorghum as part of an integrated approach to controlling silverleaf nightshade. They kept silverleaf nightshade hoed to the ground until the sorghum could form dense canopy. Application of this technique for three years was reported to eradicate silverleaf nightshade. They suggested that their approach depleted the carbohydrate reserves in the underground parts of silverleaf nightshade, but did not verify this assumption through analysis of the roots (11).

Our results indicate growth of seedling and established silverleaf nightshade is significantly reduced by shade, but shade levels greater than 63% were required for substantial reductions in vegetative and reproductive growth. Perennials were more shade tolerant than seedlings. It seems likely that this increased tolerance is linked to their established root systems and stored carbohydrate reserves.

Shade levels under the canopies of cotton and grain sorghum can reach 80% 10 to 12 weeks after planting (16). This level of shade is sufficient to markedly affect silverleaf nightshade growth if it were present prior to the onset of growth. But, the 10 to 12 weeks required for canopy formation is adequate time for the maturation of silverleaf nightshade. Thus, for shade to be an important means for silverleaf nightshade control, plant growth would have to be kept in check until the crop forms a canopy.

LITERATURE CITED

1. Abernathy, J.R. 1979. Silverleaf nightshade control in cotton with glyphosate. Proc. South. Weed Sci. Soc. 32:380.
2. Alberte, R.S. and J.P. Thornber. 1974. The correlation between chlorophyll _a/b_ ratio and proportions of chlorophyll protein complexes in green plants. Plant Physiol. 53(suppl.);63.
3. Baake, A.L. and W.G. Gaessler. 1945. The effect of reduced light intensity on the aerial and subterranean parts of European bindweed. Plant Physiol. 20.246-257.
4. Bjorkman, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. 16:889-914.
5. Boardman, N.K. 1977. Comparative photosynthesis of shade and sun plants. Ann. Rev. Plant Physiol. 28:355-377.
6. Clough, J.M., J.A. Teeri and R.S. Alberte. 1979. Photosynthetic adaptation of _Solanum_ _dulcamara_ L. to sun and shade environments. I. A comparison of sun and shade populations. Oecologia (Berlin). 38:13-21.
7. Cooper, C.S. 1966. Response of birdsfoot trefoil and alfalfa to various levels of shade. Crop Sci. 6:63-66.
8. Cooper, C.S. and M. Qualls. 1967. Morphology and chlorophyll content of the shade and sun leaves of two legumes. Crop Sci. 7:672-673.

9. Crookston, R.K., K.J. Treharne, P. Ludford and J.L. Ozbun. 1975. Response of beans to shading. Crop Sci. 15:412-416.

10. Cuthbertson, E.G. 1976. Silverleaf nightshade-a potential threat to agriculture. Agric. Gaz. N.S.W. 87:11-13.

11. D'Arcy, W.G. 1974. *Solanum* and its close relatives in Florida. Ann. Mo. Bot. Gdn. 61:819-867.

12. Davis, C.H., T.J. Smith and R.S. Hawkins. 1945. Eradication of the white horsenettle in Southern Arizona. Ariz. Agric. Expt. Stn. Bull. No. 195. 14 pp.

13. Egle, K. 1960. Menge und verhaltnis der pigmente. Pages 452-496 *in* Ruhland, *ed*. Encyclopedia of Plant Physiology. Springer-Verlag. Berlin. 1013 pp.

14. Gunn, C.R. and F.B. Gaffney. 1974. Seed characterisitics of 42 economically important *Solanaceae* in the United States. U.S.D.A. Tech. Bull. No. 1471. 31 pp.

15. Keeley, P.E. and R.J. Thullen. 1978. Light requirements of yellow nutsedge (*Cyperus esculentus*) and light interception by crops. Weed Sci. 26:10-16.

16. Knake, E.L. 1972. Effect of shade on giant foxtail. Weed Sci. 20:588-592.

17. Moosavi-Nia, H. and J. Dore. 1979. Factors affecting glyphosate activity in *Imperata cylindrica* (L.) Beauv. and *Cyperus rotundus* L. 2. Effect of shade. Weed Res. 19:321-327.

18. Meyer, B.S., D.B. Anderson, R.H. Bohning, and D.G. Fratianne. 1973. Introduction to Plant Physiology. D. Vanostrand Co. New York. 565 pp.

19. Pallas, J.E., J.D. Neves, and E.R. Beaty. 1971. Light quality under saran shade cloth. Agron. J. 63:657-658.

20. Patterson, D.T. 1979. Methodology for measurement of light in weed studies-a review. Weed Sci. 27:437-443.

21. Patterson, D.T. 1979. Effects of shading on the growth and development of itchgrass (*Rottboellia exaltata*). Weed Sci. 27:549-553.

22. Patterson, D.T. 1980. Effects of shading on growth and partitioning of biomass in cogongrass (*Imperata cylindrica*) from shaded and exposed habitats. Weed Sci. 28:735-740.

23. Smith, D. 1969. Removing and analyzing total nonstructural carbohydrates from plant tissue. Res. Rep. No. 41. College of Agric. and Life Sci. Univ. Wisc. Madison. 24 pp.

24. Smith, D.T., A.F. Wiese, and A.W. Cooley. 1973. Crop losses from several annual and perennial weeds. Weed Sci. Soc. Am. Abstr. 21. p. 53-54.

25. Spiro, R.G. 1966. Analysis of sugars found in glycoproteins. Complete carbohydrates. 8:4-5 *in* Methods in Enzymology. Academic Press. New York. 759 pp.

26. Taylorson, R.B. and H.A. Borthwick. 1969. Light filtration by foliar canopies: significance for light controlled weed seed germination. Weed Sci. 17:48-51.

27. Wintermans, J.F.G.M. and A. deMots. 1965. Spectrophotometric characteristics of chlorophyll *a* and *b* and their pheophytins in ethanol. Biochem. Biophys. Acta. 109:448-453.

Table 1. Effects of shade on the growth of seedling silverleaf nightshade.

Plant characteristic[a]	Time (days after planting)	Shade (%)			
		0	47	63	92
(1979)					
Height (cm)	56	23a	20a	13b	0c
Leaves (per plant)	56	16a	9b	6b	0c
Internode (cm)	56	1.7a	1.9a	2.0a	0c
Height (cm)	66	41a	33b	21c	0d
Leaves (per plant)	66	32a	18b	12b	0c
Internode (cm)	66	2.3a	2.4a	2.2a	0b
Height (cm)	87	71a	69a	56b	0c
Internode (cm)	87	2.6a	2.6a	2.7a	0b
(1980)					
Height (cm)	42	3.0a	2.5a	1.8b	1.8b
Leaves (per plant)	42	4.0a	2.9a	3.3a	3.3a
Height (cm)	54	5.3a	4.8a	2.5b	0.0c
Leaves (per plant)	54	9.8a	6.3a	4.3a	0.0b
Height (cm)	69	14.3a	10.8ab	9.3ab	0.0c

[a] Values sharing the same letter within a row are not significantly different at the 0.05 level.

Table 2. Effects of shade on the growth of established silverleaf nightshade.

Plant characteristic[a]	Time (days after planting)	Shade (%)			
		0	47	63	92
Height (cm)	20	12a	7b	7b	5b
Leaves (per plant)	20	7a	7a	6a	6a
Height (cm)	33	21a	23a	23a	25a
Height (cm)	48	44a	56a	46a	42a
Plants flowering (per plot)	48	3a	2ab	0b	0b

[a] Values sharing the same letter within a row are not significantly different at the 0.05 level.

Table 3. Effects of shade on the chlorophyll content, specific leaf area (SLA), and photosynthetic rate of established silverleaf nightshade.

Plant characteristic[a]	Shade (%)			
	0	47	63	92
Chlorophyll a (mg/g)[b]	0.052a	0.58a	0.61b	0.51ac
Chlorophyll b (mg/b)	0.35a	0.39ab	0.42bc	0.48c
Chlorophyll a+b (mg/g)	0.96a	1.09b	1.15b	1.10b
Chlorophyll a+b (mg/dm^2)	2.47ab	2.68a	2.32b	1.61c
Chlorophyll a/b ratio (mg/g)	1.49a	1.47a	1.47a	1.09b
SLA (dm^2/g)	3.88a	4.05b	5.01c	6.75d
Photosynthetic rate at average ambient irradiance (mg $CO_2 dm^{-2} h^{-1}$)	10.4a	4.60b	3.30c	0.90d
mg $CO_2 g^{-1} h^{-1}$	40.3a	18.6b	16.5c	6.08d

[a] Values sharing the same letter within a row are not significantly different at the 0.05 level.

[b] Values presented were calculated on a fresh weight basis.

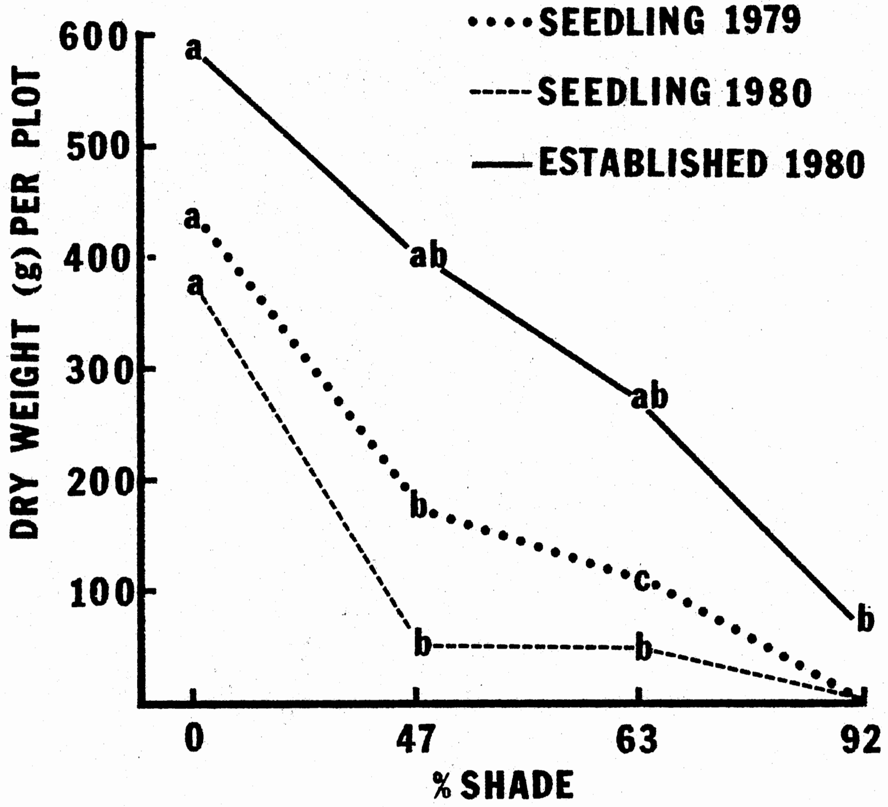

Figure 1. Effect of shade on dry matter production of seedling and established silverleaf nightshade. Values sharing the same letter within a line are not significantly different at the 0.05 level.

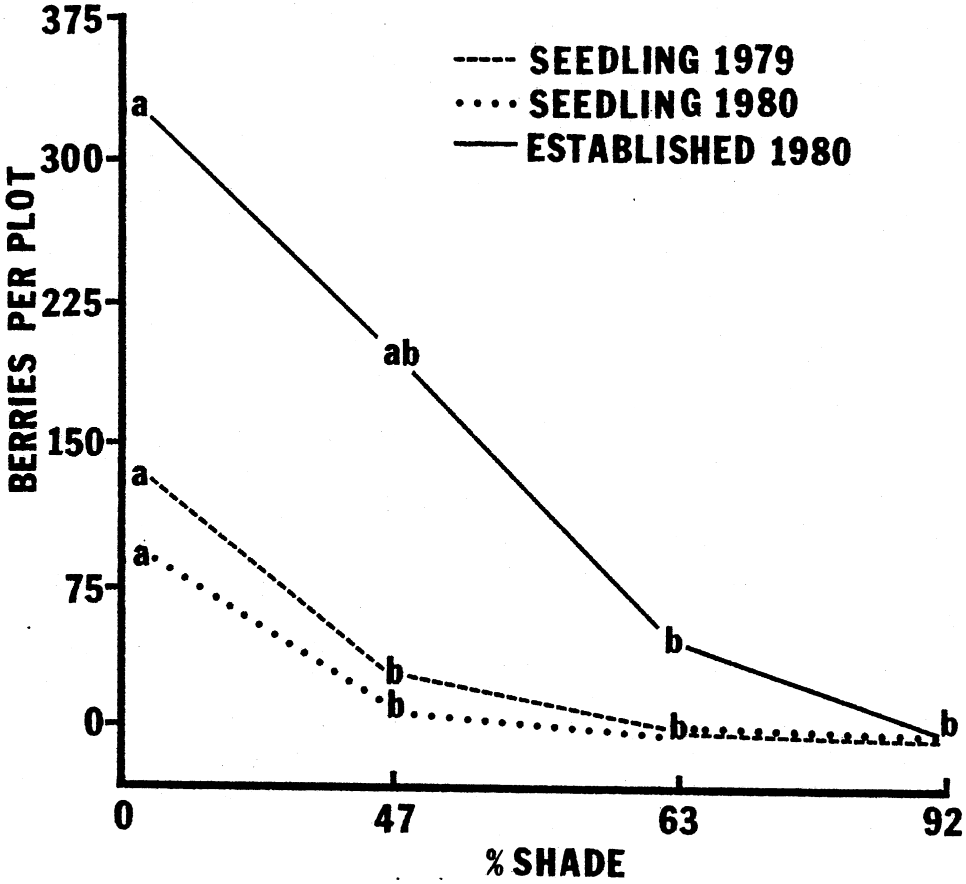

Figure 2. Effect of shade on fruit production of seedling and established silverleaf nightshade. Values sharing the same letter within a line are not significantly different at the 0.05 level.

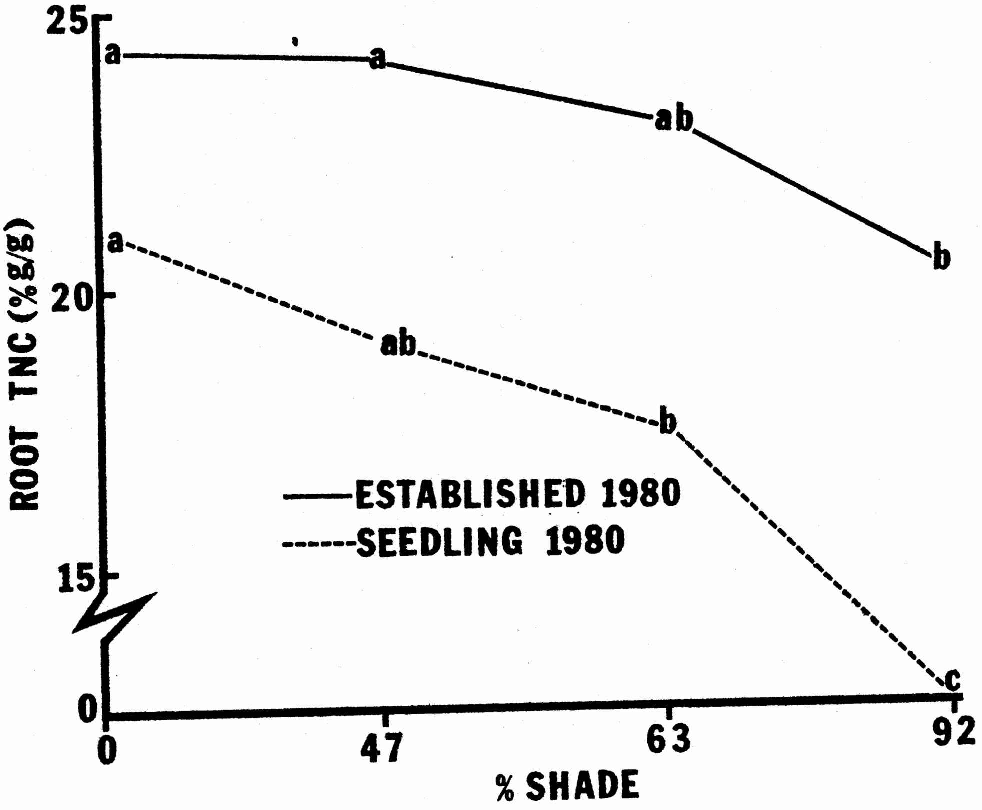

Figure 3. Effect of shade on the total nonstructural carbohydrate (TNC) content of seedling and established silverleaf nightshade roots. Values sharing a letter within a line are not significantly different at the 0.05 level.

VITA

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Candidate for the Degree of

Doctor of Philosophy

Thesis: EFFECTS OF CERTAIN ENVIRONMENTAL FACTORS ON THE GROWTH AND DEVELOPMENT OF SILVERLEAF NIGHTSHADE (*SOLANUM ELEAGNIFOLIUM*)

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