

NATIVE NORTH AMERICAN SPECIES OF  
LESPEDEZA (LEGUMINOSAE)\*

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The genus *Lespedeza* occurs in eastern North America, eastern Asia, and Australia. The native American species are perennial herbs, mostly occurring in dry, open sites, such as old fields, roadsides, prairies, and savannahs. The Asian species include shrubs and annuals, the latter sometimes being separated into *Kummerowia* Schindl. (Hutchinson 1964). Two annuals, *L. striata* (Thunb.) H. & A. and *L. stipulacea* Maxim., and one herbaceous perennial, *L. cuneata* (Dumont) G. Don, have been introduced widely in eastern North America from Asia as forage for cattle and wildlife, for preventing soil erosion, and for green manure. All three species have become well-established weeds along roadsides and in similar sites. An Asian shrub, *L. bicolor* Turcz., has become much less widely established after its introduction for purposes of wildlife management, and several other Asian introductions either have not escaped or have remained local. None of the Asian species are treated in this paper; Wilbur (1963) has described the common Asian introductions in detail. I have examined

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specimens of about 36 Asian species; more have been described. Van Steenis (1957) pointed out that certain Asian species intergrade and are in need of revision. Hiroyoshi Ohashi (pers. com.) at the University of Tokyo recently began studying the Japanese species.

Until the Asian species are satisfactorily circumscribed, attempts to divide the genus into subgenera or sections will be premature; Isely (1955) has summarized the previous attempts. *Lespedeza* has long been considered a member of the *Hedysareae* which, according to Isely (1955) and authors cited by him, is an arbitrarily defined tribe of polytypic origin. Hutchinson (1964) has redefined the tribes of the *Leguminosae* and has described a new tribe, the *Lespedezae*, to which *Lespedeza* and several other genera belong (but not *Desmodium*).

#### LITERATURE

Important contributions from the older literature to a taxonomic understanding of the American species include those by Maximowicz (1873) who prepared the first synopsis on a world-wide basis after most of the species had been discovered; Britton (1893) who first revised the North American species; and Schindler (1913) who wrote the only comprehensive world-wide monograph of *Lespedeza*. More recent critical treatments of the North American taxa are by Blake (1924) on selected species, Fassett (1939) on those occurring in Wisconsin, Fernald (1941) the white-flowered species, Gambill (1953) the species from Illinois, Isely (1955), a detailed account of those occurring in the north-central United States, Turner (1959) the Texas species, and Wilbur (1963), accurate, detailed descriptions of the species in North Carolina. Papers concerned with population studies, breeding systems, cytology, ecology, hybridization, and evolution are Clewell (1964b, 1966). Many of the data in those papers and in this one came from a dissertation, Clewell (1963). Many references to other papers on *Lespedeza* are cited in the Botany Subject Index (compiled by the U.S.D.A. Library, 1958) vols. 5: 4467-69 and 7: 7060-62.

## AN EVALUATION OF SOME TAXONOMIC CHARACTERS

To characterize and identify species, it is important to distinguish cleistogamously-formed pods from chasmogamous pods. With rare exceptions cleistogamous and chasmogamous flowers occur on separate racemes. In contrast to racemes with chasmogamous flowers, cleistogamous-flowered racemes generally are shorter, are borne farther down the stem, and bear a few more flowers. Hanson (1943) and Hanson & Cope (1955) have described cleistogamous

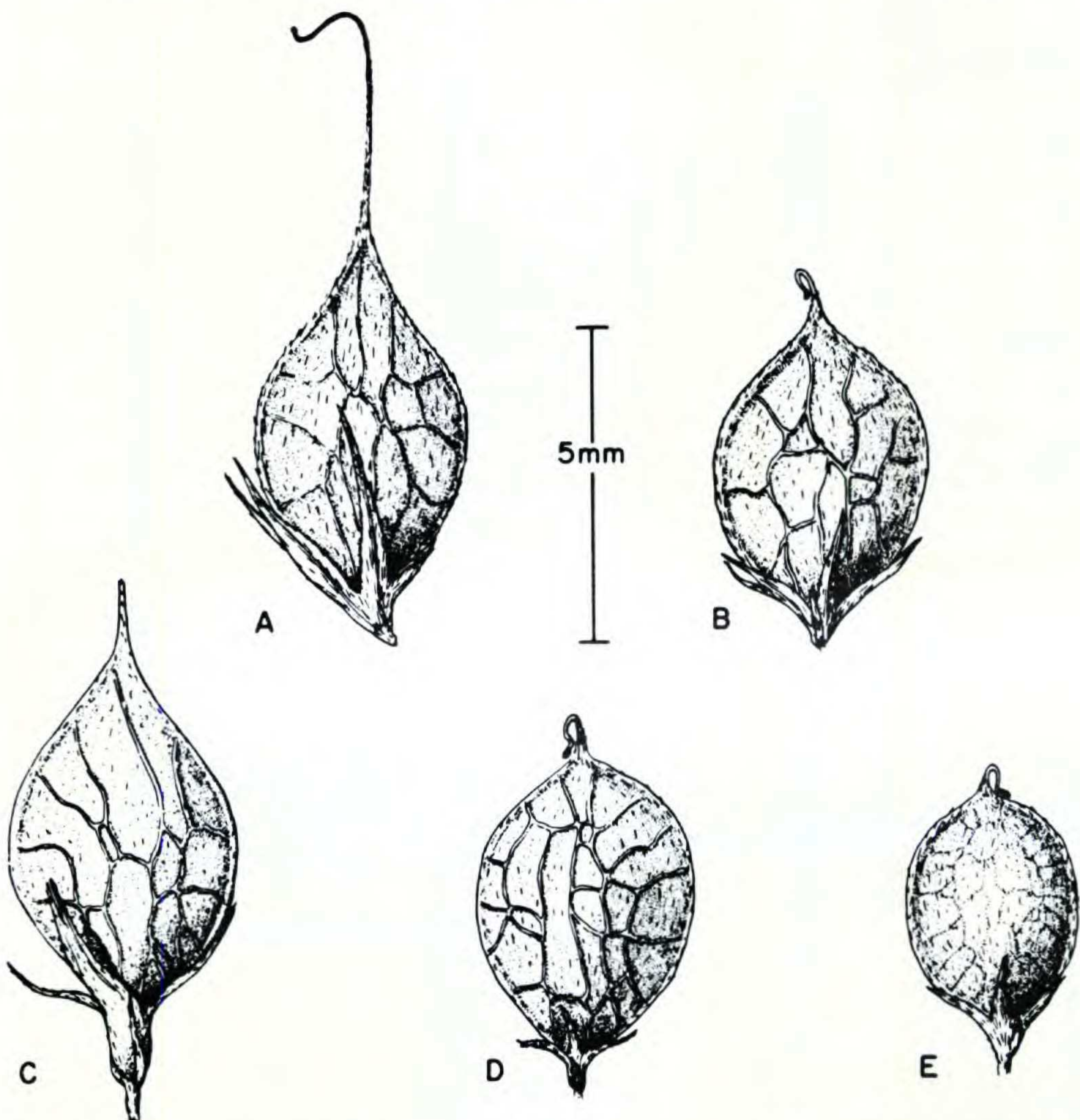


Fig. 1. Chasmogamous and cleistogamous pods. 1a: *Lespedeza intermedia* (chasmogamous); 1b: *L. intermedia* (cleistogamous); 1c: *L. violacea* (chasmogamous, style broken); 1d: *L. violacea* (cleistogamous); 1e: *L. repens* (cleistogamous).

flowers of *Lespedeza* in detail. They pointed out that in bud the style recurves until the stigma rests upon one or more anthers, the filaments of which do not elongate. Pollen grains germinate within the anthers upon which the stigma rests and the tubes grow through the indehiscent anther wall into the stigma (cleistantheric pollination). The style is persistent on mature pods and reflects its mode of development by being sharply recurved. Sometimes an anther adheres to the stigma of a mature pod, evidently held there by the pollen tubes. Styles persistent on chasmogamous pods are longer and either erect or variously curved but not sharply recurved. Cleistogamous pods can be distinguished from chasmogamous ones primarily by the shape of the style and secondarily by the slightly shorter length of the calyxes (Fig. 1). Cleistogamous pods also tend to be shorter and more orbicular, rather than elliptic.

Pollen grains, taken from dried plants and stained with cotton blue in lactophenol, revealed only nominal variation both within and between species. The grains have 3 pores and no ornamentation. Most are 27-33 microns in diameter; however, some plants have slightly larger grains, particularly certain plants of *Lespedeza capitata* and *L. violacea*. Gross pollen morphology is not taxonomically significant.

Chromosome numbers cannot be employed in distinguishing the American taxa, because all plants examined had 10 pairs of chromosomes (Clewell 1966). Pierce (1939) found the chromosomes to be small and rather uniform with no significant variation between species. My own observations confirm his conclusions, thereby negating karyotypic variation as a useful character.

D. A. Levin (pers. com.) has prepared chromatograms from pigments extracted from the leaves of several *Lespedeza*s that I sent to him. Included were a specimen of a hybrid and specimens of its parental species and of several other species, including one native to Asia. He concluded that, "the patterns of the different species are quite similar and further study of *Lespedeza* using the present techniques does not appear warranted." Levin discovered a close simi-

larity between some of the chromatograms of the lespedezas and a chromatogram of a plant of *Desmodium ciliare* (Muhl.) DC. This suggests that a comparative chromatographic study of representatives of the *Hedysareae* might be rewarding in assessing relationships between genera.

#### CONCEPT OF SPECIES

I have observed many populations of *Lespedeza* over a period of 8 years on the Atlantic Coastal Plain and adjacent physiographic provinces from the Carolinas to the Mississippi River, in most of Indiana, and in parts of Texas, Iowa, and the Ozark Plateau. Field observations and analysis led me to my recognition of 11 species. Subsequently progeny tests yielded data supporting my concepts of these species, as did observations on wild plants transplanted and grown in a greenhouse. Each progeny test consisted of removing seeds from one plant, which was collected in a natural population, and planting them under uniform conditions in a garden. The mature offspring were then compared with each other and with their parental plant. With the exception of 6 obvious hybrids, all 378 sibs of the 24 progeny tests clearly resembled their respective parental plants. The species tested were *L. angustifolia*, *L. capitata*, *L. hirta* (both subsp.), *L. intermedia*, *L. procumbens*, *L. stuevei*, *L. violacea*, and *L. virginica* (Clewell 1966). Examination of herbarium specimens from throughout the geographic ranges of all species has contributed further to the recognition of each species and has yielded information which has allowed not only the precise delimitation of the species but also the assessment of the geographic variation existing within each species.

Usually a few plants in each population are difficult to identify. Some of these have proved to be shade forms which one can learn to correlate with the variation in the "good" species (see notes on *L. intermedia* in the taxonomic treatment). Other plants appear to be hybrids. Virtually every population of about 50 plants or more consisted of 2-7 species and contained at least one hybrid. Not infrequently

hybrids composed 1% or more of the plants present. The parentage of nearly all hybrids was determined easily in the field, even though several hybrid combinations were present. This was possible because most hybrids appeared to be  $F_1$ s, and hybrid swarms with many notomorphs were rare. The parentages of hybrids that have been deposited in herbaria are less easily postulated than of hybrids seen in the field with their parental species. My identifications of *Lespedeza angustifolia*  $\times$  *hirta* and *L. procumbens*  $\times$  *stuevei* have gained credence through comparisons with artificially synthesized hybrids of these combinations. The identifications of 24 plants of hybrid origin representing 9 hybrid combinations have been verified through progeny tests yielding a total of 175 mature sibs. These sibs comprised a series of segregants, often with forms characteristic of one parent or the other and including various forms between them (Clewell 1966). My success in having field identification of both hybrids and species verified by progeny tests has convinced me that with a few exceptions hybrids can be distinguished easily from species and that the parentages of hybrids can be postulated accurately. Only one of the 48 plants upon which progeny tests were run proved to be misidentified in the field.

I have used two criteria for circumscribing species: First, plants of any species must be morphologically distinct from plants of other species in a population. Exceptions are shade forms and hybrids. Second, the morphological variation within a species throughout its geographic range has precise limits, and no species seemingly merges into another species in any region. If taxa merge, then they are assigned subspecific status. This species concept applies to *Lespedeza* as it presently occurs and not necessarily to other genera or to *Lespedeza* at other times in its evolutionary history.

In the taxonomic treatment the descriptions of species are prepared so that almost any character of one species can be compared with the same character as it occurs in every other species. Only the more important diagnostic characters are described, thereby emphasizing specific de-

limitation. I have omitted lists of specimens examined. My annotations on the great majority of the specimens I examined serve as documentation of this study. These specimens are deposited in the herbaria listed in the acknowledgements. Mimeographed lists of specimens serving as vouchers for the distribution maps (Figs. 2-13) are available from me on request; a copy will be deposited in the library of Florida State University. No index to exsiccatae was prepared. Identification of duplicate specimens in other herbaria by consulting such an index would be hazardous, because in many instances duplicates under one collection-number represent more than one species and, more commonly, hybrids.

#### TAXONOMIC TREATMENT\*

*Lespedeza* Michx. Fl. Bor.-Amer. 2: 70 (1803). (Type species: *L. procumbens*).

*Hedysarum* L. Sp. Pl. 2: 745 (1753). (in part).

*Medicago* L. Sp. Pl. 2: 778 (1753). (in part).

*Lespedezia* Hornem. Hort. Reg. Bot. Hafn. 2: 699 (1815).

Perennial herbs from woody rhizomes bearing 1-45 aerial stems, usually branched, and occasionally a short, underground stolon terminating in a new plant; INDUMENT of appressed trichomes (appressed-pubescent, sometimes silvery or sericeous) or soft, erect or spreading trichomes (pilose if short, villous if long and undulating); LEAVES trifoliolate (rarely some with 4-5 leaflets); LEAFLETS entire, nearly equal in shape, often mucro-tipped, the terminal one often slightly longer than the lateral ones; STIPULES inconspicuous, persistent, the longer ones linear or setaceous, the shorter ones subulate; STIPELS minute, usually absent; RACEMES axillary, sometimes spicate or capitate, commonly some or all reduced to axillary fascicles, rarely paniculate; FLOWERS borne in pairs, each pair subtended by 3 bracteoles on the peduncle, each flower pedicellate to nearly sessile and subtended by 2 bracteoles borne near or at the apex of the pedicel opposite the flat surfaces of the pod; CHASMOGAMOUS FLOWERS showy, CALYX campanulate, persistent in fruit, the lobes subequal, the upper 2 being more connate than the others, COROLLA violet, roseate, cream-colored, or white with a purplish spot near the base of the standard; STANDARD suborbicular to oblong, clawed; WINGS falcate-oblong, about equaling the keel; STAMENS diadelphous; ANTHERS uniform; STYLE long, fili-

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\*Synonyms of *Lespedeza* are limited to those used for native American plants. The generic description also applies only to native American plants.

form, often persistent in fruit; PODS ovate to orbicular, sometimes somewhat asymmetrical, lenticular or laterally compressed, reticulate, mostly indehiscent; CLEISTOGAMOUS FLOWERS often present, sometimes exclusively, about 0.1 the size of chasmogamous flowers, nearly always in separate racemes from chasmogamous flowers, often axillary and averaging a few more flowers per raceme than racemes of chasmogamous flowers; CALYX as in chasmogamous flowers though often slightly shorter; COROLLA greatly reduced; STYLE short, usually persistent in fruit, the distal half sharply recurved and (nearly) touching the proximal half; PODS as in chasmogamous flowers, sometimes tending to be more orbicular and slightly shorter than in chasmogamous flowers; PODS of both chasmogamous and cleistogamous flowers 1-seeded; SEEDS straw-colored to black, sometimes mottled, oval and somewhat laterally compressed.

Ricker (1934) explained that Michaux commemorated the governor of East Florida, 1784-1790, in the name, *Lespedeza*. The governor's name was not D. Lespedez, as stated by Michaux (1803) but Vincente Manuel de Cespedes. Ricker suggested that the change in spelling may have stemmed from an inability of Michaux's son or of L. C. M. Richard to interpret Michaux's notes which were damaged in a shipwreck. The spelling of *Lespedeza* must be retained under Article 73 of the International Code of Botanical Nomenclature (Lanjouw 1961). Through the efforts of Hochreutiner (1934), *Lespedeza* now serves as an illustration for the application of this Article.

I was unable to examine the types of several names applied to the lespedezas, because these types are deposited in European herbaria and were unavailable to me. I have justified the identification of some of these names with certain species in the commentaries on these species. I have associated the remainder of these names with various species both on the basis of the original descriptions and from the comments of Schindler (1913). Schindler examined the type specimens in the European herbaria, and he identified the names in nearly all previous treatments of the genus with the corresponding taxa in his monograph. His lucid discussions made it possible for me to compare my species concepts with his and to gain insight into the concepts of prior authors.



## KEY TO NATIVE AMERICAN SPECIES OF LESPEDEZA

1. Stems procumbent to weakly ascending.
  2. Stems procumbent, pilose throughout (uncommonly mostly pilose in *L. texana*). ..... *L. procumbens*
  2. Stems appressed-pubescent.
    3. Stems erect up to 1.5 dm, then trailing; the longer stipules 4-8 mm long; leaflets firm-textured, gray-green beneath; plants of central Texas. .... *L. texana*
    3. Stems procumbent to weakly ascending; the longer stipules 1.5-6 mm long; leaflets membranous, green beneath.
      4. Stems procumbent; keel about equaling wings; calyx of the cleistogamous pods 0.25-0.5 times the length of the pod; stipules mostly subulate, 1.5-4 mm long. .... *L. repens*
      4. Stems weakly ascending; keel usually longer than wings; calyx of cleistogamous pods up to 0.25 mm long, mostly shorter; stipules mostly filiform, 2.5-6 mm long. ....  
..... *L. violacea*
1. Stems erect or strongly ascending.
  5. Calyx nearly equaling or exceeding the mature pod; flowers white with a purple throat (*L. leptostachya* sometimes has light purple flowers); racemes with 10-44 flowers.
    6. The larger terminal leaflets more than half as wide as long. .... *L. hirta*
    6. The longer terminal leaflets less than half as wide as long.
      7. Rachises longer than their petioles; racemes included within or exserted up to 1.5 times beyond their subtending leaves; calyx mostly 8-13 mm long. .... *L. capitata*
      7. Rachises of the longer terminal leaflets equaling or generally shorter than their petioles; racemes 1-4 times longer than their subtending leaves; calyx 4-9 mm long.
        8. Leaflets glabrous above and stems appressed-pubescent or leaflets pubescent and stems densely pilose; racemes dense, the flowers limited usually to the terminal third of the peduncle; plants of the Atlantic Coastal Plain. ....  
..... *L. angustifolia*
        8. Leaflets above and stems appressed-pubescent; racemes open, the flowers scattered on the terminal half of the peduncle; plants of the upper Mississippi Valley. ....  
..... *L. leptostachya*
  5. Calyx half as long as the mature pod or shorter; flowers purple; racemes with 4-14 flowers.
    9. Keel often noticeably longer than wings; some racemes usually exserted 2-5 times beyond their subtending leaves; calyx of the cleistogamous pods up to 0.2 (rarely 0.25) times the length of the mature pod; stems sparsely appressed-pubescent;

- stipules 2.5-6 mm long. .... *L. violacea*
9. Keel equaling or shorter than wings; racemes included within or slightly exserted beyond their subtending leaves; calyx of the cleistogamous pods 0.2-0.4 times the length of the mature pod; stems appressed-pubescent or pilose; stipules rarely exceeding 4 mm long.
10. Leaflets glabrous above (rarely appressed-pubescent along the midrib), the longer ones more than 0.3 times as wide as long; stems moderately appressed-pubescent. ....  
..... *L. intermedia*
10. Leaflets appressed-pubescent, at least along the midrib, to pilose, the longer ones 0.1-0.5 times as wide as long; stems appressed-pubescent to pilose.
11. Terminal leaflets 0.1-0.3 times as wide as long, sparsely appressed-pubescent above, sometimes only along the midrib. .... *L. virginica*
11. Terminal leaflets 0.3-0.5 times as wide as long, appressed-pubescent to pilose above. .... *L. stuevei*

***Lespedeza angustifolia*** (Pursh) Ell. Sketch Bot. S. C. 2: 206 (1824). (T.: Clayton 934 [BM]).

*Lespedeza capitata* var. *angustifolia* Pursh Fl. Amer. Sept. 480 (1814).

*Lespedeza hirta* var. *angustifolia* Maxim. Acta Horti Petr. 2: 379 (1873).

*Lespedeza angustifolia* var. *brevifolia* Britt. Trans. N.Y. Acad. Sci. 12: 68 (1893). (T.: A. W. Chapman s. n., Florida [NY!]).

*Lespedeza angustifolia* f. *subvelutina* Fern. Rhodora 42: 457 (1940). (T.: M. L. Fernald & Bayard Long 9077, sphagnous bog about 1 mile n. w. of Dahlia, Greenville Co., Va., 20 August 1938 [GH!]).

*Lespedeza hirta* var. *intercursa* Fern. Rhodora 43: 572 (1941). (T.: M. L. Fernald, Ludlow Griscom, & Bayard Long 6622, argillaceous & siliceous swales & swaley thickets, south of Zuni, Isle of Wight Co., Va., 20, 22 Aug. 1936 [GH!]).

STEMS erect or ascending to about 1.8 m tall, short-appressed-pubescent or sometimes short-pilose; STIPULES filiform to narrowly subulate, 2-4 mm long; PETIOLES short, the terminal leaflets of the larger leaves mostly being at least 2 times longer than the combined lengths of their petiole and rachis and at least 3 times longer on leaves among the racemes; RACHISES of terminal leaflets of the petiolate leaves equaling or shorter than their petioles; TERMINAL LEAFLETS linear or narrowly oblong, the longer ones up to 6 cm long and .07-.25 times as wide, glabrous or occasionally appressed-pubescent above, if appressed-pubescent above, then stems short-pilose; STIPELS often present on some leaves, up to 1 mm long; RACEMES 1-3.5 times longer

than their subtending leaves and mostly bearing 10-26 flowers on the terminal 0.3-0.25 of the peduncle; BRACTEOLES mostly exceeding the base of the lobes of the calyx; PEDICELS 1-2 mm long; FLOWERS 5-7 mm long; CALYX 5-9 mm long, nearly chorisepalous, about equaling to much exceeding the mature pod which is easily visible between the lobes; COROLLA white or cream-colored; WINGS equaling or slightly exceeding the keel; STANDARD equaling or slightly exceeding the wings; PODS oval or elliptic, 3.5-5 mm long, moderately to densely appressed-pubescent; CLEISTOGAMOUS PODS commonly present, generally oval, 3-4 mm long, appressed-pubescent, exceeded by the calyx; SEEDS greenish-yellow to black.

Commonly on moist sand in open pine flatwoods, wet savannahs, along railroad tracks, and in open flood plains; occasionally on drier long leaf pine-scrub oak-wire grass sand ridges, particularly where disturbed; uncommonly on loam soils of pinelands, old fields, and roadsides; from Cape Cod along the Atlantic coast to southeastern Virginia and then both coastal and inland on the Atlantic Coastal Plain to northern Florida; disjunctions in the Georgia Piedmont (Walton Co.), western North Carolina (Henderson Co.), central Tennessee (Coffee, Warren Cos.) central Florida (Hillsborough Co.), and coastal Mississippi (Jackson Co.) (Fig. 2). Flowers from early August through mid-November.

N. K. B. Robson (pers. com.) has examined the holotype and said that it "agrees well" with the key characters.

Whether or not Britton (1893) intended to publish the name, *Lespedeza angustifolia* var. *brevifolia*, is uncertain; his only mention of that name is the following: "I have specimens of a peculiarly short-leaved form of the plant from Florida, communicated by Dr. Chapman, which may claim recognition as var. BREVIFOLIA." The type is a fragment of typical *L. angustifolia*, which Britton received from Chapman in April, 1891.

Most plants of *Lespedeza angustifolia* have leaflets glabrous above and scattered, appressed pubescence on their stems; however, some have both stems and leaflets densely short-pilose. Both types occur sympatrically throughout the range of the species. The latter, pilose type has been recognized as *L. angustifolia* f. *subvelutina*. If this form is

recognized, then it is reasonable that many other forms of equal insignificance in the genus should be named, causing a cumbersome and impractical classification.

Eight specimens annotated as *Lespedeza hirta* var. *intercursa* by Fernald, all of which were collected by Fernald in southeastern Virginia and deposited in GH and US, are typical *L. angustifolia*.

I have searched without success for *Lespedeza angustifolia* from the Choctawhatchee River in western Florida into eastern Louisiana. It occurs sympatrically with *L. capitata* in Florida. The occurrence of *L. capitata* westward near the Gulf coast into eastern Texas is in the same kinds of habitats occupied by both species in Florida while *L. angustifolia* occurs in old fields and roadsides and in frequently burned-over pineland in the Tallahassee Red Hills, an area resembling the Piedmont in soil and physiography. The disjunct populations in central Georgia and western North Carolina might owe their appearance to migrations inland along the flood plains of the major river systems. I hesitate to explain the occurrence of the populations in Tennessee. A. J. Sharp (in verb.) stated that several coastal plain species of other genera occur there. Relatively little morphological variation exists in the species, and no variation is associated with any particular geographic region or habitat.

Closely allied morphologically to *Lespedeza angustifolia* is *L. leptostachya*, an upland prairie endemic of the north-central states. The latter differs from *L. angustifolia* by having a uniformly appressed pubescence on both stems and leaves and densely so on the cleistogamous pods; flowers less densely arranged on the peduncles; narrower calyx lobes subtending the cleistogamous pods; and corolla sometimes light purple.

***Lespedeza capitata*** Michx. Fl. Bor.-Amer. 2: 71 (1803). (T.: Michaux [P]).

*Hedysarum umbellulatum* Walt. Fl. Car. 184 (1788), non L. 1753.

*Hedysarum frutescens* Muhl. in Willd. Sp. Pl. 3: 1193 (1803), non L. 1753.

- Hedysarum conglomeratum* Poir. in Lam. Encycl. 6: 416 (1804).  
*Lespedeza frutescens* Ell. Sketch Bot. S. C. 2: 206 (1824).  
*Lespedeza stuevei* DC. Prodr. 2: 349 (1825), non Nutt. 1818.  
*Lespedeza capitata* var. *sericea* Hooker Comp. Bot. Mag. 1: 23 (1835). (T.: Drummond 227, Jacksonville, herb. not indicated).  
*Lespedeza capitata* var. *vulgaris* T. & G. Fl. N. Amer. 1: 368 (1840).  
*Lespedeza velutina* Bickn. Torreyia 1: 102 (1901). (T.: E. P. Bicknell s. n., Woodlawn, N. Y., 28 Aug. 1898 [NY!]).  
*Lespedeza bicknellii* House Torreyia 5: 167 (1905). (T.: E. P. Bicknell s. n., Woodlawn, N. Y., 28 Aug. 1898 [NY!]).  
*Lespedeza capitata* var. *velutina* Fern. Rhodora 10: 51 (1908).  
*Lespedeza capitata* var. *stenophylla* Bissell & Fern. Rhodora 14: 92 (1912). (T.: F. E. McDonald s. n., open, dry ground, rare, Peoria, Peoria Co., Ill., Sept., 1904 [GH!]).  
*Lespedeza capitata* var. *typica* Fern. Rhodora 43: 576 (1941).  
*Lespedeza capitata* var. *stenophylla* f. *argentea* Fern. Rhodora 43: 579 (1941). (T.: H. A. Gleason s. n., sanddunes, Havana, Mason Co., Ill., Aug. 1903 [GH!]).

STEMS erect or ascending, to about 2 m tall, short appressed-pubescent to long-villous with scattered to dense hairs; STIPULES filiform to narrowly subulate, to about 7 mm long; PETIOLES short, the terminal leaflets of the larger leaves being at least 2 times longer than the combined lengths of their rachises and petioles and 3-9 times longer on leaves among the racemes; RACHISES of terminal leaflets rarely equaling and mostly longer than their petioles; TERMINAL LEAFLETS linear, oblong, narrowly rhombate, or elliptic, the longer ones up to 5 cm long and 0.1-0.45 times as wide, glabrous, glabrate, appressed-pubescent, or sericeous above; STIPELS rarely present; RACEMES capitate, included or exserted by a stout peduncle up to 1.5 times beyond their subtending leaves and generally bearing 14-30 flowers; PEDICELS 1-3 mm long; BRACTEOLES mostly exceeding the base of the lobes of the calyx; FLOWERS mostly 7-9 mm long; CALYX (7-)8-13 mm long, deeply lobed and nearly chorisepalous, the sinuses often very narrow, partially hiding and greatly exceeding the pod; COROLLA white or cream-colored; STANDARD longer than the keel and longer than to nearly equaling the wings; PODS narrowly elliptic, often somewhat asymmetrical, mostly 5-7 mm long; moderately pubescent; CLEISTOGAMOUS PODS common, elliptic, often somewhat asymmetrical, mostly 4-5 mm long, moderately pubescent; SEEDS greenish-yellow to black.

On upland prairies, sand dunes, old fields, dry roadsides, and well-drained, disturbed habitats throughout most of its range; in wet savannahs, open flood plains, and moist ditches along roads and railroads on the Atlantic Coastal Plain and distributed from Maine to northern Minnesota, central Kan-

sas, and the Texas Panhandle south to southeastern Georgia, western Florida, and southeastern Texas. Common in western prairies and in glaciated regions, less common on the Atlantic Coastal Plain, uncommon on the Appalachian Plateau (Fig. 3). Flowers from early July until mid October, mostly in August and September.

The type specimen is mounted on the same sheet with plants of *Lespedeza angustifolia* and intermediates, probably hybrids, between *L. angustifolia* and either *L. capitata* or *L. hirta* (see photograph of this sheet in Fassett, 1939). Fernald (1941) designated the shoot to the extreme right as the holotype of *L. capitata*.

As *Lespedeza capitata* is highly polymorphic, all of the synonyms published since 1835 reflect attempts to delimit various segregates of the species. The indument, the shape of the leaflet, and the length of the peduncle in relationship to the length of the subtending leaf are three of the more conspicuously variable characters. Fassett (1939, p. 102) planted seeds from different varieties of *L. capitata* and obtained offspring which segregated widely in pubescence and leaflet shape from both their parental plants and their sibs. He found that there would be eight morphological races (varieties) of *L. capitata* in Wisconsin by using the same characters of pubescence and leaflet-shape that were used in describing the four varieties recognized by Fernald. Pierce (1939) planted seeds from cleistogamously formed pods from two widely divergent specimens of *L. capitata* and obtained considerable variation among each of their progenies.

Little sense can be made of this variation until several hundred specimens of *Lespedeza capitata* from all parts of its geographic range are amassed for comparisons. After making such comparisons, two conclusions become evident: that populations of *L. capitata* near or above the southern limit of the Wisconsin glaciation are highly polymorphic and populations below this region are relatively uniform; and that certain forms of *L. capitata* are much more char-

acteristic of particular geographic regions than they are of other regions. This geographic variation is as follows:

1. *Lespedeza capitata* with nearly linear leaflets, tapering gradually from the middle to the base and apex, glabrous above, and stems with appressed trichomes (*L. c.* var. *stenophylla* Bissell & Fern.). This form occurs primarily from northeastern Indiana to eastern Iowa, south to southwestern Illinois; however, individuals have been collected in Rhode Island, Virginia and elsewhere.

2. *Lespedeza capitata* with narrowly elliptic or oblong leaflets, sericeous above, and with stems densely pubescent with very short, nearly straight trichomes, giving a silvery or cinnamon-colored appearance. (*L. c.* var. *capitata* sensu Gl.; var. *sericea* Hook., var. *typica* Fern.). This is the most common form and occurs frequently in all parts of the range of the species with the possible exception of the Appalachian Plateau. It is by far the most common type in western Iowa, South Dakota, Nebraska, Kansas, Oklahoma, and along the Atlantic Coastal Plain from North Carolina to Florida and westward to Louisiana. The populations from the Southeast are strikingly uniform. There is a slight tendency for southeastern plants to have oblong leaflets, while midwestern plants of this form have narrowly elliptic leaflets. In Iowa and Illinois many plants have been collected that resemble this form except that they have leaflets glabrous above. I have also observed a few populations in the Southeast with glabrous leaflets. Many plants from Ontario have exceptionally long, appressed trichomes on the leaflets, and these plants are not quite as silvery as others of this form and appear velutinous. These plants from Ontario and others like them, especially from coastal New England, have been named *L. velutina* Bickn. (*L. c.* var. *velutina* (Bickn.) Fern.). Prostrate forms of what might otherwise be called var. *velutina* have been observed by F. C. MacKeever (pers. com.) on Nantucket Island, Massachusetts. Attempts to grow living plants of this prostrate form which were sent to me by MacKeever were unsuccessful. Intergrades between plants that have been called var. *capitata* and var.

*stenophylla* are named *L. c. var. stenophylla f. argentea* Fern.

3. *Lespedeza capitata* with (narrowly) elliptic leaflets, glabrous above, stems with variable pubescence, usually (short-)villous (*L. c. var. vulgaris* T. & G.). This is the most common form in the Appalachians; however, I have examined only a few specimens from the southern Appalachians, and some of these have been anomalous forms with leaflets glabrous above.

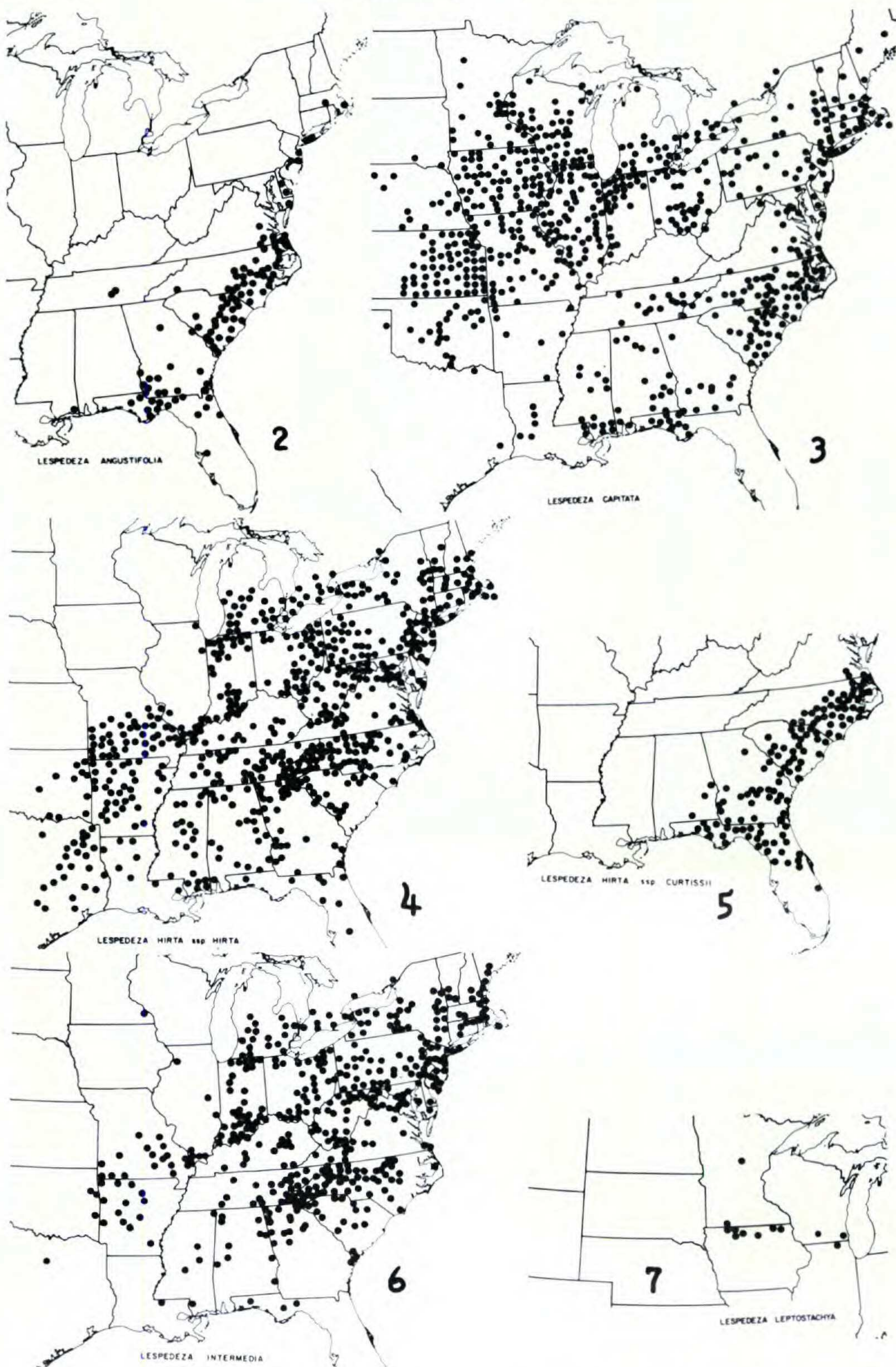
Intergradations between the various forms, the occurrence of many anomalous forms, and the heterogeneity encountered by Fassett (1939) and Pierce (1939) in progeny tests preclude the practicability of naming each form. Delimitation of forms would have to be arbitrary, a "waste basket" taxon would be necessary for anomalous forms, and identification would remain difficult for many plants.

An excellent character separating *L. capitata* from all other American species has been overlooked by previous authors: the distinctly greater length of the rachis as compared to the length of its petiole, especially of the larger leaves.

From the distribution of *L. capitata* (Fig. 3) it seems logical that the plants occurring in the northern part of the lower peninsula of Michigan arrived there recently via a post-glacial migration through Wisconsin and the upper peninsula of Michigan, not northward through southern Michigan. Heard (1962) reported a similar migration route for certain sphaeriid clams. Range extensions of *L. capitata* in Michigan in the future will be noteworthy.

***Lespedeza hirta* (L.) Hornem.** Hort. Reg. Bot. Hafn. 2: 699 (1815). STEMS erect or ascending, to 1.8 m tall, short-appressed-pubescent to long-villous; STIPULES filiform to subulate, 3-6 mm long; PETIOLES long, the terminal leaflets of the longer leaves being 1-2.5 times longer than the combined lengths of the petiole and rachis and mostly 2-4 times longer on leaves among the racemes; RACHISES of the longer terminal leaflets equaling or shorter than their petioles; TERMINAL LEAFLETS elliptic or (ob-)ovate, the longer ones up to 4 cm long and (0.45-)0.5-0.8 times as wide, glabrous, appressed-pubescent, or pilose above; STIPELS rarely present; RACEMES open, mostly 1.5-4 times





Figs. 2-7. Distribution by county of 6 taxa. Fig. 2, *Lespedeza angustifolia*; Fig. 3, *L. capitata*; Fig. 4, *L. hirta* subsp. *hirta*; Fig. 5, *L. hirta* subsp. *curtissii*; Fig. 6, *L. intermedia*; Fig. 7, *L. leptostachya*.

longer than their subtending leaves and bearing up to 16-44 flowers on the terminal half of the peduncle; BRACTEOLES extending to, or slightly beyond, the sinuses of the calyx; PEDICELS 1-2 mm long; FLOWERS 5-8 mm long; CALYX 6-12 mm long, lobed about 0.75 of its length or more, about equaling or slightly exceeding the pod which is easily visible between the lobes; COROLLA white or cream-colored; WINGS about equaling the standard and longer than the keel; PODS ovate or elliptic, 5-8 mm long, moderately to densely appressed-pubescent or appressed-pilose; CLEISTOGAMOUS PODS ovate or elliptic, mostly 5-7 mm long, moderately to densely appressed-pubescent or appressed-pilose, their calyces about equaling the pods; SEEDS mostly black, sometimes tan.

## KEY TO SUBSPECIES

Leaflets glabrous, strigose, or pilose above, not silvery; stems villous or pilose ..... subsp. *hirta*  
 Leaflets silvery with fine, dense, appressed hairs; stems appressed-pubescent or densely short-pilose ..... subsp. *curtissii*

**Lespedeza hirta** (L.) Hornem. subsp. *hirta*

*Hedysarum hirtum* L. Sp. Pl. 748 (1753). (T.: Clayton 510, Va. [LINN, microfiche!]).

*Lespedeza polystachya* Michx. Fl. Bor.-Amer. 2: 71 (1803).

*Lespedeza hirta* var. *sparsiflora* T. & G. Fl. N. Amer. 1: 368 (1840).

*Lespedeza hirta* var. *typica* Schindl. Bot. Jahrb. 49: 623 (1913).

*Lespedeza hirta* var. *calycina* Schindl. Bot. Jahrb. 49: 624 (1913). (T.: J. Reverchon s. n., Dallas Co., Tex., Aug., 1874 [GH!]).

*Lespedeza capitata* var. *calycina* Fern. Rhodora 43: 572 (1941).

In open, well-drained old fields, roadsides, sand dunes, and borders of woods from southern Maine, southern Ontario, southern Michigan, northeastern and southern Illinois, southern Missouri, and central Oklahoma south to central Florida and eastern Texas; rare on sandy soils of the Atlantic Coastal Plain (Fig. 4). Flowers from (June) mid-August through October.

Michaux cited *Hedysarum hirtum* L. as a synonym of *L. polystachya*, and his description and plate of *L. polystachya* are identifiable as *L. hirta* (L.) Hornem. Linnaeus (1753) cited Gronovius (1739, p. 173, *Trifolium fruticosum hirsutum* etc.) who, in turn, cited Clayton 510 which thus serves as the lectotype. Hornemann published *Lespedezia hirta*, incorrectly spelling the name of the genus but validly

publishing the combination. Hornemann described the species and cited the description by Muhlenberg (in Willdenow 1803) who cited *Hedysarum hirtum* L.

I have been unable to locate the type of *Lespedeza hirta* var. *sparsiflora* but have examined a photograph (GH) of it. This plant resembles a shade form of *L. hirta* or possibly the hybrid, *L. hirta* × *violacea*.

Cleistogamous pods occur much less frequently in this subspecies than in *Lespedeza hirta* subsp. *curtissii*. Comments on variation within subsp. *hirta* are included in the discussion under subsp. *curtissii*.

***Lespedeza hirta* subsp. *curtissii*** Clewell *Brittonia* 16: 75 (1964).

(T.: Clewell 532, sandy field along State hwy. 24, 4.5 mi. e. of Ocean, Carteret Co., N. C. 12 Sep. 1961 [IND!]).

*Lespedeza hirta* sensu Ell. *Sketch Bot. S. C.* 2: 207 (1824); non (L.) Hornem. (1815).

In wire grass — long leaf pine — turkey oak sand ridges, among sand pine of the Florida scrub, along roadsides and old fields in dry, sandy soils, and occasionally on loam in frequently burned-over pinelands from southeastern Virginia south along the Atlantic Coastal Plain to central Florida and west to southeastern Alabama and adjacent Florida (Fig. 5). Flowers from mid-August through October.

Plants of this coastal subspecies have been identified as *Lespedeza hirta* var. *appressipilis* Blake. The type of this variety has narrow leaflets, glabrous above, and is identifiable as *L. hirta* × *angustifolia*, and therefore the silvery plants of *L. hirta* from the coastal plain cannot be ascribed to it. Since the coastal plain plants of *L. hirta* are distinct morphologically, geographically, and ecologically from other plants of *L. hirta*, they were recognized as a subspecies (Clewell 1964a). Much of the apparent geographic overlap of these two subspecies (Figs. 4 & 5) reflects the irregular boundary between the Piedmont and the Atlantic Coastal Plain, as well as piedmont-like regions, such as the Tallahassee Red Hills, surrounded by coastal plain sands. I have studied populations of *L. hirta* on the coastal plain from

North Carolina to Louisiana and have discovered a few populations which include plants of both subspecies (Long Co., Ga., *Clewell* 923, 937, 939; Allendale Co., S. C., *Clewell* 863, 867, 868 (FSU)). These plants might owe their occurrence to dispersal by man, or they may represent local genetic variation in a subspecies that is generally much more uniform on the coastal plain.

Intergradation between the two subspecies may occur locally where their ranges meet; however, they often remain distinct. On deposit at FSU is a folder with plants from many populations of *Lespedeza hirta* from near the common boundary of the ranges of these subspecies, mostly collected in North Carolina. The nature of the variation encountered near this boundary may be examined from these specimens. Some plants from the pine barrens of New Jersey appear to be intergrades between the subspecies. If this intergradation were more extensive or if the silvery, coastal plain plants occurred with frequency within the range of subsp. *hirta*, then the variation would parallel that existing in *L. capitata*. If this situation occurred, then the identification of too many plants would be arbitrary, and to recognize distinct taxa would be impractical.

I have searched without success for plants of this subspecies near the Gulf Coast from Pensacola to New Orleans.

I can distinguish seven geographic races of *Lespedeza hirta*, which are not distinct enough to be recognized nomenclaturally but which may indicate the directions of evolution within the species. The first two races comprise subsp. *curtissii*, the others subsp. *hirta*.

1. Plants of subsp. *curtissii* from the Carolinas and northern Georgia have stems with erect trichomes, often with the tips of the trichomes bent upwards, and leaflets with trichomes longer than 0.25 mm above.
2. Plants from western Florida have stems appressed-pubescent and leaflets with trichomes mostly shorter than 0.25 mm above. Intergrades between this and the first race occur in southern Georgia and in northeastern and peninsular Florida.

3. Plants roughly from within the Gray's Manual range (New England south to Virginia and west to northern Arkansas) usually have stems densely villous and leaflets moderately appressed-pubescent above.
4. Plants from the same range as race 3 less commonly have stems moderately villous and leaflets glabrous above. Seeds from a plant of race 4 yielded offspring representing both forms (Clewell 1964a).
5. Off the coast of Massachusetts on Nantucket and Martha's Vineyard Islands plants of *L. hirta* resemble those of race 3 but with denser, longer trichomes. On these islands other species of *Lespedeza* tend to have more pronounced induments than elsewhere.
6. In Texas, plants have induments approaching that of subsp. *curtissii* but are not as silvery. In addition the calyces tend to be longer than in other areas, and the calyx lobes are slightly broader, tending to have a cuspidate, rather than an acute, apex. These plants have been recognized as *L. hirta* (or *L. capitata*) var. *calycina*. Fernald (1941, p. 579) discussed the typification of this name.
7. On the Piedmont of the Carolinas and Georgia and extending westward into nearly all of Alabama, Mississippi and southeastern Arkansas are plants with leaflets which are 10% narrower, on the average, (0.6 times as wide as long) and with shorter and denser trichomes on the stems than plants of races 3 and 4.

This variation within *Lespedeza hirta* is correlated with geological provinces and is not clinal. Most of this variation exists in the southern half of its range, while northern populations are uniform. This contrasts with *L. capitata* which is polymorphic in the North and uniform in the South. It seems plausible that geographic differentiation has occurred to a noticeable degree in *L. hirta*, and the activities of man in dispersing seeds and in modifying habitats have caused minor amounts of intergradation to occur between these races. In contrast, *L. capitata*, which is just as polymorphic as *L. hirta*, appears to be a species in which much

less racial differentiation has occurred, or if considerable differentiation had occurred previously, then it was primarily in the North and was mostly obliterated by glaciation.

***Lespedeza intermedia*** (S. Wats.) Britt. Trans. N. Y. Acad. Sci. 12: 63 (1893). (T.: *M. A. Howe s. n.*, Brattleboro, Windham Co., Vt., Sept., 1891 (GH!)).

*Hedysarum violaceum* Muhl. in Willd. Sp. Pl. 3: 1195 (1803).

*Lespedeza sessiliflora* Nutt. Gen. Amer. Pl. 2: 107 (1818).

*Lespedeza violacea* var. *sessiliflora* G. Don, Gen. Syst. 2: 307 (1832).

*Lespedeza reticulata* var. *sessiliflora* Maxim. Acta Horti Petrop. 2: 365 (1873).

*Lespedeza reticulata* S. Wats. Bibliog. Index 233 (1878), non Pers. 1807.

*Lespedeza stuevei* var. *intermedia* S. Wats. in Gray, Man. Ed. 6 141 (1890).

*Lespedeza frutescens* Britt. Mem. Torrey Bot. Club 5: 205 (1894).

*Lespedeza virginica* var. *sessiliflora* Schindl. Bot. Jahrb. 49: 614 (1913).

*Lespedeza frutescens* var. *acutifruca* Farwell, Rep. Mich. Acad. Sci. 22: 184 (1921).

STEMS erect or ascending, to about 1 m tall, appressed-pubescent; STIPULES filiform to narrowly subulate, mostly 2-4 mm long; PETIOLES long, the terminal leaflets of the larger leaves being 1-2.5 times longer than the combined lengths of the petiole and rachis and mostly 1-5 times longer on leaves among the racemes; RACHISES of longer terminal leaflets shorter than their petioles, often by 2 times; TERMINAL LEAFLETS oblong, elliptic, or narrowly ovate, the longer up to 4 cm. long and 0.3-0.55 times as wide, glabrous above or, rarely, glabrate along the midvein; RACEMES included or exserted up to 1.5 times beyond their subtending leaves and bearing 4-10 flowers; BRACTEOLES extending up to the sinuses of the calyx; PEDICELS 2-3 mm long; FLOWERS 5-7 mm long; CALYX 3-4.5 mm long and 0.3-0.5 times the length of the pod, lobed about half of its length; COROLLA purple; WINGS at anthesis (nearly) equaling the standard and distinctly longer than the keel; PODS ovate or elliptic, 5-7 mm long, short-appressed-pubescent; CLEISTOGAMOUS PODS commonly present, somewhat orbicular, 2.5-5(-6) mm long, the calyx being 1-2.5 mm long, mostly 0.2-0.33 times longer than the pod.

Dry roadsides, old fields, sand dunes, and borders of woods from southern Maine, southern Ontario, northern Indiana, central Missouri, and eastern Oklahoma south to

Georgia, western Florida, and eastern Louisiana with disjunctions in southeastern Minnesota, northwestern Illinois, and central Texas (Fig. 6). Flowers from late July through early October.

*Lespedeza intermedia* has long been called *L. frutescens* (L.) Britt., based on *Hedysarum frutescens* L. (T.: Clayton 174). Schindler (1913) identified Clayton 174 as what is now known as *L. violacea* on the basis of its long keel. Blake (1924) recognized the name, *L. intermedia*, and pursued its nomenclatural history. I agree with his position and will not be able to elaborate further on the typification of this species until such time as I am able to examine Clayton 174.

Both from the description and a photograph of the type of *Lespedeza frutescens* var. *acutifructa* I am unable to detect any differences between it and typical *L. intermedia*.

*Lespedeza intermedia* is remarkable for its lack of geographical variation.

A study of phenotypic plasticity in *L. intermedia* by means of reciprocal transplants showed that the size of the leaflets and the length of the internodes vary considerably according to the degree of shading but that pubescence and the floral characters are stable (Clewell 1964b). Leaflet shape may vary nominally but not to the point that it becomes significant in separating species. An understanding of this plasticity is important for accurate identification of species. From observations in the field and from comparisons of field- and greenhouse-grown shoots from the same rhizome, other species exhibit similar plasticity. I have examined a number of specimens which had been misidentified, evidently because they were shade forms of *L. virginica*, that superficially resembled plants of *L. intermedia*, or because they were shade forms of *L. intermedia* that resembled fruiting plants of *L. violacea*.

Chasmogamous and cleistogamous pods of *L. intermedia* can be compared in Fig. 1, a and b.

I have yet to see a specimen of, or visit a population of, *L. intermedia* in sandy pinelands in the Southeast. It is

uncommon in the Southeast except in the Blue Ridge and on the adjacent Piedmont.

**Lespedeza leptostachya** Engelm. in A. Gray, Proc. Amer. Acad. 12: 57 (1876). (T.: *C. E. Bessey s. n.*, Emmet Co., Iowa, 1871 [MO 146617!]). STEMS erect or ascending, to about 1 m tall, appressed-pubescent; STIPULES filiform to narrowly subulate, up to 5 mm long; PETIOLES short, the terminal leaflets of the larger leaves mostly 1-4 times longer than the combined lengths of the petiole and rachis and at least 4 times longer on leaves among the racemes; RACHISES of the longer leaves shorter than their petioles, often 4 times shorter; TERMINAL LEAFLETS linear or narrowly oblong, up to 3.5 cm long and 0.15-0.25 times as wide, appressed-pubescent above; RACEMES open, mostly 1.5-4 times longer than their subtending leaves, bearing up to about 16-30 flowers; FLOWERS 5-6 mm long; BRACTEOLES equaling or exceeding the bases of the lobes of the calyx; CALYX 4.5-5 mm long, nearly chorisepalous; COROLLA white to light purple; WINGS at anthesis equaling or slightly shorter than the standard and longer than the keel; CLEISTOGAMOUS PODS commonly present in open racemes, nearly orbicular, 3-4 mm long, densely pubescent, exceeded by the calyx, the calyx 4-6 mm long, nearly chorisepalous, the lobes very narrow, bracteoles greatly exceeding the base of the lobes of the calyx; SEEDS greenish-yellow to dark tan.

In upland prairies on gravelly moraines from central Minnesota south to northeastern Illinois and northwestern Iowa (Fig. 7). Flowers from late July through mid September.

Extant specimens of *Lespedeza leptostachya* mostly were collected before 1900, thereby reflecting the intolerance of this species to plowing and grazing. In 1964 I searched for it for two days in the northern tier of counties in Iowa along railroad tracks, in unplowed strips between fields, and in other prairie remnants, including where it had been collected previously. I discovered only one population, that being on a moraine of black, gravelly soil in Cayler Prairie, a preserved virgin prairie about 3 miles west of Lake Okoboji, Dickinson Co., Iowa. Roughly 500 plants grew in a three acre area, and a few plants were scattered elsewhere. *Lespedeza capitata* was also present. Recent plowing of remnant virgin tracts by farmers interested in capitalizing on the Federal Soil Bank Program probably has contributed to the pending extinction of *L. leptostachya*.



Gleason and Cronquist (1964, p. 197) reported *L. leptostachya* near Hawarden, Sioux Co., Iowa. In addition to the two collections from Wisconsin (Fig. 7) Fassett (1939) reported seeing specimens collected in the 1860's from Grant and La Crosse counties. He searched all four localities without discovering plants of *L. leptostachya*. He also saw specimens which I have not seen from northwestern Illinois and from southeastern Minnesota. Steyermark and Swink (1955) reported a recent collection from a dry, gravelly prairie in Cook Co., Illinois.

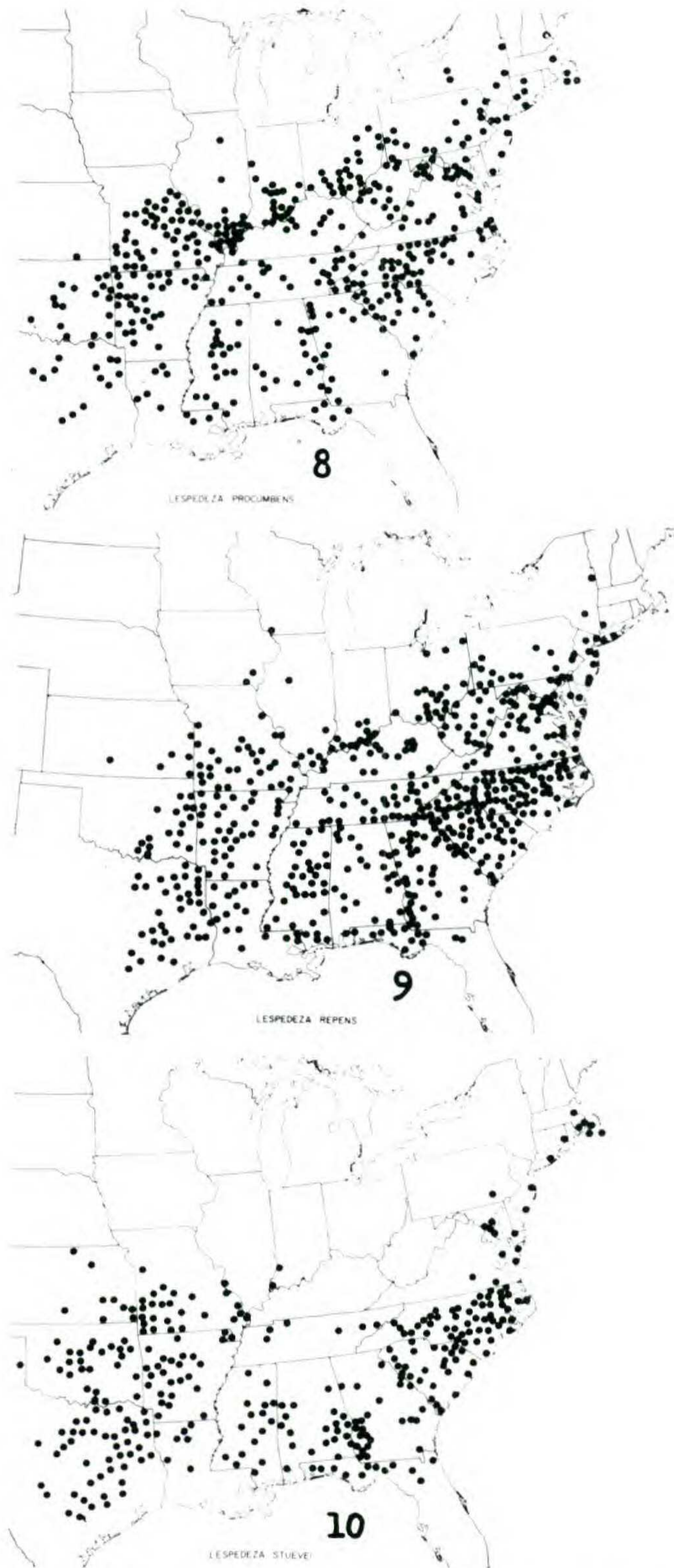
Most collections have cleistogamous pods. This degree of self-pollination helps explain the lack of variation between individuals.

See the comments under *Lespedeza angustifolia* for a comparison with that species.

***Lespedeza procumbens*** Michx. Fl. Bor.-Amer. 2: 70 (1803). (T: *A. Michaux* [P]).

STEMS procumbent, to about 1.8 m long, short-pilose to nearly villous, usually dense; STIPULES filiform to narrowly subulate, 2-4(-5) mm long; PETIOLES long, the terminal leaflets of the larger leaves mostly 0.5-1.5 times longer than the combined lengths of their petioles and rachises and mostly 1.5-5 times longer on leaves among the racemes; RACHIS of the longer terminal leaflets equaling or shorter than their petioles; TERMINAL LEAFLETS ovate, sometimes elliptic or oblong, the longer ones up to 2.5 cm long and 0.45-0.7 times as wide, sparsely appressed-pubescent, pilose, or rarely densely pilose above; RACEMES mostly 2-7 times longer than their subtending leaves, occasionally 2 per node, bearing up to 8-12(-14) flowers scattered along the terminal half of the peduncle; PEDUNCLES pilose; PEDICELS 0.5-1.5(-2) mm long; FLOWERS 5-9 mm long; BRACTEOLES extending about to the base of the lobes of the calyx; CALYX 2-4 mm long and extending (nearly) half the length of the pod, lobed 0.5-0.7 of its length; COROLLA purple; WINGS at anthesis about as long as the keel and shorter than the standard; STANDARD equaling or slightly longer than the keel; PODS elliptic, about 5 mm long, short appressed-pubescent to nearly glabrous; CLEISTOGAMOUS PODS commonly present, in axillary clusters or clustered near the apexes of peduncles, elliptic to orbicular, 3.5-5 mm long, mostly sessile, their calyces 1-2 mm long and 0.2-0.3 times the length of the pod; SEEDS greenish-yellow to dark tan.

Dry roadsides, old fields, and open woods from southern New England, central Illinois, and central Oklahoma south to Georgia, western Florida, and eastern Texas (Fig. 8).



Figs. 8-10. Distribution by county of 3 taxa. Fig. 8, *Lespedeza procumbens*; Fig. 9, *L. repens*; Fig. 10, *L. stuevei*.

Flowers from (mid-June) late August through September.

Mlle. A. Lourteig kindly compared a typical plant of *L. procumbens* from Brown Co., Indiana, with the type in the Michaux Herbarium (P) and wrote me that, "it matches perfectly." She said it did not match a plant of typical *L. repens* which I had also included. On the Atlantic Coastal Plain I have seen *L. procumbens* only on clays and loams, not on soils of pure sand. I have not detected any geographic variation in *L. procumbens*.

There is close resemblance between *Lespedeza procumbens* and *L. repens*. While *L. procumbens* has stems and peduncles pilose, typically 8-12 flowers per raceme, and cleistogamous pods either pedunculate or axillary, *L. repens* has stems and peduncles sparsely short-appressed-pubescent, typically 4-8 flowers per raceme, and cleistogamous pods commonly pedunculate. Pubescence alone is quite sufficient in distinguishing them.

***Lespedeza repens* (L.) Bart.** Prod. Fl. Phil. 2: 77 (1817) in part. (T.: Clayton 85, Va. [BM]).

*Hedysarum repens* L. Sp. Pl. 749 (1753).

*Hedysarum prostratum* Muhl. in Willd. Sp. Pl. 3: 1200 (1803).

*Lespedeza prostrata* Nutt. Gen. Amer. Pl. 2: 107 (1818).

**STEMS** procumbent or sometimes ascending when young, to about 1 m long, sparsely short-appressed-pubescent; **STIPULES** subulate, 1.5-3(-4) mm long; **LEAVES** generally of the same size on a stem, gradually becoming smaller towards the tip with an occasional axillary bud expanding into one very small leaf; **PETIOLES** long, the terminal leaflets of the larger leaves being mostly 1-4 times longer than the combined lengths of their petioles and rachises and mostly 2-5 times longer on leaves among the racemes; **RACHISES** of the longer terminal leaflets equaling or shorter than their petioles; **TERMINAL LEAFLETS** membranous, elliptic to (ob-)ovate, the longer ones up to 2.5 cm long and 0.33-0.8 (mostly 0.45-0.7) times as wide, glabrous or sparsely appressed-pubescent above, green in color below; **RACEMES** mostly 2-7 times longer than their subtending leaves, sometimes 2 per node, bearing 4-8(-12) flowers; **PEDUNCLES** filiform, appressed-pubescent; **PEDICELS** 0.5-3(-4) mm long; **BRACTEOLES** extending up to the base of the lobes of the calyx; **FLOWERS** 5-7(-8) mm long; **CALYX** 2-4 mm long, lobed about half its length and extending (nearly) half the length of the mature pod; **COROLLA** purple; **WINGS** about equaling or shorter than the keel; **STANDARD** equaling or slightly exceeding the keel; **PODS** ovate or orbicular, sometimes slightly asymmetrical, 4-5 mm long,

sparsely short-appressed-pubescent; CLEISTOGAMOUS PODS commonly present, orbicular or occasionally somewhat elliptical, rarely asymmetrical, 3-4(-5) mm long, mostly pedunculate, sometimes a few pods in axillary clusters, their calyces being up to 0.25-0.5 times the length of the mature pod; SEEDS greenish-yellow.

Dry roadsides, old fields, borders of woods, and sandy pinelands from Long Island, Ohio, central Missouri and south-central Kansas south to northern Florida and eastern Texas, also along the Mississippi River to southwestern Wisconsin (Fig. 9). Flowers from (mid-April) late May through October.

The lectotype of *Lespedeza repens*, Clayton 85 (BM), was cited by Gronovius (1739, p. 86) as *Hedysarum caulibus procumbentibus*, etc. Gronovius also cited a plant from Ceylon under this name by referring to a plate in Dillenius' Hortus Elthamensis. The plant from Ceylon is not a *Lespedeza* but might be an *Alysicarpus* (Robson, pers. com.) or a *Desmodium* (Britton 1893). Robson, who kindly examined Clayton 85 for me, questioned the name, *Lespedeza (Hedysarum) repens*, because Linnaeus' description matches more closely the plant from Ceylon than Clayton 85 which lacks obcordate leaflets described by Linnaeus. Two possibilities may explain this discrepancy; over the years the lower leaflets, which are often the only obcordate ones in *L. repens*, were lost from Clayton 85, or Linnaeus based his description on additional plants that he did not cite, such as 921-42 in the Linnaean Herbarium. Since Linnaeus referred to Clayton 85 by citing Gronovius and since he described *H. repens* as occurring only in Virginia, then I recognize the Linnaean name as legitimate. Britton (1893) and Schindler (1913, p. 593) both examined Clayton 85 and recognized it as the lectotype.

Plants of *Lespedeza repens* in the southeastern states often bloom in the late spring. These plants may have at least some of their stems ascending while in flower. Later in the year continued growth of these same stems will provide sufficient weight to make them lie procumbent. Otherwise, I have detected no geographic variation in *L. repens*; however, I have seen an occasional specimen from the lower

Mississippi Valley with fruits resembling those of *L. violacea* in size and shape.

Plants of *Lespedeza repens* are easily distinguished from *L. violacea* in the field; however, pressed specimens of these species in fruit are often misidentified. The most reliable character in separating such specimens is the ratio between the length of the mature, cleistogamous pod and its subtending calyx. In *L. repens* (Fig. 1e) the calyx extends at least a quarter of the way up the pod (not including the style). In *L. violacea* (Fig. 1d) the calyx reaches up to two tenths of the way up the pod, usually much less. Other characters are: length of stipules — 1.5-3 mm in *L. repens*, up to 2.5-6 mm long in *L. violacea*; cleistogamous pods — mostly pedunculate, 3-4 mm long, and symmetrical in *L. repens*, mostly axillary, 3-7 mm long, and often asymmetrical in *L. violacea*; leaves generally of one size, though gradually becoming somewhat shorter towards the apex of the stem in *L. repens*, leaves of two or more distinct sizes, attributable to one or few smaller leaves of different sizes occurring in the axils of the larger leaves in *L. violacea*.

*Lespedeza stuevei* Nutt. Gen. Amer. Pl. 2: 107 (1818). (T.: W. Stüve [PH.]).

STEMS erect or ascending, to about 1.8 m tall, densely appressed-pubescent or pilose; STIPULES filiform to narrowly subulate, up to 5 mm long; PETIOLES long, the terminal leaflets of the larger leaves being 0.5-2 times longer than the combined lengths of the petiole and rachis and mostly 1-5 times longer on leaves among the racemes; RACHISES of the longer terminal leaflets shorter than their petioles; TERMINAL LEAFLETS elliptic or oblong, the longer ones up to 4 cm long and 0.3-.55 times as wide, uniformly appressed-pubescent, occasionally pilose, rarely sparsely appressed-pubescent along the midvein above; RACEMES included or exserted up to 1.5 times beyond their subtending leaves and bearing up to (6-)8-14 flowers; PEDICELS up to 2 mm long; BRACTEOLES extending about to the base of the lobes of the calyx; FLOWERS 4.5-6.5 mm long; CALYX 3-5 mm long, extending (nearly) half the length of the pod; lobed about 0.5-0.6 of its length, COROLLA purple; WINGS at anthesis (nearly) equaling the standard and distinctly longer than the keel; PODS ovate or elliptic, mostly 5-6 mm long, sparsely short-appressed-pubescent to densely appressed-pilose; CLEISTOGAMOUS PODS commonly present, ovate or elliptic, mostly 4-6 mm long, sparsely short-appressed-pubescent to densely appressed-pilose, the calyx being 0.3-0.4 times the length of the pod.

Dry roadsides and old fields, borders of dry woods, and open sandy pinelands along the Atlantic Coast from Massachusetts to North Carolina, then west to southern Indiana and eastern Kansas and south to northern Florida and central Texas (Fig. 10). Flowers from (June) August through October.

*Lespedeza stuevei* was named for W. Stüve and was spelled *L. stüvei* by Nuttall (1818) and some subsequent authors. Article 73 of the International Code of Botanical Nomenclature (Lanjouw 1961) necessitates the orthographic change to *stuevei*. N. K. B. Robson (pers. com.) stated, "*Medicago caule erecto vix ramoso, racemo dense spicato terminatrice* (Gronov., Fl. Virgin.: 86) appears to belong to this species, according to the Clayton specimen in our Herbarium (BM). Linnaeus did not take it up in Sp. Pl."

Geographic variation within *Lespedeza stuevei* is pronounced and recognition of two subspecies is perhaps warranted. Plants from the Ozark Plateau and from along the Atlantic coast above North Carolina have long trichomes. The stems of these plants are often pilose, and the otherwise brown pods at maturity are often hoary with appressed trichomes. Plants from much of Texas and from the southeastern states, particularly in dry pinelands, have exceptionally fine, short, appressed trichomes which, though dense, may barely be discerned without a lens. Specimens of these southeastern plants sometimes have been mistaken for *L. intermedia*. I have seen two nearly glabrous plants of *L. stuevei*: *Kral 8159* (LAF) and *Cocks in 1900* (NO) from Jackson and Rapides Parishes, respectively, Louisiana.

Plants of *Lespedeza stuevei* or *L. virginica* with the larger terminal leaflets about 0.3 times as wide as broad must be identified arbitrarily. Most collections of such plants are probably hybrids. I have examined many populations in which both species were present, and in nearly all populations the great majority of plants can be identified easily to one or the other species. Undoubtedly these species are closely related, both phenetically and genetically, but there is little reason to consider lumping them.

*Lespedeza texana* Britt. in Small, Fl. S. E. U. S. 641 (1903). (T.: A. Arthur Heller 1914, Kerrville, Kerr Co., Tex., 19-26 June 1894 [NY!]).

STEMS erect up to about 1.5 dm, the more distal portions procumbent, up to 1.5 m long, appressed-pubescent to short-pilose; STIPULES filiform, the longer ones (3-)4-8 mm long; PETIOLES long, the terminal leaflets of the larger leaves being 1-3 times longer than the combined lengths of their petioles and rachises and mostly 2-5 times longer on leaves among the racemes; RACHISES of the longer terminal leaflets mostly shorter than, or about equaling, their petioles; TERMINAL LEAFLETS firm-textured, elliptic, the longer ones up to 3.5 cm long and 0.35-0.55 times as wide, glabrous, glabrate, or sometimes short-pilose, above, gray-green to white below; RACEMES mostly 2-7 times longer than their subtending leaves, sometimes 2 or 3 per node, bearing 4-8(-10) flowers; PEDUNCLES appressed-pubescent or short-pilose; PEDICELS (1-)3-5 mm long; BRACTEOLES extending to the base of the lobes of the calyx; FLOWERS 5.5-8.5 mm long; CALYX 2-4 mm long, and extending (nearly) half the length of the pod, lobed about half its length; COROLLA purple; WINGS shorter than or about equaling the keel; STANDARD equaling the keel; PODS ovate, 6-7 mm long; sparsely short-appressed-pubescent; CLEISTOGAMOUS PODS commonly present, 4-6.5 mm long, ovate, sometimes asymmetrical, axillary or pedunculate, their calyces being 0.1-0.3 times the length of the pod.

In thin, rocky soil of scarp woodlands on or near the Edwards Plateau in central Texas; disjunction in eastern Coahuila, Mexico (Fig. 11). Flowers from mid-June through mid-October.

I did not recognize *Lespedeza texana* as a species until I saw living plants of it in natural populations. Its most distinctive characters are not preserved in dried specimens. Its long stipules, up to 4-8 mm, often break off when dry. The somewhat coriaceous texture to the leaflets is easily overlooked on mounted specimens. The greenish-gray to white undersurface of the leaflets contrasts with the green undersurfaces in related species; this color escapes attention or is disregarded until seen in the field. The habit, which is entirely unlike that of any other American species, is the most striking character in the field, yet it cannot be recognized from pressed specimens. The stems are erect up to about 15 cm high, the next 10 cm are arching, and the rest of each stem, which may extend over a meter in length, is trailing. Other distinctive characters are the long, cleistog-

amous pods, 4-6.5 mm long (as compared to 3-4 mm long in *L. repens*), and the keel and wing petals which are about of equal lengths (in contrast to *L. violacea*). I have seen only one plant in flower, and it was greenhouse-grown. Its flowers were uniformly dark purple and were more deeply pigmented than the flowers of plants of the other species.

Although I do not know *Lespedeza texana* in the field as well as I know the other species, I believe that *L. texana* tends to be less weedy than the other species and does not invade roadsides. It is essentially allopatric; I have collected *L. procumbens* with it in Robertson Co., Texas, and know of no other sympatric populations. The collection from Coahuila is *Palmer 249* (PH) from Mt. Caracol, 21 miles southeast of Monclova.

***Lespedeza violacea*** (L.) Pers. Syn. 2: 318 (1807). (T.: *Kalm* [LINN 921-41]).

*Hedysarum frutescens* L. Sp. Pl. 748 (1753), non Muhl. in Willd. 1803.

*Hedysarum violaceum* L. Sp. Pl. 749 (1753).

*Hedysarum divergens* Muhl. in Willd. Sp. Pl. 3: 1196 (1803).

*Lespedeza divergens* Pursh, Fl. Amer. Sept. 2: 481 (1814).

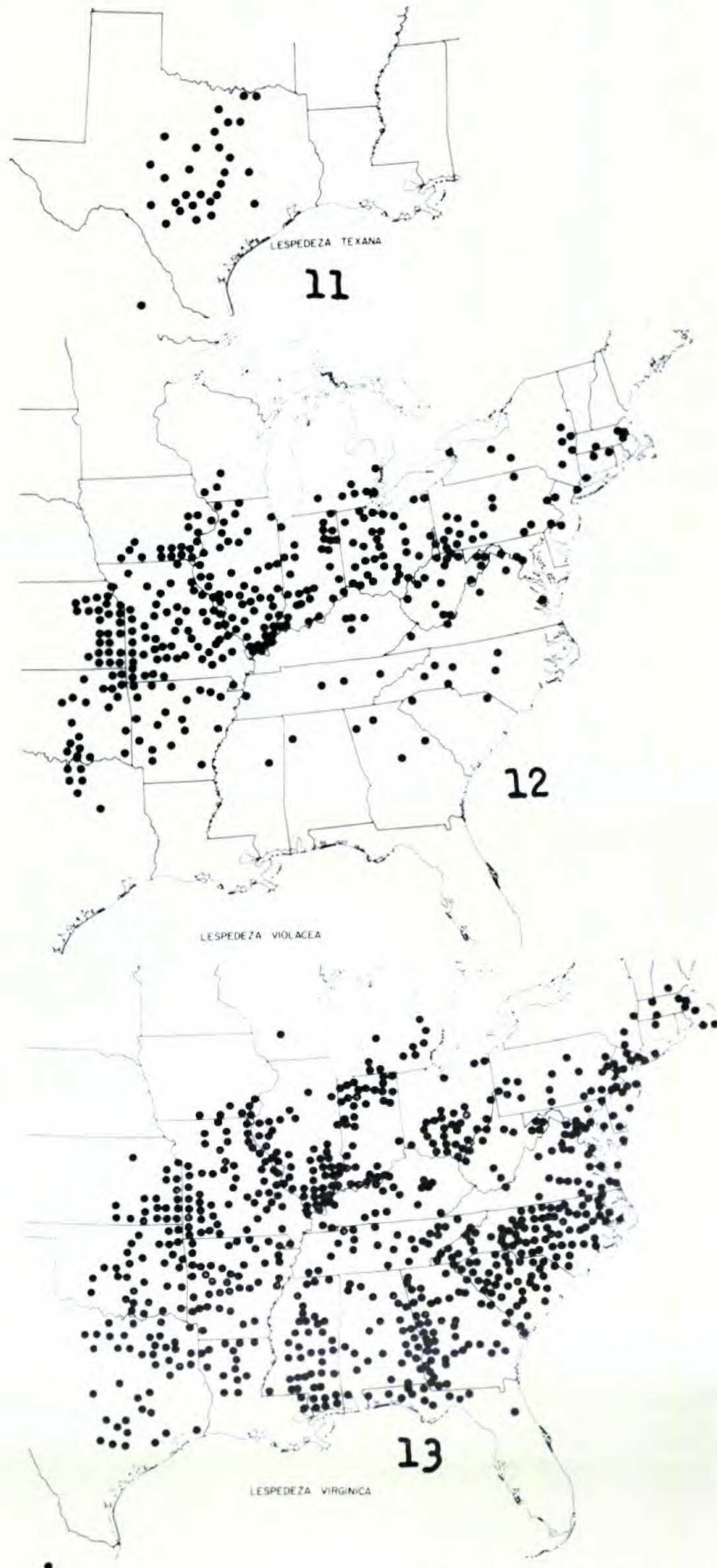
*Lespedeza violacea* var. *divergens* G. Don, Gen. Syst. 2: 307 (1832).

*Lespedeza violacea* var. *prairea* Mackenz. & Bush, Trans. Acad. Sci. St. Louis 12: 14 (1902). (T.: *B. F. Bush 93*, common, Lee's Summit, Jackson Co., Mo., 2 Sept. 1895 [MO!, isotype NY!]).

*Lespedeza prairea* Britt. in Small, Fl. S. E. U. S. 641 (1903).

STEMS erect to weakly ascending, to about 0.7 m tall, sparsely appressed-pubescent; STIPULES filiform, up to 2.5-6 mm long; LEAVES generally of several different sizes on a stem with axillary buds commonly expanding into single, smaller leaves of various sizes; PETIOLES long, terminal leaflets of the larger leaves mostly 0.5-1.5 times longer than the combined lengths of their petiole and rachis and mostly 1-4 times longer on leaves among the racemes; RACHISES of the longer leaflets shorter than their petioles; TERMINAL LEAFLETS membranous, elliptic or ovate, the longer ones up to 4.5 cm long and 0.35-0.7 times as wide, glabrous or sometimes glabrate above, light green or green below. RACEMES exserted up to 2-5 times beyond their subtending leaves or, uncommonly, all included within their subtending leaves, often 2 per node, bearing 4-6(-8) flowers; PEDUNCLES filiform, appressed-pubescent; PEDICELS 0.5-3 mm. long; BRACTEOLES extending about to the base of the lobes of the calyx; FLOWERS 5.5-9 mm long; CALYX 3-6 mm long, about half the length of the mature pod; lobed about 0.6 of its length, COROLLA purple; WINGS and STANDARD distinctly shorter than,





Figs. 11-13. Distribution by county of 3 taxa. Fig. 11, *Lespedeza texana*; Fig. 12, *L. violacea*; Fig. 13, *L. virginica*.

or, uncommonly, nearly equaling the keel; PODS 5-7.5 mm long, glabrate, sometimes asymmetrical; CLEISTOGAMOUS PODS commonly present, elliptic to orbicular, sometimes asymmetrical, (3-)4.5-6 mm long, usually axillary, sometimes (short-) pedunculate, their calyces being up to 0.2 (rarely 0.25) times the length of the pod, mostly shorter.

In dry old fields, roadsides, prairies, and open woods from southern New England to southern Wisconsin and eastern Kansas south to central Georgia and northeastern Texas (Fig. 12). Flowers from (mid-July) August through September.

Determining the correct name and its typification for this species is difficult, and I cannot feel certain that *L. violacea* is the legitimate name, since I have not seen the pertinent specimens in European herbaria. I am dependent upon the discussion by Schindler (1913, pp. 591-593) and personal correspondence received from N. K. B. Robson and D. Ockendon. *Lespedeza violacea* is based on *Hedysarum violaceum* L. Linnaeus' description of *H. violaceum* fits *L. intermedia*, *L. procumbens*, and *L. repens*, as well as *L. violacea*. He referred to Gronovius (1739, p. 87) where *Clayton 103* is cited. This specimen is identifiable as *Psoralea psoraloides* (Walt.) Cory (= *P. melilotoides* Michx.). Linnaeus probably did not have *Clayton 103* before him when he described *H. violaceum*. More than likely he described *H. violaceum* from the Kalm specimen, 921-41, in the Linnaean Herbarium. This sheet bears Linnaeus' annotation, "violaceum", and the number, 21, which corresponds to the number of *H. violaceum* in *Species Plantarum*. I was unable to determine from the microfilm of 921-41 whether this specimen was of *L. violacea* or was a shade form of *L. intermedia*. Britton (1893) and Schindler (1913) both identified it as *L. intermedia* of this paper. For purposes of nomenclatural stability I am assuming that it is *L. violacea* until I have occasion to examine it in person. If this specimen is not what I now call *L. violacea*, then *L. frutescens*, based on *Hedysarum frutescens* L., would be the next name in priority. In describing *H. frutescens*, Linnaeus referred to Gronovius (1739, p. 174) who cited *Clayton 174* (BM), a specimen identified as *L. violacea* by Schindler (1913) on

the basis of the long keel. The epithet, *frutescens*, has been applied to *L. capitata* and more recently to *L. intermedia* by Britton (1894), Robinson & Fernald (1908), and others. I would consider *L. frutescens*, applied to what I am now calling *L. violacea*, a *nomen confusum* and would reject it under Article 69 of the Code of Nomenclature (Lanjouw 1961). *Lespedeza divergens* (Muhl.) Pursh would then become the name of this species.

By noting the year of collection of specimens identified as *L. prairea* deposited at NY, I assume that Britton had 17 collections before him when he first recognized them as a species. These plants, as well as the type, resemble closely typical *L. violacea* as it occurs in full sunlight. Field observations indicate that the lengths of the internodes and leaflets are highly variable, depending upon the amount of shading, just as was determined in *L. intermedia*. Four plants of *L. violacea* grown in full sunlight from seeds of *Clewell 1563* had internodes and leaflets about three times shorter than did the parent plant which was collected in a woods in Martin Co., Indiana.

See the discussion under *L. repens* for a comparison with that species. Chasmogamous and cleistogamous pods can be compared in Fig. 1, c and d.

*Lespedeza violacea* is common west of the Mississippi River and fairly common north of the Ohio River. It becomes increasingly rare in the southeastern states and to my knowledge has not been collected on the sandy soils of the Atlantic Coastal Plain.

***Lespedeza virginica* (L.) Britt.** Trans. N. Y. Acad. Sci. 12: 64 (1893). (T.: Clayton 191 [BM]).

*Medicago virginica* L. Sp. Pl. 778 (1753).

*Hedysarum reticulatum* Muhl. in Willd. Sp. Pl. 3: 1194 (1803).

*Lespedeza sessiliflora* Michx. Fl. Bor.-Amer. 2: 70 (1803).

*Hedysarum sessiliflorum* Lam. Encycl. 4: 414 (1804).

*Lespedeza reticulata* Pers. Syn. 2: 318 (1807), non S. Wats. 1878.

*Lespedeza angustifolia* Darl. Fl. Cestr. 81. (1826), non Pursh 1814.

*Lespedeza violacea* var. *reticulata* G. Don, Gen. Syst. 2: 307 (1832).

*Lespedeza violacea* var. *angustifolia* T. & G. Fl. N. Amer. 1: 367 (1840).

*Lespedeza reticulata* var. *angustifolia* Maxim. Acta Horti Petrop. 2: 366 (1873).

*Lespedeza virginica* var. *typica* Schindl. Bot. Jahrb. 49: 614 (1913). STEMS erect or ascending, to about 1.6 m tall, appressed-pubescent or sometimes short-pilose; STIPULES filiform to narrowly subulate, up to 6 mm long; PETIOLES long, the terminal leaflets of the larger leaves being 0.5-1.5 times longer than the combined lengths of their petioles and rachises and mostly 1.5-3 times longer on leaves among the racemes; RACHISES of the longer terminal leaflets generally half as long as their petioles; TERMINAL LEAFLETS linear or narrowly oblong, the wider ones sometimes narrowly lanceolate, the longer ones up to 4 cm long and 0.1-0.3 times as wide, sparsely appressed-pubescent, sometimes only along the midvein, or rarely glabrous above; RACEMES included or exserted up to 1.5 times beyond their subtending leaves and bearing 4-8(-14) flowers; PEDICELS up to 2 mm long; BRACTEOLES extending about to the base of the lobes of the calyx; FLOWERS 5-7 mm long, CALYX 2-4 mm long, and extending (nearly) half the length of the pod; lobed about half its length, COROLLA purple; WINGS nearly equal or slightly shorter than the standard and slightly longer than the keel; PODS 4-7 mm long, sometimes slightly asymmetrical, minutely to densely appressed-pubescent; CLEISTOGAMOUS PODS commonly present, 4-5 mm long, sometimes slightly asymmetrical, their calyces being 0.2-0.3 times the lengths of the pods.

In dry old fields, roadsides, prairies, borders of woods, and open sandy pineland from central New England, southern Michigan, southern Iowa, and eastern Kansas south to northern Florida and eastern Texas; disjunctions in southern Wisconsin and central Nuevo León, Mexico (Fig. 13). Flowers throughout August and September.

N. K. B. Robson (pers. com.) said that the lectotype, *Clayton 191* (BM), is identifiable as *Lespedeza virginica* as I have described the species. Darlington (1826) published a name, "*L. angustifolia* ? Ell." which from description is most likely a hybrid between *L. capitata* and a purple flowered species. I have cited this name with *L. virginica*, because Torrey and Gray (1840) evidently used Darlington's citation for the basionym of *L. violacea* var. *angustifolia*, and Maximowicz (1873) cited the Torrey and Gray name as a synonym of his *L. reticulata* var. *angustifolia*. It is clear from the discussion by Torrey and Gray that they were describing *L. virginica*.

The Mexican collection is *C. H. Muller 2820*, scattered in open pine forest, LaTrinidad, Municipio de Montemorelos, Nuevo León, 18 Aug. 1936 (LL, MO, TENN). Of the plants

of *Lespedeza virginica* that I have examined from Tennessee north into the Ohio River Valley, many appear to have the denser pubescence of *L. stuevei*. These plants have been identified as *L. virginica* var. *deamii* M. Hopkins; an example is *Bartley & Pontius*, Jackson Co., Ohio, 1935 (OS). Although rare or absent in much of this region, *L. stuevei* may have been more common there recently, and the pubescent forms of *L. virginica* might represent the products of introgression with *L. stuevei*.

#### PUTATIVE HYBRIDS

Natural hybridization in *Lespedeza* has been suspected by many authors, including Mackenzie (1907), Wiegand & Eames (1925), Palmer & Steyermark (1935), and Fernald (1950). Of the 55 possible interspecific hybrid combinations between the 11 native American species, 19 are not expected because the ranges of three, *L. angustifolia*, *L. leptostachya*, and *L. texana*, do not overlap with the ranges of some of the other species and each other. Of the remaining 36 possible combinations, I have observed 17 in natural populations and have identified 16 additional combinations from dried specimens (Table I, Figs. 12-16).

The high frequency of populations containing hybrids of *Lespedeza* makes the genus suitable for the study of hybridization in the field by autumn classes in taxonomy. In trying to locate hybrids, one should familiarize himself with the species in a large population. Such populations are common on top of road embankments in hilly country. If both white- and purple-flowered species are present, pink-flowered plants are likely to be hybrids. If both procumbent and erect species are present, plants with weakly ascending stems may be hybrids. All species have calyces extending either about half the way up the chasmogamous pods or exceeding the pod. Plants with calyces extending about two thirds of the way up the pods usually are hybrids.

Since a few hybrids occur in nearly every population, it is not surprising that some have been named as species or infraspecific taxa. Sixteen names have been applied to various hybrid combinations by other authors; I have recog-

TABLE I

The Naturally Occurring Putative Hybrids of *Lespedeza*, Their Relative Abundance, and the Number of Progeny Tests Completed on Each.

Hybrid	Figure	Abundance	Progeny Tests
angustifolia × capitata	15	rare	
angustifolia × hirta	16	common	1
angustifolia × repens	15	rare	
angustifolia × stuevei	15	rare	2
angustifolia × virginica	—	rare	
capitata × hirta	16	abundant	
capitata × intermedia	15	rare	
capitata × leptostachya	16	rare	
capitata × repens	17	rare	
capitata × stuevei	15	rare	
capitata × violacea	14	common	
capitata × virginica	16	common	
hirta × intermedia	14	abundant	8
hirta × procumbens	16	abundant	2
hirta × repens	18	common	1
hirta × stuevei	17	abundant	4
hirta × violacea	15	rare	
hirta × virginica	18	abundant	5
intermedia × procumbens	17	rare	1
intermedia × repens	15	rare	
intermedia × stuevei	18	rare	
intermedia × violacea	14	rare	
intermedia × virginica	14	rare	
procumbens × repens	15	rare	
procumbens × stuevei	18	rare	
procumbens × violacea	15	rare	
procumbens × virginica	17	abundant	
repens × stuevei	17	rare	
repens × violacea	17	rare	
repens × virginica	18	abundant	2
stuevei × violacea	17	rare	
stuevei × virginica	18	abundant	
violacea × virginica	15	common	

} identifications  
very tentative

Relative abundance probably reflects the abundance of the parental species more than their genetic compatibility.

nized only 12 "good" taxa, including subspecies. Most of the previous taxonomic difficulties encountered in *Lespedeza* have stemmed from a failure to recognize hybrids. Only a small portion of the difficulties in conceptualizing and

identifying the "good" taxa during this century have resulted from phenotypic plasticity (c.f. *L. violacea*, sun and shade forms) or from failure to delimit taxa precisely.

Whether or not any of these hybrid combinations merit nomenclatural recognition is a matter of opinion. I choose not to recognize any hybrids with binomials or infraspecific names. If one combination is named, then the remaining 31 combinations logically should be named. The recognition of even one hybrid would tend to confuse specific delimitations and make the construction and use of keys difficult at best. If only the common hybrids are named, or if only the rather distinctive hybrids from contrasting parental species are named, then the decision as to which are common or which are distinctive becomes arbitrary, not biological, because most possible hybrids exist, many with frequency. It could be argued that those hybrids that are similar could be lumped under one name. For example, the name *Lespedeza* × *nuttallii*, based on *L. hirta* × *intermedia*, could also apply to *L. hirta* × *stuevei* and *L. hirta* × *virginica*. I do not favor this procedure, because the binominal becomes meaningless in denoting the parental species involved. Furthermore, the decision as to what hybrid combinations should be applied to which binomial would be arbitrary. For example, enough similarity exists to include plants of *L. capitata* × *intermedia* under two names, *L.* × *nuttallii* and *L. simulata* (based on *L. capitata* × *virginica*). Even if only one hybrid combination was applied to one name, in practice it would be impossible to identify many hybrids correctly. For instance, many notomorphs of *L. hirta* × *intermedia*, *L. hirta* × *stuevei*, and *L. hirta* × *virginica* are indistinguishable from one another. Regardless of how many epithets are applied to hybrids, each clutters the nomenclature, since formulas can be employed just as easily. The only possible justification for applying names to hybrids in *Lespedeza* would be to ease the filing of herbarium specimens, but hybrids can be filed conveniently in one or more covers at the end of the genus.

The only hybrid combinations that are treated further are

those which have been given previous nomenclatural recognition.

***Lespedeza angustifolia* × *hirta***

*Lespedeza hirta* var. *oblongifolia* Britt. Trans. N. Y. Acad. Sci. 12: 66 (1893). (T.: *J. B. Brinton s.n.*, sandy pine barrens, Egg Harbor, Atlantic Co., N. J., 10 Aug. 1879 [NY!]).

*Lespedeza oblongifolia* W. Stone, Pl. So. New Jersey 509 (1912).

*Lespedeza hirta* var. *apressipilis* Blake, Rhodora 26: 32 (1924). T.: *A. H. Curtiss 639*, dry pine barrens, Duval Co., Fla., Oct. [US 517623!]).

Plants that I assign to *Lespedeza hirta* subsp. *curtissii* have been called *L. hirta* var. *apressipilis* Blake by Fernald (1941, 1950), Wilbur (1963), and others. Blake cited three specimens of var. *apressipilis*, two of which matched his diagnosis and my concept of subsp. *curtissii*. The third specimen, *Curtiss 639* which he assigned as the type, does not resemble subsp. *curtissii* or match his diagnosis. Its leaflets are glabrous above (not silvery with dense, fine, appressed trichomes), and the leaflets are narrowly obovate and slightly less than half as wide as long (not ovate and more than half as wide as long). It appears to be a notomorph of *L. angustifolia* × *hirta*. Blake's choice of a type for var. *apressipilis* was unfortunate, because it necessitated another name for the taxon he delineated.

***Lespedeza capitata* × *hirta***

*Lespedeza longifolia* DC. Prodr. 2: 349 (1825). (T.: *Bonjean, s. n.* in Louisiana [G]).

*Lespedeza capitata* var. *longifolia* T. & G. Fl. N. Amer. 1: 368 (1840).

*Lespedeza capitata* var. *hirtiformis* Fern. Rhodora 40: 437 (1838). (T.: *M. L. Fernald & Bayard Long 7481*, border of dry woods, Zion's Church, n. w. of Whaleyville, Nansemond Co., Va., 17 Sept. 1937 [GH!]).

*Lespedeza hirta* var. *longifolia* Fern. Rhodora 43: 585 (1941).

*Lespedeza hirta* var. *dissimulans* Fern. Rhodora 43: 585 (1941). (T.: *M. L. Fernald & Bayard Long 13966*, valley of the Penobscot River, dry thickets on clay terraces, Veazie, Penobscot Co., Maine, 9 Sept. 1916 [GH!, ex NEBC]).

Without having seen the *Bonjean* specimen, it is problematic whether the epithet, *longifolia* DC., is a synonym of the above formula or of *Lespedeza capitata*. A photograph



of this specimen in the Gray Herbarium resembles *L. angustifolia* × *hirta*, but *L. angustifolia* has been collected no further west than Mississippi. That DeCandolle recognized *L. angustifolia*, *L. capitata*, and *L. hirta*, as well as *L. longifolia*, is evidence that the Bonjean collection represents something else than the first three species mentioned. From DeCandolle's descriptions I am not convinced, though, that he understood *L. angustifolia* or the variation in *L. capitata*. Torrey and Gray (1840), Britton (1893) and others have extended *L. capitata* var. *longifolia* to include certain typical specimens of *L. capitata*. Fernald (1941) and others have considered the epithet *longifolia* DC. in its various combinations synonymous with the epithet *oblongifolia* Britt. in its combinations. The latter epithet I believe applies to *L. angustifolia* × *hirta*. The Drummond specimen from Louisiana (photograph in Fernald, 1941) appears to be *L. capitata* × *hirta*, in that it has the elongate rachis of *L. capitata* and the elongate raceme of *L. hirta*.

Fernald cited only the type and an isotype with his diagnosis of *Lespedeza capitata* var. *hirtiformis*, and he re-assigned these specimens to *L. capitata* var. *calycina* (Schindl.) Fern. three years later (Fernald 1941). Of the four specimens at the Gray Herbarium which were annotated by Fernald as *L. hirta* var. *dissimulans*, one is *L. capitata* and the rest are probably *L. capitata* × *hirta*, including the type.

***Lespedeza capitata* × *violacea***

*Lespedeza manniana* Mackenz. & Bush, Trans. Acad. Sci. St. Louis 12: 15 (1902). (T.: *Kenneth K. Mackenzie s. n.*, frequent on dry hills, Swope Park, Jackson Co., Mo., 23 Aug. 1896 [NY!]).

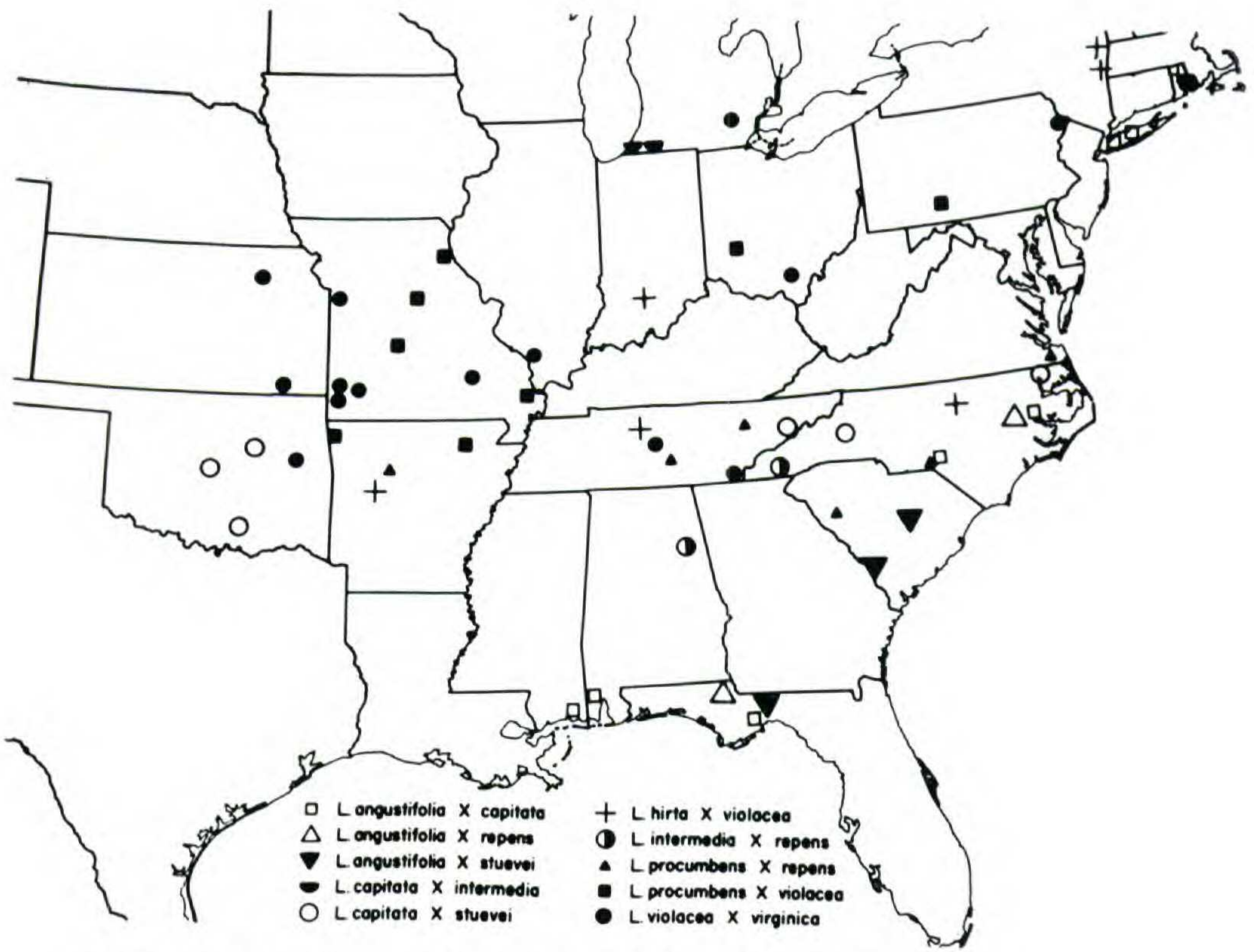
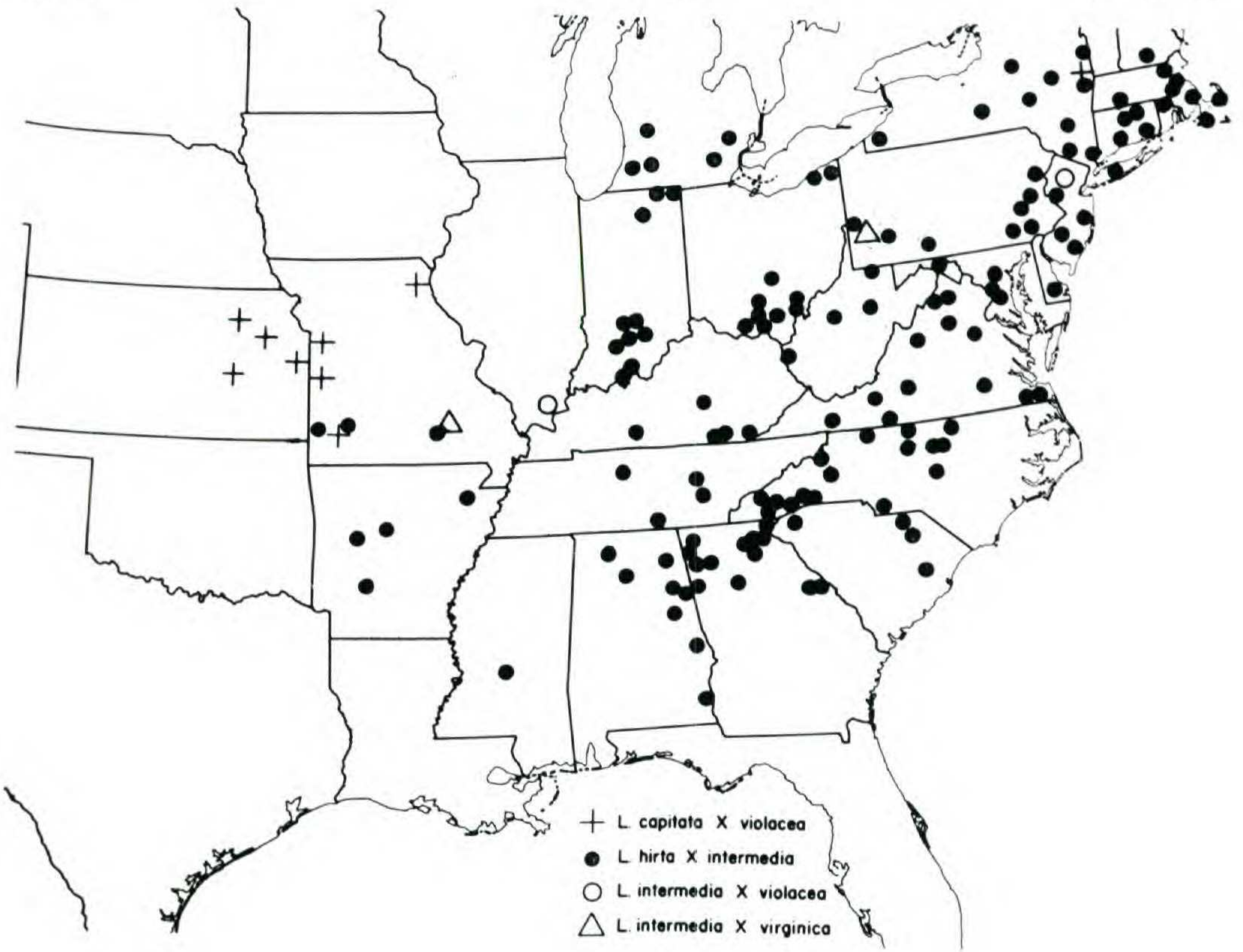
*Lespedeza nuttallii* var. *manniana* Gl. Britt. & Brown Fl. 2: 434 (1952).

***Lespedeza capitata* × *virginica***

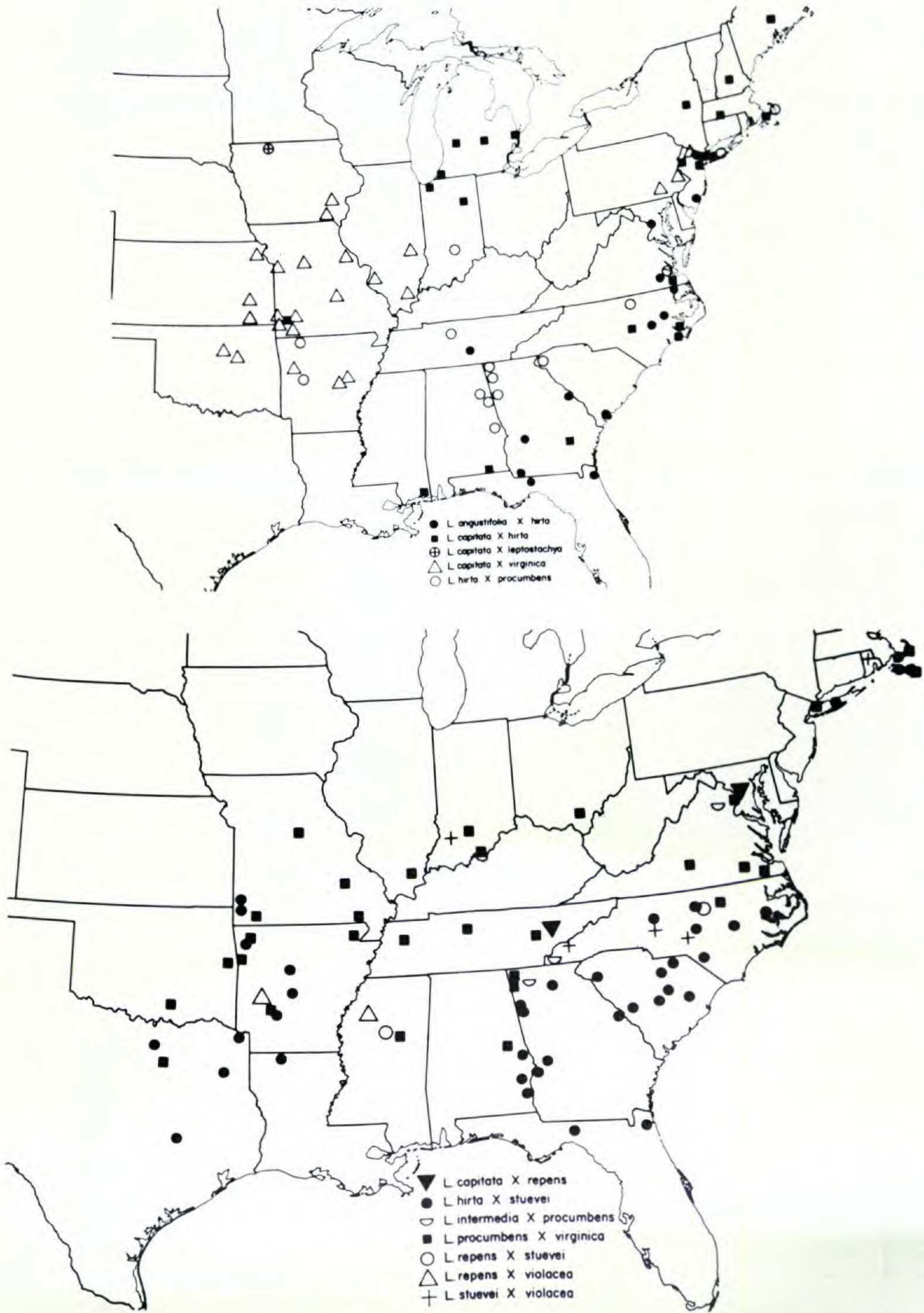
*Lespedeza simulata* Mackenz. & Bush, Trans. Acad. Sci. St. Louis 12: 15 (1902). (T.: *B. F. Bush s. n.*, Newton Co., Mo., 29 Aug. 1893 [MO 146712!]).

***Lespedeza hirta* × *intermedia***

*Lespedeza nuttallii* Darl. Fl. Cestr. Ed. 2, 420 (1837). (T.: *Nuttall s. n.*, Sussex Co., Delaware [PH!]).



Figs. 14-15. Distribution by county of 14 hybrids.



Figs. 16-17. Distribution by county of 12 hybrids.

*Lespedeza virgata* Nutt. in 'T. & G. Fl. N. Amer. 1: 368 (1840), non DC. 1825. (T.: Nuttall s. n., cited above).

*Lespedeza intermedia* var. *hahnii* Blake, *Rhodora* 26: 32 (1924).

T.: *W. L. Hahn s. n.*, vicinity of Bascom, Ohio Co., Ind., Aug., 1906 [US 609738!]).

*Lespedeza intermedia* f. *hahnii* M. Hopkins, *Rhodora* 37: 265 (1935).

*Lespedeza nuttallii* var. *nuttallii* Gl. Britt. & Brown Fl. 2: 434 (1952).

The epithet, *hahnii*, has been applied to notomorphs approaching *L. intermedia*.

The results of biosystematic studies on *Lespedeza hirta* × *intermedia* are reported in Clewell (1964b). Fox (1945) claimed that *Hayden 9908* (GH!, TEX!) from Davis Co., Iowa, was probably introduced to the experimental farm on which it was collected.

#### ***Lespedeza procumbens* × *virginica***

*Lespedeza brittonii* Bickn. *Torreyia* 1: 103 (1901). (T.: *Bicknell s. n.*, Bronxville, Bronx Co., N. Y., 16 Sept. 1893 [NY!]).

*Lespedeza procumbens* var. *elliptica* Blake, *Rhodora* 26: 26 (1924). (T.: *S. F. Blake 8621*, in meadow, Lorton, Fairfax Co., Va. 16 Sept. 1923 [US 1111347!]).

#### ***Lespedeza stuevei* × *virginica***

*Lespedeza stuevei* var. *angustifolia* Britt. *Trans. N. Y. Acad. Sci.* 12: 63 (1893) non Pursh 1814. (T.: *J. K. Small & A. A. Heller, s. n.*, Heilig's Mill P. O., Rowan Co., N. C., 13-18 Aug. 1891 [NY!]).

*Lespedeza stuevei* var. *neglecta* Britt. *Mem. Torrey Bot. Club* 5: 206 (1894). (T.: *Small & Heller*, cited above).

*Lespedeza neglecta* Mackenz. & Bush, *Trans. Acad. Sci. St. Louis* 12: 17 (1902).

*Lespedeza stuevei* f. *angustifolia* M. Hopkins, *Rhodora* 37: 265 (1935).

*Lespedeza virginica* f. *deamii* M. Hopkins, *Rhodora* 37: 265 (1935). (T.: *C. C. Deam 55645*, in a wooded sand ridge in the Herschel Green woods about 4 miles north of Washington, Davies Co., Ind., 19 Sept. 1934 [GH!; isotype IND!]).

Britton (1893) described *Lespedeza stuevei* var. *angustifolia* Britt. as having "leaves linear or linear-oblong", not "oval, oblong, or suborbicular" as in typical *L. stuevei*. The following year Britton (1894) renamed such plants as *L. stuevei* var. *neglecta*, possibly because the epithet, *angustifolia*, had been used previously in the genus as *L. angustifolia* (Pursh) Ell. He did not assign types or cite specimens when publishing these names, and no specimens at NY are marked as types of these names. One specimen (*Small &*

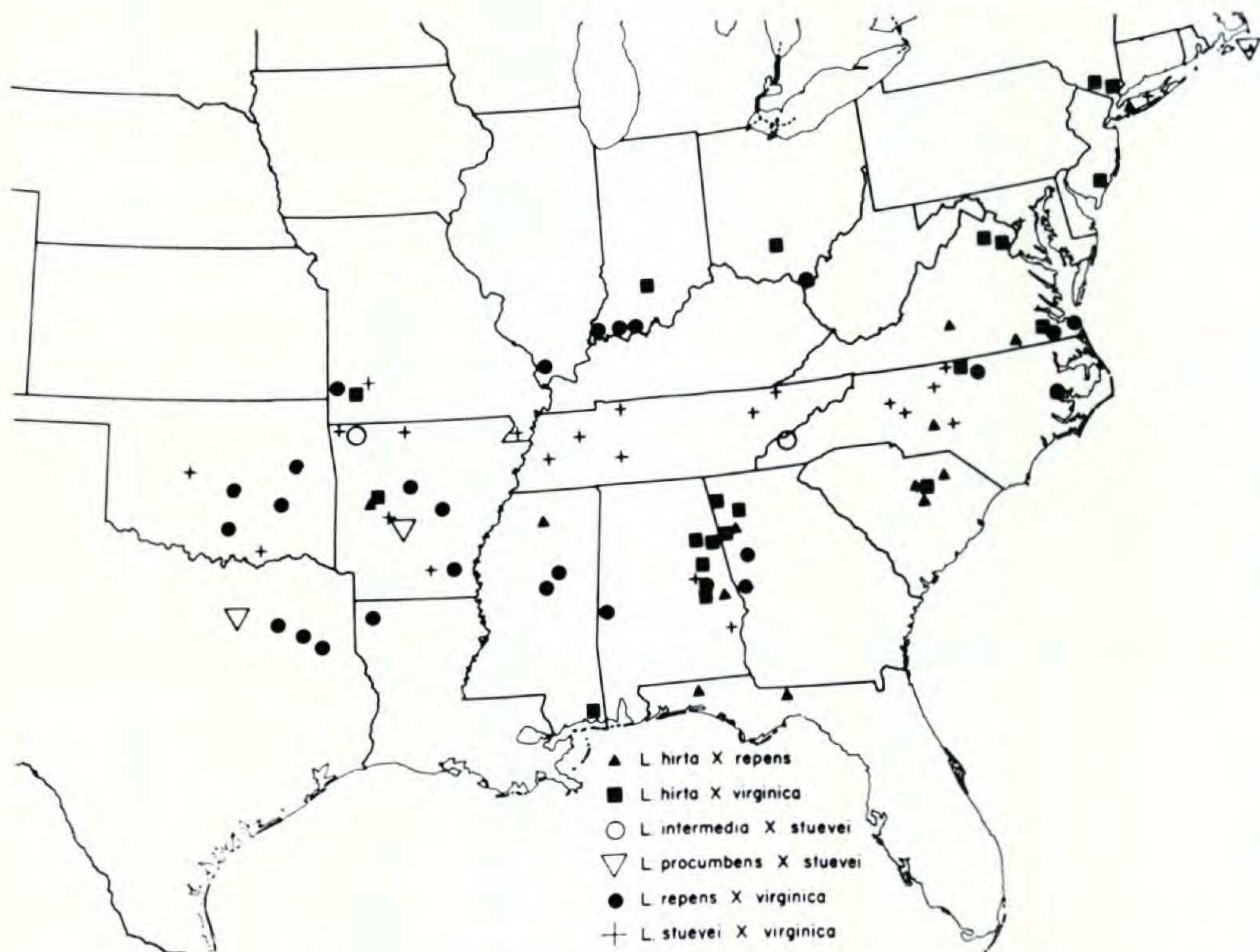


Fig. 18. Distribution by county of 6 hybrids.

*Heller*, Rowan Co., N. C., 1891 (NY!) bears the following annotations in Britton's hand: *L. stuevei* var. *angustifolia* Britton; *L. stuevei neglecta* Britton; *L. neglecta* (Britton) Mack. & Bush. A second specimen (*Beardslee & Kofoid*, Swain Co., N. C., 1891 (NY!)) Britton annotated as *L. neglecta* Mack. & Bush. Both specimens fit Britton's description of *L. stuevei* var. *angustifolia*, and both are probably *L. stuevei* × *virginica*. I have chosen the *Small & Heller* specimen as the type of these names.

Hopkins (1935) distinguished *L. stuevei* f. *angustifolia* (based on *angustifolia* Britt.) from *L. virginica* f. *deamii* on minute differences in pubescence and lengths of petioles, both being variable characters.

*Lespedeza violacea* × *virginica*

*Lespedeza acuticarpa* Mackenz. & Bush, Trans. Acad. Sci. St. Louis 12: 16 (1902). (T.: *Mackenzie* 449, frequent, limestone barrens at Swope Park, Jackson Co., Mo., 13 Sept. 1901 [MO 148552!]).

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