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SOKAL R. R., and F. J. ROHLF. 1969. Biometry. The Principles and Practices of Statistics in Biological Research. W. H. Freeman & Co. San Francisco. 776 p.

TILLET, S. S. 1967. The maritime species of *Abronia* (Nyctaginaceae). Brittonia 19: 229–327.

WILLIAMS, W. T., and J. R. POTTER. 1972. The Pacific coastal strand community at Morro Bay State Park, California. Bull. Torrey Bot. Club 99:163–171.

Convolvulus sepium in old field succession on the New Jersey Piedmont

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QUINN, JAMES A. (Dept. Bot., Rutgers Univ., New Brunswick, N.J. 08903). *Convolvulus sepium* in old field succession on the New Jersey Piedmont. Bull. Torrey Bot. Club 101: 89–95. 1974.—The purpose of the study was to investigate the possibility that allelopathic and autotoxic phenomena influence the results of competitive interactions between *Convolvulus sepium* and associated species on the Piedmont of New Jersey. Field observations and greenhouse experiments were performed on the effects of soil from patches of *C. sepium* on germination and growth and the effects of leachate of this species on growth. Past reports and field observations indicated that (1) certain species growing in areas inhabited by *C. sepium* appear inhibited even during its dormant period and even after hand-weeding removes it as a competitor, and (2) when initially dominant, the species often declines in importance during the early stages of old field succession. Allelopathic effects of *C. sepium* varied with the species tested. *Amaranthus retroflexus, Chenopodium album, Digitaria sanguinalis,* and *Triticum aestivum* were significantly inhibited at all stages of development investigated. *Portulaca oleracea* was inhibited only during germination and seedling development. Autotoxicity was statistically significant in all controlled environment studies. The interaction of such allelopathic and autotoxic effects in the early stages of secondary succession is discussed.

Hedge bindweed (*Convolvulus sepium*), an agricultural weed, is a common component of the initial vegetation occupying abandoned cropland on the Piedmont of New Jersey. It has been generally assumed that it was persistent under these conditions because of its competitive prowess in the struggle for moisture and nutrients. Its rapid vegetative growth and extensive root system are consistent with a strong competitive ability, but several observations suggest that its success is not completely explained by conventional modes of competition. The growth of *Danthonia sericea* in replicate plots in a transplant garden at the William L. Hutcheson Memorial Forest (HMF) seemed to be inversely related to the occurrence and abundance of hedge bindweed. This difference in *Danthonia* growth developed over a span of time (September 1967 to May 1968) during which bindweed was dormant and thus would not have been shading or competing with *Danthonia* for moisture or nutrients. Furthermore, hand-weeding starting in March removed bindweed as a competitor in the vicinity of individual *Danthonia* plants. The persistence in the soil of an allelopathic chemical from bindweed could provide a mechanism by which *Danthonia* growth was reduced by dormant or absent bindweed.

In her study of secondary succession on the Piedmont of New Jersey, Bard (1952) found the peak coverage, frequency, and presence values for *C. sepium* in her 2-yr-old fields. At HMF, Shure (1969) reported hedge bindweed as a dominant producer during the early summer in 1-yr-old fields in both 1967 and 1968. Kricher (1970), working in the same areas as Bard, found that relative coverage values of *C. sepium* in his 3-yr-old field plots averaged 15.4, while the species was not recorded in

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his 30-yr-old field or HMF forest plots. Lewis (1971) in an HMF study utilizing fields aged one to five years reported a cover value for *C. sepium* in the 1-yr-old field at least three times greater than that for any of the other fields. It thus appears that hedge bindweed declines in importance during old field succession and that particularly significant declines occur when it is initially dominant over considerable area. The decline of a strong competitor, such as bindweed, in a density-dependent manner might well be produced by an autotoxic reaction.

The objective of this study was to investigate the possibility that allelopathic and autotoxic phenomena influence the results of competitive interactions between *C. sepium* and associated species.

Materials and methods. All field observations, bindweed materials, and soils came from old field study areas at the William L. Hutcheson Memorial Forest at East Millstone, New Jersey, on the Piedmont. These areas are underlain by Triassic red shale of the Brunswick formation (Kummel 1940) and are slightly rolling to level in topography with moderately well-drained silt loam soils (ranging around *p*H 5.0) of 46 to 61 cm in depth (Ugolini 1964). Annual precipitation totals approximately 112 cm (climatological standard normal based on the period 1931–1960).

All greenhouse observations and experiments were conducted in one room under semi-controlled environmental conditions. Temperature ranged between 21 and 29 C, with the maximum during a 24-hr period generally exceeding the minimum by at least 5 degrees. Relative humidity varied between 50 and 80%. Pots and flats were watered regularly for maintenance of a moderate soil moisture level (12–18% of dry soil weight). Seeds, seedlings, and plants of pigweed, *Amaranthus retroflexus*; lamb's quarters, *Chenopodium album*; hedge bindweed, *Convolvulus sepium;* crabgrass, *Digitaria sanguinalis*; carpetweed, *Mollugo verticillata*; purslane, *Portulaca oleracea*; and wheat, *Triticum aestivum* were used in one or more experiments, depending on their availability and on greenhouse space limitations. All seeds (except for wheat—soft red winter type, "Redcoat" variety, harvested in New Jersey and obtained from the Farmers' Cooperative Association of N.J., Inc., of New Brunswick) and plant materials were collected either at HMF or within a 16-km radius of the forest on comparable sites. Nomenclature follows Gleason and Cronquist (1963).

BINDWEED SOIL VS. NON-BINDWEED SOIL. Soil (upper 15 cm) was collected from dense bindweed patches and from immediately adjacent non-bindweed areas in a 2-yr-old field, sifted with 6 mm hardware cloth to remove large pieces of organic material (especially rhizomes), and stored in closed garbage cans for use in the following experiments. Replicate samples of these soils and similar samples from a one-year old field were analyzed for texture, *p*H, cation exchange capacity, and available nutrients by the Rutgers Soil Testing Laboratory. Textural analysis was by the hydrometer method (Bouyoucos 1953); soil *p*H was determined using a Photovolt model Digicord meter on a soil-water (1:1) suspension. Cation exchange capacity was obtained by the ammonium acetate method (Schollenberger and Simon 1945), and techniques for determination of NH_4-N and NO_3-N followed those of Hanna and Purvis (1955). Concentrations of P, K, Mg, and Ca were determined according to the procedures outlined by Flannery and Markus (1970).

To determine if the bindweed exerted a lasting effect in the soil on residual seeds, 18 pots (15 cm dia) were filled with bindweed soil and 18 with soil from areas free of bindweed, and germination was noted. The number of individuals and air-dry shoot weights of seedlings arising from these residual seeds were determined after one month's growth in the greenhouse.

In a further test one year later of the effect of prior bindweed occupancy of the soil, the same bindweed and non-bindweed soils were placed in wooden flats ($31 \times 45 \times 7$ cm deep), and seeds of pigweed, crabgrass, and wheat were planted. For each species, four flats (two with bindweed soil and two with non-bindweed soil) were utilized. In each flat, 200 seeds were planted in four rows (50/row). Percent germination, mean height, and air-dry shoot weight were determined after variable periods of growth in the greenhouse (38, 20, and 15 days for pigweed, crabgrass, and wheat, respectively). The variable of residual seeds was removed by extracting their seedlings from both within and between the rows. This was made possible by consistent source-related differences in seedling morphology and pigmentation.

LEACHATE COLLECTION AND APPLICATION. Leachates were collected from flats containing a dense growth of bindweed and from flats containing only the standardized soil (control leachate). These flats ($50 \times 35 \times 10$ cm deep) were of galvanized sheet steel with perforated bottoms and were arranged in sets of four on frames supporting polyethylene sheeting which funneled the leachate into a bucket. On the average, 375 ml of the leachates were applied every three days to paired 15-cm clay pots of lamb's quarters, wheat, purslane, and hedge bindweed. A standardized 1:1:1 mixture of loam, sand, and sphagnum peat was used for the above flats and pots. Three sets of four bindweed and four non-bindweed flats furnished the necessary leachate for these experiments beginning in June and terminating in September, 1969.

Previously thinned pots of plants were paired on the basis of comparable vigor and size of the plants at the following stages of height growth: lamb's quarters, 3–6 cm; wheat, 18–22 cm; and purslane, 8–21 mm. One pot of each pair was randomly selected to receive the bindweed leachate; the other received control leachate. To test for autotoxicity, paired pots of comparable shoot number and vigor of hedge bindweed were also subjected to this treatment. The number of pots per species, plants or shoots per pot, the determinations made, and the duration of each trial are cited in Table 4.

MEASUREMENT OF LEAF SIZES. Six flats of hedge bindweed (two each of 1, 12, and 18 months in age) were utilized for one-surface leaf area measurements. In each case, 50 leaves per flat were randomly selected and measured with a transparent grid divided into ¼ cm^2 units.

Results and discussion. EFFECT OF SOIL FROM BINDWEED PATCHES. Source of soil produced striking differences in the number and size of individuals germinating from residual seeds present in the soil (Table 1). Pigweed, crabgrass, and purslane (species commonly associated with hedge bindweed in the early stages of old field succession) had from 10–44 times more individuals on the non-bindweed soil, and shoot weight per individual was considerably greater even at these higher densities (6, 16, and 1.3 times for pigweed, crabgrass, and purslane, respectively). Although there were 8 times the carpetweed plants on non-bindweed soil, individuals weighed less than those on the bindweed soil. This may have been an effect of density stress since the non-bindweed pots averaged 62.4 plants as against 4.1 plants per bindweed pot.

There could be two explanations for the greater number of individuals on the non-bindweed soil—(1) a persistent effect of bindweed growth not detectable by standard soil analyses, and (2) different numbers of residual seeds in the soils. Analyses of the soils from the bindweed patches and bindweed-free areas (Table 2) did not show *p*H or nutrient differences large enough to explain the large differences in germination and growth among seeds of these associated species. The texture was a loam in each case, and the cation exchange capacity varied between 6.9 and 11.4 meq/100 g and was not correlated with presence or absence of bindweed. The soil factors examined are those commonly found to limit crop growth in New Jersey, but unexamined factors cannot of course be eliminated. The presence of allelopathic chemicals is one such factor. As the entire area prior to plowing had been covered by a diverse vegetation, seed levels were presumed to be similar in the areas which ultimately developed as bindweed patches. The greater weight of seedlings in the non-bindweed soils, even at levels producing competitive stress, strongly suggests an inhibitive effect present in the bindweed soil, even if initial seed levels were different.

To overcome the difficulty imposed by

Table 1. Number of individuals and mean air-dry shoot weight of seedlings arising from residual seeds in 18 pots each of bindweed (B) and non-bindweed (N) soils.

Species	Total no.		Weight (mg/plant)	
	B	N	B	N
Amaranthus retroflexus	5	55	8	49
Chenopodium album	0	3	0	33
Digitaria sanguinalis	2	90	5	80
Mollugo verticillata	46	364	9	6
Portulaca oleracea	16	607	11	15
Miscellaneous	5	4	120	50

Table 2. Nutrient levels and pH of soil samples (upper 15 cm) taken from adjacent bindweed and non-bindweed areas in one- and two-year-old fields on June 20, 1969, at the study areas of the William L. Hutcheson Memorial Forest.

Source and sample number		pH	Available nutrients[a] ppm NH_4-N	NO_3-N	K	Mg	Ca
ONE-YEAR OLD FIELD							
Bindweed	1	5.4	10.8	4	56	62	160
	2	5.3	12.0	8	48	76	208
	3	4.9	17.6	4	58	50	144
Non-bindweed	1	5.3	13.6	8	39	61	160
	2	5.1	14.0	4	48	75	192
	3	5.5	12.0	4	50	73	192
TWO-YEAR OLD FIELD							
Bindweed	1	5.0	13.6	8	30	50	160
	2	4.8	14.0	4	30	55	80
	3	5.1	11.2	8	36	80	160
	4	5.2	11.2	4	33	56	91
Non-bindweed	1	4.9	12.4	4	45	56	91
	2	4.9	11.2	4	23	60	80
	3	5.1	12.0	8	38	91	144
	4	4.9	12.4	4	27	67	96

[a] Concentration of P was < 10 ppm in each sample.

the imprecise number of residual seeds in the soil (designated [2] in the above paragraph), the effect on given numbers of pigweed, crabgrass, and wheat seeds planted in flats of bindweed and non-bindweed soil was determined. Although not significantly different, percentage germination was slightly lower in pigweed and crabgrass in soil from bindweed areas (Table 3). For all three species, plants on soil from bindweed patches were yellow-green and spindly, i.e., shorter in height, with short, narrow leaves, and lower in shoot weight. The differences in height and weight between the control plants and those grown in bindweed soil were statistically significant in crabgrass and wheat (Table 3). Much poorer development of root systems of all species was noted in the soil from bindweed patches, and this observation, together with the preceding data, point to an inhibitory effect of the bindweed soil on root development and growth.

EFFECTS OF LEACHATES. Except for purslane, mean shoot weights for plants receiving bindweed leachate were significantly less than for those receiving the control leachate (Table 4). Lamb's quarter plants receiving bindweed leachate often showed yellowing or yellow-green leaves, and their air-dry shoot weights were also less, primarily because of significantly shorter heights. Wheat plants receiving bindweed leachate were generally smaller, with significantly fewer tillers and with leaf blades slightly shorter and narrower than the controls. Although weights were slightly greater for purslane receiving control leachate, no consistent visible differences between plants treated with leachate from

Table 3. Percent germination, mean height, and air-dry shoot weight of three species grown in bindweed (B) or non-bindweed (N) soil.

Species	Duration of trial (Days)	Germination[a] %		Mean height (cm)		Weight g/50 plants	
		B	N	B[b]	N	B[b]	N
Amaranthus retroflexus	38	69	79	2.9	3.0	0.29	0.41
Digitaria sanguinalis	20	66	71	6.3**	13.7	0.14*	0.48
Triticum aestivum	15	85	82	16.3*	22.8	2.90**	5.30

[a] Summary of the results from two flats each planted with 200 seeds.
[b] Significance of difference from control: *, $P \leq 0.05$; **, $P \leq 0.01$.

Table 4. Mean air-dry shoot weight of plants grown in paired pots receiving either the bindweed (B) or the control (N) leachate.

Species	No. of pots per treatment	Plants per pot	Duration of trial (Days)	Shoot weight (mg/plant)	
				B[b]	N
Chenopodium album	18	2	48	730**	1295
Triticum aestivum	17	3	48	573*	707
Portulaca oleracea	17	1	37	681	780
Convolvulus sepium	20	3–7[a]	94[c]	442**	791

[a] Range in number of shoots at beginning of experiment. Pots were paired as to number and vigor of shoots.
[b] Significance of difference from control: *, $P \leq 0.05$; **, $P \leq 0.01$.
[c] The shoots were clipped to an 8-cm level 16, 38, 63, and 94 days after initiation of leachate application and the clippings air-dried and weighed.

bindweed or control flats could be detected. The lack of differential response here, in the case of plants already 8–21 mm tall when leachates were first applied, provides an interesting contrast to the marked inhibition of purslane germination in soil from bindweed patches (Table 1) and thus suggests that the allelopathic agent of bindweed may be more effective against the germination of purslane than against the development of the seedlings once germinated. Soil analyses at the termination of the leachate experiments indicated no differential depletion or buildup of nutrients in either the flats utilized to provide the two leachates or the pots receiving them.

The air-dry weight of shoot clippings of bindweed derived from four harvests during a three-month growing period were significantly less for plants receiving bindweed leachate (Table 4). These differences in shoot weights were due to the production of fewer shoots, a slower growth rate of existing shoots, and a significant decrease in individual leaf size of the plants receiving leachate from the bindweed flats. Measurements on six flats of hedge bindweed from a common source demonstrated similar decreases in leaf size with increased time of growth in the flats (Fig. 1). This decrease in leaf size and vigor with time had been observed in the HMF old field study areas but was attributed to either depletion of nutrients and/or interspecific competition. However, in the greenhouse the same phenomena were consistently observed under conditions of no interspecific competition, regular watering, and periodic application of liquid fertilizer.

Ecological significance. Hedge bindweed is commonly one of the dominant producers in the early stages of old field succession on the Piedmont (Shure 1969, Kricher 1970, Lewis 1971, Small et al. 1971). Its rapid vegetative growth from fleshy, creeping rootstocks and the tendency of the long creeping stems (1–3 m) to twine about or overtop other herbaceous plants certainly contribute to its success. Shure (1971) observed that hedge bindweed formed a dense vegetative mat during early summer when most other seedlings

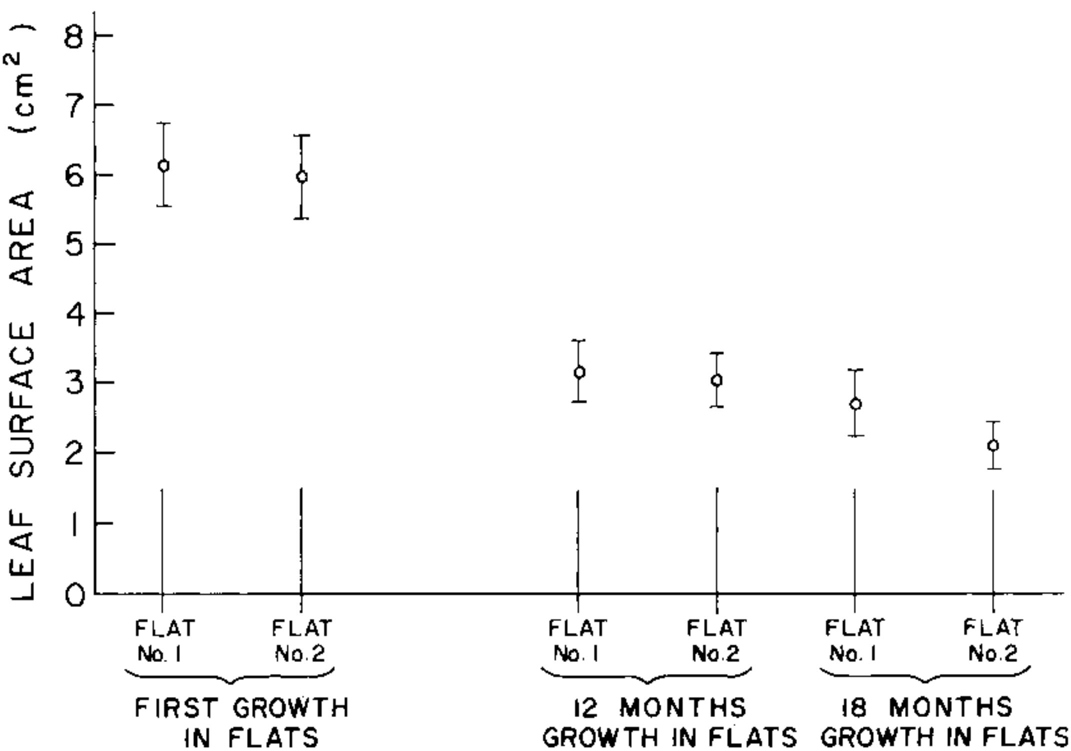

Fig. 1. Means (circles) and 95% confidence intervals (vertical lines) of upper leaf surface area of *Convolvulus sepium* grown in flats for 1, 12, and 18 months.

were appearing and that growth forms of other species were altered, depending on the degree of bindweed cover. I had accepted these characteristics as satisfactorily explaining its early success in abandoned croplands until I happened to discover the effect of soil from bindweed patches on the growth of *Danthonia sericea*. Subsequently, a series of soil samples from bindweed and non-bindweed areas in different fields at different seasons revealed no evidence for nutrient depletion or differences in ammonium and nitrate-N levels. One possible explanation of my results would be the presence of inhibitory concentrations of phenolic acids in the soils from bindweed areas. An inhibitory substance in the creeping stem of hedge bindweed in France appeared to be a complex coumarin derivative (Tronchet 1961). Phenolic acids (such as p-coumaric) at concentrations found in many soils have been found to suppress the growth of young wheat (Wang, Yang, and Chuang 1967). The significant effects in this study of soil source (bindweed vs. non-bindweed area) and bindweed leachate on the germination, seedling development, and growth of species commonly associated with hedge bindweed in the early stages of old field succession provide an explanation for the inhibition of *D. sericea* and suggest the addition of allelopathy to the total competitive interactions between *C. sepium* and associated species.

Hedge bindweed declines in importance during old field succession and often is not recorded in plots of fields more than 30 years past abandonment (Bard 1952, Kricher 1970). Much earlier, however, the species drops from a dominant status (Lewis 1971); and although it may continue to be commonly recorded in quadrats 16 years after abandonment (Small, Buell, and Buell, unpublished data from HMF sites), a plotting of cover values of *C. sepium* on the same quadrat through time often produces a "ripple" effect of high-low-high cover values or of *C. sepium* peaking at high values, disappearing, and then re-entering the quadrat in subsequent years and again peaking (C4, C5, D1, and D3 fields of Small et al. 1971). Evidence from the effects of the bindweed leachate on the growth of bindweed and from the observations of declining vigor with time of growth in one place (pot, flat, or field quadrat) strongly suggest autotoxicity. Significantly, hedge bindweed thrives with regular cultivation, which would facilitate microbial activity, breakdown of inhibitors, and leaching. Another explanation of the field results could be a depletion of nutrients or perhaps an inhibition of nitrification (Rice 1964, Blum and Rice 1969), but the phenomenon also occurred under high nutrient (including added nitrates) levels in the greenhouse. In addition, analyses of soil from non-bindweed and bindweed areas of one and two years of age provided no support for this alternative (Table 2).

In conclusion, evidence has been presented which indicates that allelopathic inhibition of associated species could contribute to the detrimental effects of *C. sepium* as a weed during regular cultivation and to its occasional dominance for several years following cultivation. Eventually, autotoxic effects begin to override the benefits of allelopathic inhibition, and *C. sepium* declines in importance as shading and other competitive stresses increase during secondary succession.

Literature Cited

BARD, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecol. Monogr. 22:195–215.

BLUM, U., and E. L. RICE. 1969. Inhibition of symbiotic nitrogen-fixation by gallic and tannic acid, and possible roles in old-field succession. Bull. Torrey Bot. Club 96:531–544.

BOUYOUCOS, G. J. 1953. An improved type of soil hydrometer. Soil Sci. 76:377–378.

FLANNERY, R. L., and D. K. MARKUS. 1970. Simultaneous determinations of phosphorus, potassium, calcium and magnesium in soil extracts by AutoAnalyzer. *In* Advances in automated analysis. Volume 2. Pp. 29–37. Mediad, Inc., White Plains, N.Y. 346 p.

GLEASON, H. A., and A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand Co., Inc., Princeton, N.J. 810 p.

HANNA, W. J., and E. R. PURVIS. 1955. Techniques for determining the nutrient status of soils and crops. Rutgers Univ. Agr. Exp. Sta. Bull. 780. 15 p.

KRICHER, J. C. 1970. Bird species diversity in relation to secondary succession on the New Jersey Piedmont. Ph.D. dissertation, Rutgers University, New Brunswick, N.J. 123 p.

KUMMEL, H. B. 1940. The geology of New Jersey. N.J. Dep. Conserv. and Devel., Geol. Ser., Bull. 50. 203 p.

LEWIS, A. J. 1971. The effects of chemical and mechanical manipulation of old-field plant populations; An evaluation of ragweed control techniques. Ph.D. dissertation, Rutgers University, New Brunswick, N.J. 101 p.

RICE, E. L. 1964. Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants. (I.) Ecology 45:824–837.

SCHOLLENBERGER, C. J., and R. H. SIMON. 1945. Determination of exchange capacity and exchangeable bases in soil—ammonium acetate method. Soil Sci. 59:13–24.

SHURE, D. J. 1969. Insecticide contamination and trophic relationships in a first-year, old-field ecosystem. Ph.D. dissertation, Rutgers University, New Brunswick, N.J. 163 p.

————. 1971. Insecticide effects on early succession in an old field ecosystem. Ecology 52:271–279.

SMALL, J. A., M. F. BUELL, H. F. BUELL, and T. G. SICCAMA. 1971. Old-field succession on the New Jersey Piedmont—the first year. William L. Hutcheson Memorial Forest Bull. 2(4):26–30.

TRONCHET, J. 1961. Étude par chromatographie sur papier d'une substance inhibitrice présente dans les tiges rampantes de *Convolvulus sepium.* Bull. Soc. Hist. Nat. Doubs 63(1):11–13.

UGOLINI, F. C. 1964. Soil development on the red beds of New Jersey. William L. Hutcheson Memorial Forest Bull. 2(1):1–34.

WANG, T. S. C., T. K. YANG, and T. T. CHUANG. 1967. Soil phenolic acids as plant growth inhibitors. Soil Science 103:239–246.