

AN ABSTRACT OF THE THESIS OF

CHERYL ALISON CROWDER for the degree of MASTER OF SCIENCE
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Title: THE ECOLOGY AND REPRODUCTION OF SOPHORA LEACHIANA PECK
(FABACEAE)
Abstract approved: *Redacted for Privacy* -
Dr. Kenton L. Chambers

The goal of the study was to collect data on the ecology and reproduction of Sophora leachiana in order to help explain the rarity and restricted range of this species. There are 13 known populations of S. leachiana, occurring in a 29 by 6.4 km area in the Siskiyou Mountains of southwestern Oregon. The species acts as a primary colonizer in disturbed areas, especially following fires. When the tree canopy becomes re-established, Sophora may persist vegetatively as rhizomes and aerial shoots, but it ceases flowering.

Most populations occur on south or west slopes, in a region of low summer rainfall. Adaptations of the plant include xeromorphic leaflet anatomy, leaflet movements to avoid high insolation, and flowering that depends on high levels of incident light.

The reproductive cycle of Sophora was analyzed, beginning with meiosis and extending through pollen maturation, pollination, seed and fruit development, seed anatomy, seed germination, and predators of the plant. Two chromosome levels were found, tetraploid (n=18) and hexaploid (n=27). Meiosis was more regular in the former than in the latter, but the hexaploids showed a higher percentage of stainable pollen. Species of Bombus are the principal pollinators, but low

levels of insect activity were seen in Sophora populations. The flowers show a typical xenogamous syndrome, including protandry, high pollen-ovule ratio, and low rate of spontaneous selfing. In controlled experiments, only intrapopulation pollinations were successful.

In a vast majority of the flowering, the pistils show no development past anthesis. Maturation of the fruit is limited to favorable sites of high insolation and low plant density. Even in maturing fruits, an average of 79 percent of the seeds abort prior to maturity. Seed abortion appears to result from endosperm failure, due perhaps to self-incompatibility. The mature seeds have the characteristic anatomy of "hard" leguminous seeds and probably are adapted to survive the heat of forest fires. In a series of tests, normal-appearing Sophora seeds showed an average germination rate of only 58 percent. Growth of the seedlings was variable, and some abnormalities were observed. The inflorescences of plants in nature were often parasitized by thrips, which caused premature dropping of the flowers. Larvae of a species of moth were a common predator in some Sophora populations, attacking both the vegetative parts and inflorescences. The rust, Uromyces hyalinus, was a plant pathogen of low incidence but sometimes high density on individual shoots.

Sophora leachiana does have vigorous asexual reproduction by stout rhizomes; but because the species eventually dies out as the forest matures, it must depend on seeds in order to persist in an area. The species is probably a Tertiary relic, depleted in biotypes and possessing a restricted gene pool. Current seed production may be adequate for continuance in the small area Sophora now occupies, but it does

not allow for expansion of the species range. Forest clear-cuts are a favorable habitat for the growth and flowering of S. leachiana. However, forest management practices that would destroy the vegetative clones and hence end seed reproduction in these sites would probably lead to the extinction of the species.

Best scan available.

The Ecology and Reproduction of
Sophora leachiana Peck (Fabaceae)

by

Cheryl Alison Crowder

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THE ECOLOGY AND REPRODUCTION OF SOPHORA LEACHIANA PECK (FABACEAE)

LITERATURE REVIEW

Taxonomic History of Sophora and Relationships of Sophora leachiana

Fabaceae is the third largest angiosperm family, containing about 590-690 genera and 12000-17000 species (Harborne et al., 1971). This family is further broken down into 11 tribes (Gleason, 1952). Characteristics of Sophoreae tribe, in which Sophora is the type genus, include free stamens or stamens united only at the base, and pinnately compound leaves. Free stamens are not unique to the Sophoreae, being also characteristic of the Podalyrieae and Adesmia in the Hedysareae (Harborne et al., 1971). Separation of the Sophoreae and the Podalyrieae is easy because the latter have ternately compound or rarely simple leaves. The possession of free stamens in a family where strongly united diadelphous or monodelphous stamens are more common, suggest a close affinity of these tribes. Both have a chromosome base number of $x = 9$ (Sophoreae in part; $x = 9, 11, 13, 14$) which is unique among legumes with the exception of Lespedeza (Senn, 1938). Other tribes possess base numbers of 6, 7, 8, 10, 11, or 12. These two characteristics, along with biochemical data collected by Alston and Turner (1963) suggest that the Sophoreae and Podalyrieae are closely related and represent early offshoots of the phyletic line of the Fabaceae (Turner and Fearing, 1959).

The Sophoreae tribe consists of about 48 genera in tropical and subtropical areas of all continents (Harborne et al., 1971). The genus Sophora includes trees, shrubs and perennial herbs; distinguishing

traits include alternate imparipinnate leaves, calyx campanulate with five subequal lobes, and a papilionaceous, glabrous corolla ranging from white to yellow or blue to violet. The style is straight and the stigma minutely capitate-penicillate. Of the approximately 75 species in the genus (Rudd, 1968), fewer than ten are herbaceous. Three of these herbaceous species are in North America:

Sophora leachiana Peck, S. nuttalliana B. L. Turner, and S. stenophylla A. Gray. The remaining herbaceous species are Asiatic: S. flavescens Ait., and S. pachycarpa C. A. Mey. The taxonomy of the last species is subject to debate. Yakovlev (1967) includes them as subspecies of S. alopecuroides L. however, in other treatments the former is maintained as a separate species (Komarov, 1945; Davis, 1970) and the latter two are treated as varieties of one species (Davis, 1970) or only as one species (Komarov, 1945).

S. alopecuroides subsp. jaubertii (Spach) Borza

S. alopecuroides subsp. tomentosa (Bliss) Yakovl.

S. alopecuroides L. subsp. alopecuroides

Table 1 lists for each herbaceous species the important synonyms encountered in the current literature, references for plant descriptions, and distribution and habitat descriptions.

The genus Sophora was first described by Linnaeus (1753, 1754) based on six species including S. alopecuroides. This species was later designated as the lectotype for the genus (Britton and Brown, 1913).

Table 1: Synonyms, Descriptive References, Habitat and Distribution, of the Herbaceous Species of Sophora.

S. alopecuroides L. subsp. alopecuroides

Descriptions: Linnaeus, 1753; Lamarck, 1806; deCandolle, 1825; Ledebour, 1833; Tutin et al. 1968; Davis, 1970.

Habitat: edges of fields, banks, rarely on sand-dunes, sea level to 1750m (Davis, 1970) "riverline and lacustrine meadows, tugaic soils (Bottomland complex with woods, bushes, and meadows in river floodplains in Soviet Central Asia.) less frequently in steppes and deserts with a high water table; as a weed among crops and in rubbish-strewn places; in dense but not extensive thickets ... especially in depressions and in river valleys on more or less saline soils with a good supply of water at least periodically". (Komarov, 1945).

Distribution: Greece, S. Russia, SW and E Asia (Davis, 1970).

S. alopecuroides subsp. jaubertii (Spach) Borza = S. jaubertii Spach = S. prodanii Anders

Descriptions: Komarov, 1945; Yakovlev, 1967; Tutin et al., 1968; Davis, 1970.

Habitat: In scrub and open communities, wood margins, sometimes a weed in fields 30-730m elevation (Komarov, 1945; Davis, 1970).

Distribution: Syria, Turkey, Romania, Russia.

S. alopecuroides subsp. tomentosa (Bge. ex Boiss.) Yakovl.

Description: Yakovlev, 1967; Davis, 1970.

Habitat: edges of fields, banks, rarely sand-dunes, sea level to 1750m (Davis, 1970).

Distribution: Iraq, Iran, Afghanistan, NW Pakistan, SW and E Asia. (Davis, 1970).

S. flavescens Ait. = S. angustifolium Sieb. and Zucc.

Description: Lamarck, 1806; Lee, 1935; Komarov, 1945.

Table 1: (Continued)

Habitat: "Scrub on mountain slopes, valleys of rivers and lakes especially of sandy soil; sometimes a weed of cultivated fields" (Komarov, 1945).
 "Open moist grassy situations by sides of streams; 6700 ft. elevation" (Diels, 1912). Elevation 1,000 - 5,000 ft (Lee, 1935).
 Streamside slopes; at the edges of broad-leaved woods (Yakovlev, 1967).

Distribution: Russia (Yakovlev, 1967).

S. leachiana Peck

Description: Peck, 1941, 1954; Rudd, 1972.

Habitat: Sparsely wooded slope above Galice Creek. (Peck, 1941)

Distribution: Southwestern Oregon, USA.

S. nuttalliana B. L. Turner = S. sericea Nutt. non Andr. = S. carnosa (Pursh) Yakovl. (incorrect name)

Description: Nuttall, 1818; deCandolle, 1825; Rafinesque, 1832; Torrey and Gray, 1840; Stevens, 1948; Rudd, 1972.

Habitat: Prairies, dry and/or rocky hillsides (Wooton and Standley, 1915; Tidestrom, 1925; Rudd, 1972; van Bruggen, 1976); at higher elevations in grama grasslands (Correll and Johnson, 1970); in cultivated fields (Kearney and Peebles, 1960); on saline soils of dry hillsides or along roads (Yakovlev, 1967); igneous or calcareous alluvial soils (Turner, 1959); at elevations of 800-3200m (Yakovlev, 1967; Rudd, 1972); or 4,000-7,000 ft. (Kearney and Peebles, 1960).

Distribution: In Great Plains from South Dakota and Wyoming to Arizona and Texas, USA; into northern Mexico. (Rudd, 1972).

Table 1: (Continued)

S. pachycarpa C. A. Mey

Description: Lee, 1935; Komarov, 1945.

Habitat: Desert foothills in loess and sandy soils; can form dense thickets over large areas as component of wormwood and ephemeral desert communities; commonly found as weed in rubbish-strewn places, increasing with overgrazing and spreading rapidly in plowrows. Populations usually occur in washout holes and depressions as the plant is dependent on a raised water table (Komarov, 1945).

Distribution: Central Asia (Komarov, 1945).

S. stenophylla A. Gray

Description: Rudd, 1972.

Habitat: Plains, dry hillsides and canyons (Wooton and Standley, 1915; Tidestrom, 1925); in sand-dunes and rocky areas (Goodding, 1939; Rudd, 1972) from 5,500-7,000 ft. elevation (Kearney and Peebles, 1960).

Distribution: S. Utah, Nevada, New Mexico, NE Arizona, USA.

The genus has been the subject of several taxonomic treatments. Auguste deCandolle (1825) divided the genus into only two sections -- Eusophora with ten entirely free stamens and Pseudosophora with slightly connate diadelphous stamens. Sophora flavescens was included as one of the ten species comprising the section Eusophora. The latter section was made on only one species -- S. alopecuroides. Sophora nuttalliana (as S. sericea) along with the arborescent S. acuminata were tentatively placed in this section. Pseudosophora was later raised to generic status by Sweet (1830).

Torrey and Gray's treatment in 1840 followed deCandolle's outline. In addition to the two sections Eusophora and Pseudosophora, Torrey and Gray included the division Styphnolobium Schott in which was placed their new species S. affinis. Whether these three divisions represented sections or were subgenera was not clarified by Torrey and Gray, and has been questioned (Rudd, 1972).

Engler and Prantl (1891) divided the genus into four sections. Section Eusophora DC was still included, although the distinguishing traits were an unwinged fruit and keel tip not pointed rather than deCandolle's "free stamens" criterion. Many of the same species, including S. flavescens, and also additional ones were placed in this section. Sophora acuminata, in deCandolle's Pseudosophora, was moved to Eusophora in this treatment.

Section Goebelia Bunge, said to have wingless fruits and keel tip pointed, was composed of the two herbaceous species S. alopecuroides and S. pachycarpa. The two additional sections were Platyosprion Maxim.,

the one species S. platycarpa Maxim. possessing a two-winged fruit, and the section Edwardsia Salisb., with four-winged fruits, included eight arborescent species.

Engler and Prantl's system was followed in the Flora of the USSR (Komarov, 1945). However, S. flavescens was moved from Sect. Eusophora DC. to Sect. Goebelia (Bge.) Taub. Komarov's section Goebelia is synonymous with Engler and Prantl's Goebelia, but the sectional characteristics given by Komarov are "perennial herbs, pods cylindrical, bulging about the seeds, raceme spiciform." Characteristics of Sect. Eusophora were constant in both treatments.

Yakovlev reviewed the entire genus in 1967 and expanded it to include eight sections. Sections Edwardsia Seem. and Pseudosophora DC. remained the same; the other sections were Cephalostigmaton Yakovl., Disemaea (Lindl.) Yakovl., Hammermannia Yakovl. Keyserlingia (Bge. ex Boiss.) Yakovl., Sophora L. and Wightia Yakovl. Ammothamus (Bge.) Yakovl. was reduced from a genus to section status. Yakovlev also recognized Styphnolobium Schott and Calia Teran et Berl. as genera under which were included several species formerly assigned to Sophora.

In Rudd's (1971, 1972) treatment for North America, Sophora was composed of five sections. Rudd and Yakovlev both included Sect. Sophora, but these sections corresponded to different ideas. Yakovlev's Sophora is replaced by Rudd's Aigialodes; Rudd's Sophora is synonymous with Pseudosophora DC., Rudd included a new section Oresbois (Rudd, 1971). Styphnolobium and Calia were reduced by Rudd from generic

status (Yakovlev, 1967) to a section of the genus Sophora.

Further changes may be necessary due to disagreement over the generic lectotype of Sophora. Britton and Brown designated S. alopecuroides as the lectotype because this species represented Linnaeus' original concept of the genus and was cited by him in Hortus Cliffortianus. However, Hitchcock and Green (1929, 1947), Hutchinson (1964) and Yakovlev (1967) considered S. tomentosa L. as the correct type. Rudd (1968) agrees with the use of the latter species, since S. alopecuroides was the only species deCandolle placed in the "discordant" section Pseudosophora, a section which Sweet (1830) raised to generic status. If S. tomentosa is selected as the type and Sweet's generic change is recognized, then the name Pseudosophora must be altered to Sophora. The species in Eusophora DC. would have to be transferred to later synonymous genera such as Styphnolobium and Calia.

Even though the sections used to organize the genus varied from author to author, the treatment of the herbaceous species was very constant. All herbaceous species except S. flavescens were usually placed in the same section together. Komarov's is the only treatment which placed all herbaceous species in the same section Goebelia. The herbaceous species are distinguished from one another on the basis of leaflet shape, size and pubescence as well as certain floral traits. Several herbaceous species bear strong resemblances to one another. Sophora alopecuroides and S. nuttalliana have long been known to possess similar morphologies. Nuttall's

(1818) original description of S. nuttalliana lacked fruits, an often important trait in Sophora. However, Nuttall stated: "Legume not seen - but the striking affinity of this plant to ... S. alopecuroides justified its admission into this genus". Yakovlev states that S. nuttalliana "is analogous to" S. alopecuroides.

Sophora leachiana is also very similar to S. nuttalliana, so similar that Yakovlev recognized S. leachiana only as a synonym of S. nuttalliana. However, I believe Yakovlev was in error and Peck was justified in assigning a new specific epithet to this Oregon endemic. Besides being geographically disjunct, S. leachiana differs from S. nuttalliana by its smaller flowers and different leaf pubescence. In addition, S. nuttalliana has diadelphous stamens briefly but conspicuously united, despite some reports that mention free stamens (Rafinesque, 1832, who also stated that the calyx was four-parted rather than the actual five-parted). Sophora leachiana's stamens are only very weakly united. Sophora alopecuroides' stamens are somewhat connate (Torrey and Gray, 1840) although Ledebour and Bentham (in Torrey and Gray, 1840, further references not given) state that they are wholly distinct. Differences in leaflet size can not be used to distinguish between species, as the size ranges of all three species overlap (S. alopecuroides subsp. alopecuroides 15-40mm x 5-15mm (Komarov, 1945; Tutin et al., 1968), about 20mm x 10mm (Lee, 1935), 20-42mm in length (Yakovlev, 1967), 10-20mm x 5-10mm (Davis, 1970); S. alopecuroides subsp. jaubertii 12-20mm x 7-10mm (Komarov, 1945); S. alopecuroides subsp. tomentosa, 10-20mm x 5-10mm (Davis,

1970); S. leachiana 10-35mm x 5-15mm (Rudd, 1972), S. nuttalliana about 15mm long (Tidestrom, 1925), 5mm x 6.3mm (Stevens, 1948), 3-20mm x 2-10mm (Rudd, 1972), commonly less than 10mm long (Kearney and Peebles, 1960)). Yakovlev's distinction between S. alopecuroides and S. nuttalliana was based on leaflet size; however, the measurements given (2.0-4.2 cm in length for S. alopecuroides; 0.7-1.7 cm for S. nuttalliana) did not reflect the full range of variability possible within each species. Misidentification of the species based on use of his key would be a common error. Depending on the effect of environmental influences on leaflet size, Sophora leachiana could key to S. alopecuroides or to what Yakovlev considered to be the synonymous S. nuttalliana.

The differences listed above support S. leachiana as a distinct species. It is correctly placed in Rudd's section Sophora and deCandolle's Pseudosophora.

Additional Studies of Sophora Species

No thorough autecological or synecological study involving any Sophora species has been performed. Several more specific taxonomic studies have been undertaken (Chock, 1956; Degener and Degener, 1971, with Hawaiian Sophoras; Markham and Godley, 1972; Markham, 1973, flavonoid composition and chemotaxonomy of three arborescent New Zealand species), as well as various studies concerning the composition of root extracts (Hatayama and Komatsu, 1971; Komatsu et al., 1970), structure of the seed (Corner, 1976), effect of salt on growth of the seedlings (Alekperov et al., 1961) and anatomical studies of

the leaflets (Northington et al., 1977). Several studies of interest here include chromosome counts (Table 2), alkaloid research, flower morphology and adaptation, and evolution of two Sophora varieties.

The poisonous nature of the foliage and seeds of many Sophora species is well known. Sophora alopecuroides was introduced into the United States by the U.S. Soil Conservation Service to use as a soil builder; however, because of the plant's high toxicity (toxic at one percent and fatal at two percent of the animal's weight) the established populations were eradicated (Kingsbury, 1964). Sophora nuttalliana was believed to possess poisonous foliage compounds, but this could not be confirmed using feeding experiments with horses (Kingsbury, 1964). This species along with S. alopecuroides and other Sophoras do possess a very poisonous alkaloid in the seeds (Pammel, 1911; Muenscher, 1949). The poisonous seeds of S. secundiflora can often be passed through the digestive tract without harm to the animal; only when the seed coat is cracked is there danger of poisoning (Muenscher, 1949; Kingsbury, 1964). The toxicity of the seeds of S. secundiflora was found to be due to a combination of pipercolic acid, 4-hydroxypipercolic acid and γ -glutamyltyrosine (Izaddoost, Harris and Gracy, 1976). Studies performed with other species show the toxic seed compounds included anagyrine, cytisine, matrine, methylcytisine, sophochrysin and sparteine (Briggs and Ricketts, 1937; Briggs and Russell, 1942; Komarov, 1945; Briggs and Morgan, 1948; Kuschmuradov et al., 1972).

Table 2. Chromosome numbers of Sophora species. Counts given are sporophytic numbers unless otherwise indicated. The herbaceous species are presented first. All synonyms reported under species name preferred by Yakovlev (1967) or by Rudd (1972).

Species

HERBS

<u>S. alopecuroides</u> L.	36	Chuxanova, 1967, in Moore, 1973.
<u>S. alopecuroides</u> subsp. <u>jaubertii</u> (Spach) Borza	36	Tarnavarschi and Lungeanu, 1970, in Moore, 1973.
<u>S. flavescens</u> Ait.	18	Tschechow, 1931, in Senn, 1938, and in Darlington and Wylie, 1955.
<u>S. flavescens</u> Ait.	8 (sic!)	Nagl, 1962, in Cave, 1963.
<u>S. flavescens</u> Ait.	n=9	Kawakami, 1930, in Senn, 1938.
<u>S. pachycarpa</u> C. A. Meyer	36	Chuxanova, 1967, in Moore, 1973.

SHRUBS AND TREES

<u>S. acuminata</u> Benth.	n=11	Mehra and Hans, 1969, in Moore, 1973.
<u>S. chinensis</u> Gray	28	Tschechow, 1931, in Senn, 1938; Kawakami, 1930, in Darlington and Wylie, 1955.
<u>S. chrysophylla</u> (Salisb.) Seem.	16	Skottsberg, 1955, in Cave, 1959.
<u>S. gypsophila</u> Turner & Powell		
var. <u>gypsophila</u>	18	Northington, 1976.
var. <u>guadelupensis</u>	18	Northington, 1976.

Table 2. (Continued)

Species

SHRUBS AND TREES

<u>S. japonica</u> L.	28	Tschechow, 1931, in Senn, 1938, and Darlington and Wylie, 1955.
<u>S. microphylla</u> Ait.	18	Rattenbury, 1957, in Cave, 1960; Sykes and Godley, 1968; Atchison, 1949, also in Darlington and Wylie, 1955.
<u>S. moorcroftiana</u> (Benth.) Baker	c.16	Lechtova-Trnka, 1931, in Darlington and Wylie, 1955.
<u>S. occidentalis</u> L.	18	Mangenot and Mangenot, 1958, in Cave, 1960.
<u>S. prostrata</u>	18	Rattenbury, 1957, in Cave, 1960.
<u>S. secundiflora</u> (Orteza) Lag.	18	Atchison, 1949, also in Darlington and Wylie, 1955.
<u>S. tetraptera</u> Ait.	18	Atchison, 1949, also in Darlington and Wylie, 1955.
<u>S. tomentosa</u> L.	n=9	Pal, 1964, in Cave, 1964.
<u>S. tomentosa</u> L.	18	Atchison, 1951, also in Darlington and Wylie, 1955.
<u>S. toromiro</u> (Phil.) Skottsberg.	18	Skottsberg, 1955, in Cave, 1959.

Further alkaloid work with chemotaxonomic implications was reported by Izaddoost (1975). Izaddoost created four unnamed subgenera of Sophora based on the presence or absence of alkaloids of the matrine series (matrine and matrine N-oxide) and cytisine series (cytisine, N-methylcytisine, and anagryne). In this classification involving 28 species, the herbaceous species were not grouped together. Sophora pachycarpa contained only matrine series alkaloids; S. alopecuroides, S. flavescens, and S. stenophylla contained both series; S. nuttalliana and S. leachiana contained only cytisine series alkaloids. These studies were based on the alkaloids extracted from 200 mg of seeds. The source of Sophora leachiana seeds for this study is very vague, being listed only as "North America".

Otto Urban (1934) reported the flower structure and development of Sophora tetraptera Ait., an arborescent member of the genus native to South America and New Zealand. The flowers are borne in short, compact racemes. The yellow, papilionaceous corolla possesses a broad, round standard that is only slightly reflexed; this standard, plus the hanging nature of the flowers furnishes ideal protection of the floral parts from the elements.

Pollinating bees are attracted to the flowers by the yellow color and by nectar secreted by the receptacle. Maximum stamen-to-insect area is assured from the positioning of the protruding anthers in that some anthers are turned slightly upwards while others point down. As a result, the insect is dusted with pollen on the abdomen as well as its back. Protection from nectar thieves is provided by a barrier

formed by the lower third of the large and strong filaments surrounding the pistil. Certain insects and ants cannot penetrate this obstacle to reach the nectar.

When the stamens first protrude from the corolla, the pistil is very small; only later does the pistil lengthen, arching upwards and above the stamens, helping to prevent self pollination. This method of flower maturation suggests that Sophora tetraptera is protandrous.

The probable origin of infraspecific disjunction of the shrubs S. gypsophila var. gypsophila and var. guadalupensis was studied by Northington (1976). These varieties are known from only two very local sites; var. gypsophila occurs in north central Mexico and the latter variety occurs 300 km north in the Guadalupe Mts. in west Texas. Chemical, ecological, cytological and morphometric data were compared for this species and for S. arizonica and S. formosa, two related species also occurring in the southwestern United States. Pleistocene bioclimatic data suggest that the present Chihuahuan Desert was a widespread pine-oak juniper forest 12,000-15,000 years of age. Northington hypothesized that the progenitor of these Sophora species could have been common in this forest. With the increasing aridity that followed, this ancestral species was reduced to isolated populations which later differentiated into the existing species and varieties.

The Siskiyou Mountains

The study area lies in the Klamath Mountains, a series of mountain ranges 129 km in width which run 322 km from north to south and

are located in Josephine and Curry Counties, southwestern Oregon, and extend into northern California. The Klamath Mountain region is bordered by the Coast Ranges of Oregon and California to the west and the volcanic Cascade Range to the east. It is delimited on the north by the Rogue River in Oregon, and on the south by the Mad River and the Sacramento River in California. This area includes the South Fork, Salmon, and Trinity Mountains in California, and the Rogue River and Siskiyou Mountains in Oregon (Diller, 1914). Sophora leachiana's range lies in the Siskiyou Mts. with the northern limit reaching the Rogue River.

The Klamath Mountains are recognized as one of the oldest land masses in western North America (Detling, 1968). Land first emerged in this area at the close of the Paleozoic, only to be eroded and submerged in the Triassic and Jurassic periods. Another cycle of uplifting and erosion occurred in the early Cretaceous; by the late Cretaceous a third uplift occurred, and the Klamath Mountains were not subsequently submerged during the Cenozoic era (Whittaker, 1960). Erosion and uplifting have continued throughout this period with the most important change being the uplifting of the Klamath peneplain during the early Pliocene. Erosion and differential uplifting of this plateau have resulted in the structures existing today (Shanon, 1933).

The Klamath Mountains have not suffered a major disturbance since their final uplift at the end of the late Cretaceous. They escaped the lava flows that were characteristic of many parts of

Oregon during the mid Miocene through the Pleistocene (Babcock and Stebbins, 1938; Whittaker, 1960). In contrast to the Cascades, Willows, and other northwest mountain ranges, this area was not extensively glaciated in the Pleistocene. Glaciation did have an effect on the vegetation of this area, however the glaciers were of the local alpine type extending down to 870 meters (Whittaker, 1961; Wells et al., 1949); the vast destructive ice sheets which characterized the Cascades were not present in the Klamath Mountains.

The Klamath area is topographically diverse as the mountains form a complex mosaic rather than a straight chain. Coupled with this is the large variety of parent materials, hence soil types, found in this area. Major rock types include diorite, gabbro, serpentine, granite, and peridotite. Climatic differences are also in operation, with the coastal influence of mild temperatures and high rainfall occurring in the western part and with steeply decreasing precipitation towards the east.

General climatic data for the area of Sophora leachiana can be gathered from weather stations at Grants Pass (29 km due east of Site Three and Barr Mine, elevation 281 meters) and Cave Junction (24 km SSE of Briggs Creek, elevation 390 m). All weather data are based on 14-20 years' monthly averages reported from each station (U.S.D.A. Weather Bureau, 1957-1977). The climate is one of cool, wet winters followed by hot, dry summers. Most of the yearly precipitation (144 cm for Cave Junction; 79 cm for Grants Pass) falls from September through May, with the summer months contributing only 2.4 cm and 3.0 cm of

the total for Cave Junction and Grants Pass, respectively. Records from Galice, Oregon, from 1909 to 1915 show a yearly average of 122 cm with 3.0 cm falling in the summer months (Department of Agriculture Weather Bureau, 1930). Snowfall totalled 53 cm for Cave Junction and 18 cm for Grants Pass. Average high and low temperatures in December and January at Cave Junction and Grants Pass are 7.2⁰C and -1.1⁰C, with extremes around -8⁰C for Cave Junction and about -6⁰C for Grants Pass, each with a high extreme of 15.5⁰C. Summer temperatures reach an average high of 32⁰C with average lows of 9.4⁰C at Cave Junction and 14⁰C at Grants Pass; daily temperature maximums were over 38⁰C at both locations with minimums of 2.7⁰C and 7.2⁰C. Cave Junction averages 143 frost-free days (temperatures \geq 0⁰C) and Grants Pass averages 167 days, with the first fall frost occurring in early October. The last spring frost occurs around the second week of May at Cave Junction and in late April at Grants Pass.

The vegetation of the Siskiyou Mts. is very fire-prone, with lightning or human activities being the major causes of fires. Indians are known to have set fires for hunting and warfare. Fire frequency increased with white man's settlement because miners, ranchers and hunters had a supreme disregard of fire and set fires to drive game, to clear land, or even for entertainment (Haefner, 1912; Butler and Mitchell, 1916; Whittaker, 1960; Haefner, 1975). In recent years man-caused fires have declined, and with modern fire-fighting methods, those caused by lightning or by neglect have been brought relatively well under control. Fires are very important to

the native plant communities, and probably in no lower elevation areas does the vegetation lack evidence of fire. The vegetation has likewise become fire adapted; fires change the age distribution present in the stand but do not tend to change the vegetation composition of an area (Whittaker, 1960).

Adequate fire records for the Siskiyou Mountains are not maintained, therefore the complete fire history is not known. The only reported fire occurring in Sophora's range is the Nome Creek fire of late June, 1938. This man-caused 4,000 acre burn started near the Illinois River and burned most of the Nome Creek drainage, spreading across the Illinois River eastward to Panther and Briggs Creek (Marquis, 1978). No records of the location of frequent, smaller fires that could have affected the area are known, although Sternes (1959) reports "literally hundreds" of lightning-caused small fires in July, 1959, and other years.

Fire is not the only factor disturbing the area. The discovery of gold on May 2, 1852, at Josephine Creek, Josephine County, ushered in the Oregon Gold Rush (Diller, 1914), and many placer mines were promptly initiated. These claims were not only for gold, but for silver, copper, chromite and platinum as well. Placer mines were first located in easily accessible locations, hence the majority of the mines were near streams. The Galice area was especially rich, and about 25 placers are known from this area, two on Rich Gulch and 12 on Galice Creek. Another popular area was along Briggs Creek drainage. Mining intensity decreased steadily past the 1860's; however, Diller

(1914) reports 119 important mines active in the Galice-Waldo-Kerby area. Mining declined and except for small private operations, it essentially stopped after World War II. The damage mining inflicted on the vegetation was not limited to the immediate placer location, as roads were often constructed to the mining sites. Another common disturbance was ditch construction, such as the five-foot deep, ten-foot wide and three-mile long waterway running from Soldiers Creek to the Gold Bond Placer 1.5 miles above the mouth of Briggs Creek. Today mining scars are still very apparent on the landscape. In the Sophora area, mining now occurs only on a small scale; new man-caused disturbances include further road construction and commercial logging.

Vegetation of the Siskiyou Mountains

The Siskiyou Mountains are known for their interesting floristics. Geographically the area links the northern, southern, and eastern portions of Pacific Coast vegetation, so that elements of these floras mingle in this region. The varied parent materials, slope, aspect, climate along with the great age of the mountains have allowed a flora rich in endemics to develop. Because of the remoteness and ruggedness of the area, vegetation studies have been few. However, several key works do describe the present vegetation patterns.

One of the first treatments of the Siskiyou area was by Peck (1940), however, his report was limited to a brief floristic list for the area. The first major study was performed by Whittaker (1960). His work encompassed the vegetation associated with three major soil types--gabbro, diorite and serpentine. The vegetation structure at a

given site was found to depend on the parent material; within a given vegetation type associated with a parent material, the moisture gradient also influenced the vegetation as did the elevation.

Whittaker divided the Siskiyou area into four formations -- a coastal forest of Sequoia sempervirens and Pseudotsuga menziesii, the Mixed Evergreen Formation, Oak Woodland, and Valley Grassland. The Mixed Evergreen Formation is transitional to sclerophyll and conifer forests, as it possesses an upper tree stratum of needle-leaved evergreen conifers and a lower tree stratum of broad-leaved evergreen or sclerophyll species. Widespread species include Pseudotsuga menziesii, Pinus lambertiana, and P. ponderosa, with the lower tree stratum of Castanopsis chrysophylla, Lithocarpus densiflora, Arbutus menziesii, Quercus kelloggii and shrubby Q. chrysolepis. Shrubs include Berberis nervosa, Rhus diversiloba, and Rosa gymnocarpa. Ceanothus integerrimus and Arctostaphylos viscida occur in drier sites.

The relative importance of each layer was dependent on the soil type and moisture conditions (see also Whittaker, 1961). Mesic vegetation included high conifer values and few sclerophylls, changing with increasing aridity to open conifer stands with a dense understory of sclerophylls. Whittaker recognized three dominant vegetation types of low elevations occurring in the Mixed Evergreen Formation. Very mesic areas support a Chamaecyparis lawsoniana--Pseudotsuga forest with few sclerophylls and many deciduous species. A Pseudotsuga--Lithocarpus--Arbutus (the "Pseudotsuga--sclerophyll") community, with other sclerophylls present and sometimes dominant, occurs along most of the moisture gradient on diorite and on less xeric gabbro sites.

More xeric gabbro supports a "Sclerophyll-Pseudotsuga" community with a sparse cover of Pseudotsuga and dense sclerophyll layer. Quercus chrysolepis is also abundant along with Rosa gymnocarpa, Rhus, Rubus ursinus, and Pteridium aquilinum in the understory.

The third dominant vegetation type is an open Pinus--Pseudotsuga--Quercus chrysolepis--Arctostaphylos on xeric gabbro and eastward from the main study area. The canopy is more open; Pinus ponderosa, P. lambertiana and Libocedrus decurrens are more important. When both strata for this vegetation type are open, the formation grades into a pine-oak woodland, followed by grasslands in the most xeric sites.

Waring's study (1969) divided the Siskiyou into two provinces delineated by the absence (or only rare presence) of several species in the eastern province and their common occurrence in areas of the western province and sometimes the southern Cascades. The approximate boundary separating the eastern and western fractions begins at Finley Bend on the Rogue River (sect. 14, T36S, R7W) and extends in a south-westerly direction through the Siskiyou Mountains. The change in species composition was correlated with a sharp increase in transpirational stress and daily temperature fluctuations just inside the western boundary of the eastern province. Waring criticized Whittaker's study, as the great majority of Whittaker's samples were in the western province; therefore Waring feels that Whittaker's formations and vegetation types apply only to the western area. This is supported by the fact that Lithocarpus densiflora was a dominant species in one of Whittaker's vegetation types of the mixed evergreen forest, but it

is characteristically not found in the eastern province of the Siskiyou Mountains. Using moisture stress measurements and a temperature-effect index (Optimum Temperature Days), Waring was able to classify eight broad and sometimes intergrading vegetation types of the eastern province.

The Lower Illinois River forest was surveyed by Emmingham (1973); this area included the southern limit of the range of Sophora leachiana. A timber management survey was made including productive capacity in relation to the represented plant communities. Emmingham's results are in basic agreement with Whittaker's, but provide amplified descriptions of the area including vegetation associated with additional parent materials.

The Rogue River Valley is the most xerophytic area in southwestern Oregon (Gratkowski, 1961). Gratkowski delineated by map the area referred to as the Rogue River Valley; Peavine Mountain occupied the western boundary of the valley. Although ecological studies are very limited, the vegetation of the area is diverse and three of the four formations proposed by Whittaker (1960) are present. A floristic description of the valley was prepared by Peck in 1940. His work, later verified by Gratkowski (1961), reported the lower elevation forest to include Pseudotsuga menziesii, Pinus lambertiana, P. ponderosa, and Libocedrus decurrens. This corresponds to the "Pseudotsuga--sclerophyll" community of the Mixed Evergreen Formation.

Drier, more sparsely wooded areas support the Oak Woodland Formation composed of Quercus sp. (Q. kelloggii, Q. garryana) and

Arbutus menziesii, with dense undergrowth of evergreen brush dominated by Ceanothus integerrimus, C. cuneatus, and Arctostaphylos viscida.

These woodlands can be succeeded by conifers at some localities within the valley. A forest of Pseudotsuga--Pinus ponderosa--Quercus may be climax in some areas (Franklin and Dyrness, 1973). Extensive areas support dense stands of climax or fire-maintained chaparral along with the Valley Grassland Formation.

MATERIALS AND METHODS

Ecological Methods

Thorough study of a plant species should include research into its ecological requirements and adaptations. Ecological factors affecting a plant's distribution can best be understood by making direct measurements of the environment, and this format has been successfully employed on a variety of species (e.g., Picea breweriana; Waring, Emmingham, and Running, 1975). However, such an approach was beyond the scope of my study. Instead, environmental parameters were inferred from the biotic environment associated with the species, as expressed in the structure and components of the vegetation associated with Sophora leachiana.

The distribution of Sophora was outlined by visiting all reported localities of the species. Potential site locations were furnished by the United States Forest Service and herbarium specimens at Oregon State University (OSC) and the University of Oregon (ORE). Additional populations were found by chance exploration of other areas. A Bureau of Land Management (BLM) map of Peavine Mountain area was used to pinpoint the locations of the three Peavine populations. The exact location of all other areas was determined from United States Geological Survey maps. Names of creeks in the Geological Survey map sometimes differed from those on the Siskiyou National Forest map; the nomenclature of the former map was followed in this report.

A general description of all site locations was prepared including such information as the nature of disturbance, the aspect, and the presence of drainage areas in and around the community. Slope gradation

was measured with an Abney handlevel; elevation was obtained from the Geological Survey maps. Several Sophora populations were located in commercially logged areas; the United States Forest Service at Grants Pass, Oregon, supplied information concerning the age of the cut and silvicultural and restoration practices at these sites. Associated species were listed with nomenclature following Peck (1940) in most instances. Hitchcock and Cronquist (1973) and Munz (1959) were also used. Voucher specimens of many species are on file at OSC.

Sophora leachiana is found in areas whose vegetation is modified by disturbance; therefore, additional sampling was done in the adjacent minimally disturbed forests. The thirteen disturbed areas were sampled to learn primarily about the structure of the Sophora populations and the surrounding vegetation. No formal community measurements were made at four locations because three of the populations were quite small and the fourth was found only along the roadside near another much larger Sophora population. At these four locations, a floristic survey of all associated species was compiled. Ranking of the species was determined by Poulton's ratings, a method useful in a preliminary survey of the community structure.

Poulton's ecological reconnaissance method involves five dominance ratings. A value of five is assigned to the species which dominates the stand, therefore not every stand will have an individual in this category. Codominants are rated as four. A three rating is given to those species which are easily seen throughout the area; species

occurring in scattered patches or as isolated individuals encountered only when walking through the area are rated as a two. Very wide-scattered species and those in isolated patches are assigned a value of one.

The remaining nine areas were sampled with the aid of three by five meter quadrats. Three locations involved five quadrats placed end to end forming a three by 25 meter area. Only five quadrats were used because the vegetation in the area sampled was rather homogeneously distributed. The analysis of Lower Peavine involved two quadrat series of five each, one series in the open sunlit roadside and the other placed within the forest. All other localities involved 15 quadrats (nine by 25m or 225m^2). Selection of quadrat position was biased towards good stands of Sophora leachiana rather than being randomly located within the site. Quadrats usually paralleled roads or pathways when applicable; all horizontally bisected the slope. Within each quadrat, the number of all species was recorded along with the diameter at breast height (DBH) of any tree. Cover, the estimated percent area shaded by a plant, was also recorded for each species. Data from the quadrats were combined for analysis (see below).

The mature vegetation of the area was studied at seven locations. The exact sites chosen for the quadrats were those of least disturbance found in the immediate surroundings of the disturbed Sophora area. Despite this prerequisite, all stands showed some signs of disturbance. Fifteen by 25 meter (375m^2) quadrats were used in all sites. Within the quadrat the DBH and estimated cover of each tree

species was recorded. The density and cover for shrubs and herbaceous species were low in every plot, therefore all individuals occurring in a five by 25m strip bisecting the center of the plot were recorded along with estimated cover. This deviated from Daubenmire's (1968) use of the 15 by 25m areas, as he confined his shrub samples to two one by 25m areas and herbs to 50 0.1m^2 units.

The data were analyzed separately for the arborescent, shrub and herbaceous layers. The DBHs of all arborescent members were changed to basal area, or biomass, using the formula πr^2 . The total biomass of each species was determined and a species' relative biomass was calculated by dividing each species value by the sum total biomass within the plot. Percent abundance equalled the number of stems of a species divided by the total number of stems in the plot; likewise, relative cover is the species cover divided by total cover. An age class spectrum with eight categories of DBH was constructed to check the reproduction of each species. Upper limits of each size class, in cm, were 0.5 DBH, 3.8, 15.25, 23, 30, 38, 50; the eighth class included all trees >50cm DBH.

An importance percentage, defined as the average of the percent abundance, percent biomass and percent relative cover of a species, was used only as a quick guide to the community standing of a species. Relative cover and not actual cover was used because the species themselves were being compared and not the sites. The use of only cover would have emphasized differences between the total canopy coverage at each location rather than a species contribution to the total cover.

The values used to compile this importance index differ from the parameters used according to Curtis' (1959, in Mueller-Dombois and Ellenberg, 1974) definition. The method of data collection did not allow frequency determinations to be calculated, therefore Curtis' relative frequency was substituted with relative cover.

Relative cover and biomass have both been used elsewhere as indicators of dominance. As a general rule the cover of an individual will increase with increasing DBH. Indeed, biomass is often calculated from cover estimates rather than from DBH measurements (Mueller-Dombois and Ellenberg, 1974). Therefore, inclusion of relative cover and biomass in the importance index may appear repetitious. However, several species were represented by low biomass but with high cover (young Corylus cornuta, various tree seedlings, shrubby Lithocarpus densiflora and Quercus chrysolepis). Relative cover was included in the importance value calculations to represent better these species. Because the importance value was the average of the three parameters rather than their sum, the addition of the cover class probably did not place undue weight on those species with high values in both parameters.

An index value should not be the sole criterion for community placement, as combining all data into a single unit tends to distort the true picture of the community (Mueller-Dombois and Ellenberg, 1974). Therefore in deciding community dominants, the values of the individual parameters along with age class spectrums, received the most emphasis.

Because the relative position of the conifer, sclerophyll and deciduous layers can be important in defining the community type, the

percent abundance, percent biomass, relative cover and importance percentage for the three respective layers were also calculated.

Shrub and herbaceous species were analyzed by percent abundance and percent relative cover. Occasionally it was unrealistic to count the number of individuals (as in a thick patch of grass); only percent cover was recorded in this instance and this was taken into account in analyzing the vegetation.

Comparative community analysis was performed to test if two or more vegetational units were present within the areas sampled. Braun-Blanquet's manual-visual table was constructed using guidelines set by Mueller-Dombois and Ellenberg (1974). Species lists for all areas were compiled into a synthesis table; species with constancy values between 10-60 percent were selected for further use. Plots were ordered so that groups of species characteristic of one vegetational unit are separated from species composing a second unit. This analysis was first attempted using only the data from the undisturbed sites; however, all species in the undisturbed and disturbed portions of an area were used in a second analysis.

Reproductive Biology Methods

A species' long term success in an area is determined by reproductive ability. A species may be able to establish in a new area; however, it will in time be eliminated from the community unless propagation is successful. A knowledge of reproductive modes is thus of utmost importance in understanding the distribution of a species. All phases of the cycle, beginning with chromosome number and behavior and

concluding with the germination of seeds, were studied to measure the reproductive success of Sophora leachiana.

Extensive studies were conducted in the spring and summer of 1976 and 1977. The first stage in this investigation was a determination of the initial reproductive output within a population. The rachis of the terminal racemose inflorescence of Sophora leachiana persists on the plant, whereas infertile flowers are deciduous. Therefore, the percent of individuals flowering in each population could be determined and their percent fruit-set measured. Only the developing fruits of fertile flowers remain on the rachis. The percent seed set within the fruits could also be measured because each maturing seed is visible as a bulge in the fruit. Very young seeds do not form bulges in the fruit walls; therefore the number of developing seeds could not be determined in stands sampled in the spring or early summer. The percent flowering, percent fruiting, and percent seed set were counted for each quadrat established at the individual sites.

The above measurements confirmed the prior reports (Peck, 1954) of a low reproductive success in Sophora leachiana. In order to shed light on the cause of low seed set and the high incidence of seed abortion, the following seven studies were performed:

1. Chromosome observations.
2. Pollen stainability.
3. Pollen germination in vitro.
4. Flower structure and pollinator activity.
5. Pollen-stigma interactions.
6. Controlled field crosses.
7. Anatomy of aborted seeds.

In addition to these studies, the germination of seeds and the effect of heat on seed viability were also explored.

In order to determine chromosome numbers and observe meiosis, young buds from four sites were fixed in a solution of 3:1:1, 100 percent ethanol: chloroform: glacial acetic acid. This solution was made up fresh every morning; before fixation the calyx enveloping the young anthers was torn open with the aid of fine-pointed tweezers. The buds were allowed to remain in the fixative for 24 hours, then rinsed and kept in 95 percent ethanol for 12 hours. At the end of this period, the solution was changed to 80 percent ethanol for an additional 12 hours. Final storage was done in 70 percent ethanol in a freezer. Staining was accomplished by placing the buds in alcoholic hydrochloric acid-carmin (Snow, 1963) overnight in a 69°C oven. Excess stain was removed by placing the inflorescence in several changes of 70 percent ethanol; buds were kept in the 70 percent ethanol solution in a freezer until further use. To prepare for examination, anthers were dissected from the buds and placed on a slide in a drop of 45 percent acetic acid. Excess solution was blotted away and the anthers were squashed in a drop of Hoyers mounting medium (Radford, Dickison, Massey, and Bell, 1974). Observations were made with a Zeiss phase-contrast microscope.

Pollen stainability was counted by crushing a mature but undehiscent anther from either a fresh or dried specimen in one drop of aniline blue in lactophenol (Radford, Massey, Dickison, and Bell, 1974). The drop was stirred before a coverslip was lowered into place. In some instances it was desirable to have stainability results from the plants used in chromosome analysis. In these cases, anthers were taken off inflorescences that had already received treatment with Snow's chromosome

stain (1963) and were being stored in 70 percent ethanol. These anthers were taken through 50 and 30 percent alcohol solutions to dH_2O before being mascerated in the analine blue-lactophenol solution. The prior addition of Snow's stain did not seem to interfere with the reaction between analine blue and the viable pollen grains. Counts were made about 24 hours after the slides were prepared. The number of pollen grains counted per anther averaged about 700; in all cases at least 400 grains were counted. In a few instances, the total number of grains per anther was tallied in order to compute the pollen-ovule ratio (Cruden, 1977).

Pollen germination in vitro was performed by placing cover slips on moist filter paper in petri dishes; on these cover slips standing drops of 1/40 ml (25 λ) of the nutrient solution were delivered using a micropipette. The nutrient solution used was that of Brewbaker and Kwacks (1963). Two additional solutions were also prepared, differing only in their sucrose concentrations. Brewbaker and Kwacks' solution called for 10 percent sucrose (along with 100 ppm H_3BO_3 , 300 ppm $\text{Ca}(\text{NO}_3)_2 \cdot 4 \text{H}_2\text{O}$, 200 ppm $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ and 100 ppm KNO_3 in dH_2O); the other solutions contained 20 and 30 percent sucrose respectively. Pollen grains were obtained from freshly dehisced anthers dissected from inflorescences collected at the Taylor Creek, Lower Peavine, Briggs Creek and Squirrel Place sites. Grains were removed from the anther with a fine-tip probe and stirred into the nutrient drop. An attempt was made to remove only a small number of grains from the anther, by touching the probe very lightly to the grains and dislodging

any large clumps seen on the probe with the aid of a dissecting scope. Nonetheless, the average number of grains was around 142. Four replicates of each different sucrose concentration were run for each site, except five replicates were run for Taylor Creek. The same anther was used to supply pollen for one 10, 20, and 30 percent sucrose series. Anthers from different flowers furnished pollen for each replication. The plates were left at room temperature for 24 hours before counting was begun. Since not all of the counts could be performed the same day, those remaining were preserved by adding a drop of FAA (18:1:1, 50 percent ethanol: glacial acetic acid: 37 percent formalin). For examination, the cover slip containing the standing drop was placed on a slide and another cover slip was lowered on top of it in order to spread out the drop. The entire area was scanned under 100x power. Germination was said to have occurred when the pollen tube was at least as long as the diameter of the grain (Dean, 1964, as reported in Stanley and Linskens, 1974). The observations were tallied into five categories:

1. Grains which exhibited no visual change.
2. Grains which were swollen but showed no tube growth.
3. Grains with a tube less than the diameter of the grain.
4. Abnormal grains (burst tube; large swollen bladder like areas in tube).
5. Normal grains possessing a tube \geq the diameter of the grain.

In the last category, the length of the pollen tube in relation to the diameter of the grain was estimated. The final percent germination figure used to compare the populations was taken to be the numbers in Group 4 and Group 5 divided by the total number of grains. The results were analyzed statistically using 95 percent confidence limits and F tests (Petersen, 1975). Group 4 was included with Group 5 because the

observed abnormalities can most likely be explained as being caused by the nutrient media. Burst tubes are usually an indication of boron deficiency in the medium (Brewbaker and Majumder, 1961; Maheshwari, 1963); and the large bladderlike areas (the 'secondary pollen grains' of Haeckel, 1951) are a function of the age of the tube (Hartmann-Dick and Muller-Stoll, 1955, as in Maheshwari, 1963). Short spherical tubes indicate a supraoptimum medium (Maheshwari, 1963).

Flower morphology was examined in the field with fresh flowers and in the lab with pressed and dried specimens. The flowers of an inflorescence were dissected, and petal condition, stamen length, anther dehiscence, pistil length, and nectar production were noted. Pollinator activity was observed in the field whenever possible; one species of pollinator was captured with an insect net, killed in carbon tetrachloride, and given to the entomology department at OSU for identification.

It was originally planned that the pollen tube growth in vivo experiment would be conducted in the field. However, due to bad weather conditions, flowering shoots from Briggs Creek, Squirrel Place, Taylor Creek, Upper Peavine, and Lower Peavine had to be gathered, placed in jars of water, and transported back to OSU. The first inflorescences were collected at Briggs Creek around 6:00 p.m. Monday, May 9, 1977. They arrived at OSU around 2:30 a.m. on May 10, and the crosses were performed at 6:00 p.m. on that date.

Each flower to be crossed was carefully emasculated and the stigma checked for pollen grains with the aid of a dissecting scope. Newly dehisced anthers were plucked from the flowers of the male parent and

rubbed across the stigma until the stigma appeared yellow to the unaided eye. The trials included crosses between the four locations, among different individuals from the same location, and selfing. Flowers at various stages of development were used as the female parent. Labeling the flowers was done by simply marking a number on the calyx with a red felt-tip pen. All crosses were allowed to go a minimum of 32 hours; the longest run was 41 hours.

The pistils of the individual flowers were fixed in Carnoy's solution (3:1:1, ethanol: glacial acetic acid: chloroform) for 12 hours. They were rinsed and stored in 70 percent ethanol in a freezer. The pistils were prepared for staining following the procedure devised by Nair and Narasimhan (1963) by placing them successively in 50 percent ethanol, 30 percent ethanol, and dH_2O , two minutes each, followed by hydrolyzation in 1N HCL at 57°C for 15 minutes. After rinsing in dH_2O , the pistils were placed in the analine blue staining solution for 20 minutes. At the end of this time period, the styles were dissected from the ovaries and cleared for 80 to 90 minutes in 45 percent acetic acid. The increase in clearing time from one hour to 90 minutes was the only deviation from Nair and Narasimhan's procedure. After clearing, the styles were mounted in lactophenol and observed under the microscope. The staining character of the stigma and style as well as the pollen grains was noted. Pressure was then gently applied to the cover slip so as to separate the stigmatic and stylar tissues to aid in observing pollen tubes.

Field crosses were performed May 6-9, 1977. A flower was emasculated, the stigma checked for pollen grains using a binocular dissecting microscope, and then an anther from the male parent was rubbed across the stigma. Deposition of pollen grains on the stigma was confirmed by observations with the dissecting scope or with a 10x hand lens. The female parent included flowers at all stages of maturity; i.e., unopened buds were used as well as all stages of opened and older flowers. The crosses included those between plants from the same site as well as from different populations. Pollen was transported around the site by placing the inflorescence in a plastic bag which was kept out of the sun at all times. Flowering shoots were transported from one population to another by placing the shoots in jars of water. Selfing was performed on some plants; other flowers were not emasculated or manipulated in any way to test if selfing could occur in the absence of a pollinator. To test for apomixis, some individuals were emasculated and not pollinated. Flowers were labeled by securely tying color-coded embroidery floss around the individual pedicles. All inflorescences were covered with a cheese-cloth bag to exclude pollinators. The bag was supported with twine tied to two or three sticks driven into the ground next to the plant, thus the weight of the bag was not carried by the plant itself.

At the end of August, seven sites were revisited and most fruits seen in each population were collected and taken back to the lab. The seeds were separated from the fruits and stored in glass vials at room temperature. Because numerous seeds aborted at varying stages of

development, eight size categories were selected and the seeds tallied according to these sizes, with the color and the presence of any fungus also noted for each seed. The average values and ranges for these eight size categories and their average weights were:

Group 1	-	1.0mm	x	0.5	mm	x	0.25mm	1.0mm	x	0.5mm	to	1.5mm	x	1.0mm	0.008mg
Group 2	-	3.0	x	1.0	x	0.75	2.0	x	0.5	to	3.0	x	1.0	0.08	
Group 3	-	4.0	x	1.5	x	2.0	3.0	x	0.5	to	5.0	x	2.0	0.43	
Group 4	-	4.0	x	2.0	x	2.0	3.0	x	2.0	to	5.0	x	1.0	0.45	
Group 5	-	5.0	x	2.5	x	2.0	4.0	x	2.0	to	6.0	x	4.0	0.95	
Group 6	-	5.0	x	3.0	x	3.5	4.0	x	2.0	to	6.0	x	4.0	1.8	
Group 7	-	6.0	x	4.0	x	3.0	3.0	x	3.0	to	6.0	x	4.0	3.5	
Group 8	-	6.0	x	3.5	x	3.5	4.0	x	3.0	to	6.0	x	4.0	3.8	

Group 3 seeds are 'clubshaped', i.e., rounded at the hilar end, tapering to a narrow point at the other end. Group 4 seeds are similar to Group 3 except they are elliptic in outline, not club shaped. Groups 5 and 6 are difficult to separate because complete intergradation occurs between the two. The values given for Groups 5 and 6 represent averages of the lower and upper limits of this gradation. These categories were maintained separately for the sectioned ovule study but they were combined for tallying, because distinguishing between some members of Groups 5 and 6 would have been unnecessarily tedious. Seeds in Groups 5 and 6 were black and shriveled.

There were essentially no size difference between Groups 7 and 8. The diagnostic trait used to separate these two classes was the nature of the seed coat, Group 7 possessing a coat with indentations of various sizes and Group 8 a smooth seed coat. Most of the individuals in Group 7 also had seed coats that were tinged with brown, sometimes quite heavily or even completely. Group eight's seed coat was usually a

mustard yellow, sometimes faintly tinged with brown, only occasionally all brown.

Six seeds from each category were selected at random, weighed, and their seed coats clipped. The seeds were placed in petri dishes on moist filter paper overnight to allow imbibition to occur. The embryos were then isolated from the seed and placed in FAA (18:1:1, 70 percent ethanol: glacial acetic acid: 37 percent formalin). Due to the small seeds in Groups 1 and 2, the embryos were not removed and the entire seed was placed in FAA. A vacuum of 25 psi was placed on these solutions to draw all air out of the tissues. The seeds were taken through a tertiary butyl alcohol (TBA) dehydration series (Sass, 1964) embedded in parafin, and sectioned at 8 μ using a microtome. Staining was with safranin and fast green following the outline presented by Sass. Several sections of seeds from Group 7 were taken through a different series of stains in order to determine the food storage product in the cotyledons. Total carbohydrates as insoluble polysaccharides were tested using the periodic-acid Schiff's technique reported in Jensen (1962), as adapted from Hotchkiss (1948) and McManus (1948). Total protein was determined using Jensen's ninhydrin-alloxan-Schiff's reagent as modified from Yasuma and Ichikawa (1953). A deamination control was run on sections from Group 6 using Jensen's procedure.

Thirty-six seeds from Group 8 and 12 seeds from Group 7 were selected to test for percent germination. In order to avoid possible pathogenic contamination, the work was done in the sterile transfer room at Oregon State University. The seeds were first surface sterilized

with a 1.2 percent sodium hypochlorite (NaOCl , or Chlorox) solution for 10 minutes (Seneca and Cooper, 1971). After thorough rinsing in sterile distilled water (dH_2O) (autoclaved 20 minutes at 21 lb pressure), the seed coats were nicked with a sharp razor blade at the anterior portion of the seed. The germination tests were carried out using four 17.8 x 12.7 x 6.35cm plastic tubes each of which had been thoroughly scrubbed with Chlorox and rinsed with sterile dH_2O before use; the soil used was collected at a population of Sophora at Site Three and had also been sterilized by autoclaving for 2 hours. The seeds were planted 1.3 to 1.9cm deep, 12 per tub, with three rows of four seeds in a tub. After watering thoroughly with dH_2O , a glass plate was taped in place over each tub. All four flats were allowed to equilibrate at room temperature for 24 hours before being placed in a 2.2°C refrigerated room for 12 weeks. At the end of this stratification period all flats were transferred to the greenhouse and maintained on a $18.3\text{-}15.5^\circ\text{C}$ day-night temperature regime. No special lighting was arranged; therefore conditions followed the natural photoperiod and intensity of light which reached the greenhouse bench. The flats were watered when necessary. The glass plates were kept on the tubs in order to retard evaporation during the early stages of germination; these plates were removed when the seedlings were tall enough to touch the glass. The flats observed daily and the seeds were recorded as having germinated when the hypocotyl hook or the cotyledons first became visible. Observations were continued periodically in order to examine seedling growth.

Many species in fire prevalent areas possess seeds which are fire adapted. The seeds can survive a fire and will often experience increased germination rates following a fire. Sophora leachiana is found in fire-prone environments. Therefore the effects of heat on the viability of Sophora seeds was of special interest. The procedure used was adopted from Quick (1935). A moist heat rather than dry heat procedure was chosen because moist heat more closely simulates conditions in a fire (Martin and Cushwa, 1966). One liter of distilled water in Erlenmeyer flasks was heated to 60°C, 70°C, 80°C, 90°C, or 100°C, removed from the heat source and the seeds immediately dropped into the hot water. The solution was allowed to cool overnight. If imbibition occurred, the seed coat was removed, the structure and size of the embryo were noted, and the embryo was placed in a one percent solution of 2,3,4-triphenyl tetrazolium chloride (TZ) for eight hours. The TZ solution was kept in the dark at room temperature; acidity paper was used to ensure the pH was at the proper level of pH 6 to pH 7 (Lakon, 1949).

Tetrazolium is colorless in solution; it is reduced in cells to the red, water insoluble formazan product. Viable embryos will stain a dark red color, although the entire embryo need not stain red to be viable. Instead, the location and extent of nonstaining necrotic tissues are the governing factors. In this study, interpretation of staining patterns was based on excellent guidelines presented by Delouche et al. (1962).

Mature seeds of Group 7 and Group 8 were used in these tests. Individual experiments were of two kinds: Seeds were placed in the

hot water treatment once, and manually scarified if imbibition did not occur. Scarification was accomplished by nicking the posterior end of the seed with a sharp razor blade. Other seeds that did not imbibe following the initial heat treatment were treated a second time at the same or at a higher temperature. The seeds were then scarified, allowed to imbibe and the embryos placed in the TZ solution.

Four potential sources of error were monitored with controls. Viability of untreated, scarified seeds was determined to estimate the percent viability present within the seeds prior to the heat treatments. Seeds used in all experiments were placed overnight in distilled water to insure none were naturally permeable. The two remaining factors dealt with the TZ solution. Tetrazolium solutions decompose in light and with bacterial action. Therefore mung beans (Phaseolus aureus) known to have a high percent germination rate were used to check the performance of the solution. Bacterial contamination in the solution or on an embryo will cause interference with the test results because bacteria can also reduce TZ to the red product. To alleviate this problem, several mung beans were killed by brief exposure to boiling water and the dead embryos placed in the TZ solution. The lack of any reaction in the dead embryos showed that color development in other tests was caused by the embryo itself and not by bacterial contamination of the solution.

RESULTS

Ecological Relations

Sophora leachiana is confined to only thirteen populations rather homogeneously distributed within a 29 by 6.4 km area in Josephine County, Oregon. The northern limit is the Mount Peavine area near Galice; the southern limit is where Briggs Creek meets the Illinois River 30.5 km west of Selma. All populations occur in close proximity to perennial streams located in one of three watershed areas - Galice Creek, Taylor Creek or Briggs Creek, and all are in heavily disturbed sites. Figure 1 furnishes the name and exact location for each population, while township, elevation, slope, and aspect are presented in Table 3.

To gain information concerning the habitat occupied by Sophora leachiana, community measurements were made at ten sites; the other two sites were surveyed for associated species. Because the sites supporting Sophora were often too highly disturbed to indicate the community type normally found at each location, seven additional sites were located in adjacent undisturbed forested areas. These community measurements also illustrated various fractions of the population structure of Sophora.

A discussion of the general vegetative patterns associated with Sophora will be presented, followed by a more detailed description of each area.

Finally, the population structure and behavior of Sophora including disease and predation patterns will be examined.

- Ba - Barr Mine
- Br - Briggs Creek
- Lp - Lower Peavine
- NH - Nobles House
- NP - New Place
- OF - Oak Flat
- S3 - Site Three
- SC - Soldier Creek
- Sq - Squirrel Place
- TC - Taylor Creek
- TH - Taylor House
- UP - Upper Peavine
- WT - West Fork Taylor

- - - - - roads
- contour lines
(intervals in feet)
- _____ creeks

One centimeter = 1.38 kilometers.

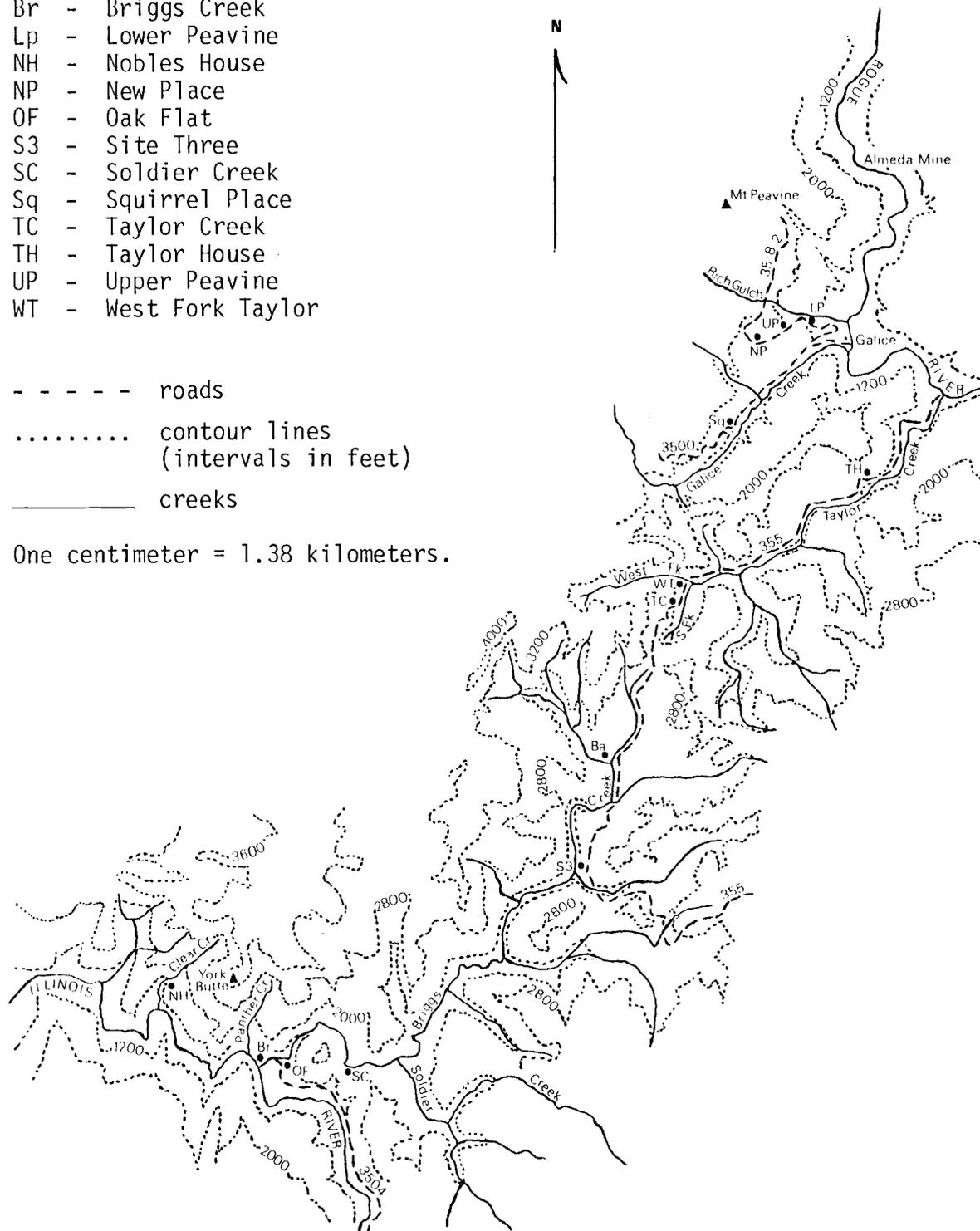


Figure 1. Map of *Sophora* populations.

Table 3. Location, slope, and aspect and elevation of the thirteen Sophora leachiana populations.

	<u>Location</u>	<u>Slope</u>	<u>Aspect</u>	<u>Elevation</u>
Barr Mine	Center Sect. 7 T36S R8W	flat		658m (2160 ft)
Briggs Creek	Lower center Sect. 6 T37S R9W	flat		280m (920 ft)
Lower Peavine	Center Sect. 35 T34S R8W	10° (18%)	290° (WNW)	381m (1250 ft)
New Place	Lower center Sect. 34 T34S R8W	-	90° (E)	647m (2125 ft)
Nobles House	Right half center Sect. 35 T36S R10W	23° (42%)	175° (S)	422m (1386 ft)
Oak Flat	Lower right Sect. 6 T37S R9W	varies		335m (1100 ft)
Site Three	Upper center Sect. 19 T36S R8W	11° (20%)	126° (SE)	640m (2100 ft)
Soldier Creek	Lower right Sect. 5 T32S R9W	1.5° (11%)	338° (N)	487m (1600 ft)
Squirrel Place	Upper left Sect. 10 T35S R8W	11.5° (20%)	120° (ESE)	381m (1250 ft)
Taylor Creek	Lower left Sect. 28 T35S R8W	31° (60%)	200° (SSW)	579m (1900 ft)
Taylor House	Lower left Sect. 13 T35S R8W	23° (43%)	210° (SSW)	365m (1200 ft)
Upper Peavine	Center left Sect. 35 T34S R8W	flat		487m (1600 ft)
West Fork Taylor	Center Sect. 28 T35S R8W	flat		449m (1475 ft)

Plant Associations

General Vegetation in Undisturbed Areas

Community measurements in undisturbed areas were done in only seven locations. The remaining six areas could not be visited for this purpose or were so highly disturbed that the plot would not have adequately represented a natural condition. Locations were chosen that showed the least signs of disturbance; however, fire and/or man-related activities were evident at all sites.

The vegetation associated with Sophora leachiana belongs to the Mixed Evergreen Forest formation. All sites supported the characteristic upper conifer stratum with a lower stratum of sclerophylls and deciduous trees. Pseudotsuga menziesii was the dominant in all seven stands as only rarely did another species possess a higher abundance, biomass or cover value (Table 4). Seedlings and young trees were numerous at all locations indicating successful reproduction. Members of the genus Pinus, represented by P. lambertiana and P. ponderosa, were present at every site. All locations had large old Pinus individuals; occasionally they were so widely scattered that they were not included within the plot itself. Only Briggs Creek possessed both species of Pinus; each was represented as large trees and saplings. (Pinus ponderosa was planted at Taylor Creek; only P. lambertiana was native). Other conifers were seen only as infrequent individuals; these species included Libocedrus decurrens, Taxus brevifolia, Thuja plicata, and Chamaecyparis lawsoniana.

Table 4. Vegetational data for undisturbed plots

		Ps me	Qu ke	Ar me	Pi la	Pi po	Litde	Qu ch	Co co	Libde	Ca ch
Sq	A	76 (81)	4 (4)	3 (3)	6 (6)		8 (9)	3 (3s)		+	1 (1)
	B	38	26	21	16		-	-			0.1
	C	58	17	13	10		1	1			1
	D	57	16	12	10		3	1			1
Br	A	33 (39)	10 (12)	+	20 (23)	3 (3)	5 (6)	28 (33)		1 (1)	
	B	30	7		4	51	0.2	9		0.3	
	C	36	14		12	19	2	17		1	
	D	33	11		12	24	3	18		0.5	
TC	A	23 (15)	5 (3)	10 (6)	23 (15)	+	28 (18)	14 (9)	+	+	+
	B	63	8	5	21		4	1			
	C	39	8	19	12		15	8			
	D	41	7	11	18		15	7			
S3	A	30 (16)	77 (4)	+	4 (2)		15 (8)	13 (7)	33 (18)		+
	B	90	9		-		-	-	-		
	C	70	22		2		1	1	4		
	D	63	13		2		5	5	12		
Ba	A	53 (18)	24 (8)	6 (1)		3 (1)			15 (5)	+	
	B	60	4	2		34			0.1		
	C	54	14	11		14			7		
	D	55	14	6		17			7		
Th	A	74 (58)	8 (4)	15 (6)	+		1 (1)	3 (2)	+		+
	B	88	9	3			-	-			
	C	68	18	14			-	-			
	D	77	12	11			0.4	1			

Table 4. (cont)

		Ps me	Qu ke	Ar me	Pi la	Pi po	Litde	Qu ch	Co co	Libde	Ca ch
LP	A	48 (39)	40 (33)	5 (4)		+	+	7 (6)			+
	B	40	16	43				-			
	C	48	39	13				-			
	D	45	32	20				2			
Mean Values	A	48 (226)	14 (68)	5 (20)	7 (46)	1 (4)	9 (42)	10 (60)	7 (23)	0.1 (1)	0.1 (1)
	B	58	11	11	6	12	1	1	0.1	0.05	0.03
	C	53	19	10	5	5	3	4	2	0.1	0.2
	D	53	15	9	6	6	4	5	3	0.1	0.1

A - percent individuals (number of individuals of that species)

B - percent biomass expressed as percent basal area

C - percent relative cover

D - importance value; sum of A, B, and C divided by three.

+ - present in area, but not included in plot.

Ps me - Psuedotsuga menziesii

Qu ke - Quercus kelloggii

Ar me - Arbutus menziesii

Pi la - Pinus lambertiana

Pi po - Pinus ponderosa

Litde - Lithocarpus densiflora

Qu ch - Quercus chrysolepis

Co co - Corylus cornuta var. californica

Libde - Libocedrus decurrens

Ca ch - Castanopsis chrysophylla

The coniferous layer was the dominant one at all locations (Table 5). Conifers possessed the highest abundance at all sites except Site Three and Taylor Creek where deciduous trees and sclerophylls respectively possessed more aerial stems. Sclerophylls totalled a higher biomass at Lower Peavine and a higher cover at Taylor Creek. Taylor Creek's biomass data of 84 percent conifer attributed basal area suggest that conifers remain dominant at this site despite the abundance and cover values. Conifers compiled 60 percent of the 531 aerial arborescent stems representing the seven plots. The actual density of conifers in number of aerial stems per hectare varied from 489 to 2364. The lower density values reflected larger, more widespread individuals with high biomass rather than smaller, closely spaced trees.

The density of sclerophylls and deciduous trees varied between 54 to 1059 and 81 to 897 stems per hectare respectively. At only two locations (Squirrel Place, Taylor House) were the deciduous species and sclerophylls of equal importance; the remaining locations had one species class of greater importance than the other. Combined data for the seven plots yielded very similar values for the sclerophyll and deciduous species; 23 and 17 percent abundance, 12.5 and 11 percent biomass 17 and 20 percent cover respectively with both species types possessing importance values of 17.

The presence list can be used to signal the suggested place of each stand along the moisture gradient. Site Three and Barr Mine are mesic; both sites are also very close to perennial streams.

Table 5. Summarized data for conifer, sclerophyll, and deciduous species in the undisturbed plots.

St/ha = aerial stems per hectare
 A = percent abundance
 B = percent biomass

C = percent cover
 I = importance value

Site	St/ha	Conifers				St/ha	Sclerophylls				St/ha	Deciduous Species			
		A	B	C	I		A	B	C	I		A	B	C	I
Ba	516	56	94	68	73	54	6	2	11	6	353	38	4	21	21
Br	1793	56	85	67	70	1059	33	9	19	20	326	10	7	14	10
LP	1059	48	40	48	45	271	12	43	13	22	897	40	16	39	32
Sq	2364	81	53	67	67	434	15	21	16	17	108	4	26	16	15
S3	489	33	90	72	65	407	27	0.2	2	10	598	40	9	26	25
TC	815	45	84	50	60	897	50	9	42	34	81	5	8	8	7
Th	1576	82	88	68	80	244	13	3	14	10	108	5	9	18	11
Mean	1230	60	76	63	66	481	23	12	17	17	353	17	11	20	17

Deciduous trees are chiefly represented by Quercus kelloggii. This species was the subdominant in four of the seven plots and stayed high in importance in the remaining three areas where Pinus was subdominant. Reproduction by Q. kelloggii was abundant; only at Squirrel Place were seedlings not of sufficient number to be included within the sample plot. Quercus kelloggii seedlings are considered to be the most shade intolerant of the major species present in this vegetation unit (Franklin and Dyrness, 1969), therefore their presence possibly indicates that the forest canopy is recovering from a fairly recent disturbance or will always remain fairly open. Corylus cornuta was another deciduous species present in four locations. Quercus garryana was present in the sites along the Illinois River (Briggs Creek and Nobles House), and Acer macrophyllum was present near the stream bank at Barr Mine.

The remaining species are the sclerophylls. One of the dominant sclerophylls is Arbutus menziesii, a fire-indicating species whose aerial portions are easily killed by fire but which forms sprouts from the root collar (Emmingham, 1973). Arbutus averaged nine percent importance value and was represented in all stands by large, widely spaced individuals as well as saplings. Lithocarpus densiflora and Quercus chrysolepis were present in all sites except Barr Mine and were not abundant at Taylor House. They were a conspicuous and often important element of the flora at the remaining sites. Both species vary in growth from being represented as shrubs as well as trees; root sprouting can occur after a fire or cutting. In order to be

consistent, and because it was difficult to tell a young tree from a shrub, these sclerophyll species were considered as trees. They attained true tree status at Taylor Creek and Briggs Creek; the remaining sites were characterized by more shrubby growth forms. Castanopsis chrysophylla, the other major sclerophyll species, occurred in a majority of stands; however it existed as scattered individuals of rather low abundance.

Shrub coverage was not high at any site. Rhus diversiloba was present at all locations, and combined data showed this was the dominant shrub with 43 percent of the aerial stems. However, the species was not of sufficient abundance at Site Three and Barr Mine to be included within the plots and was subdominant to Berberis nervosa and Lonicera hispidula at Taylor House. Berberis was present at all sites; Lonicera was absent only at Barr Mine. Other species included Whipplea modesta, Rosa gymnocarpa, Rhamnus californica var. occidentalis and Symphoricarpos albus.

Herbaceous cover was very sparse in all undisturbed plots, and at Taylor Creek and Briggs Creek herb abundances were so low that none occurred in the study plot. Sophora leachiana did extend into the study area at Site Three, Squirrel Place and Lower Peavine; this species was the dominant herbaceous member at the two latter populations. Sophora possessed 53 percent of the 57 herbaceous aerial shoots found in all populations sampled. Polystichum munitum and Pteridium aquilinum were other important species as were Hieracium albiflorum and Fragaria vesca.

Species present in one of the two areas that indicate a mesic or submesic state include Salix sp., Taxus, Linnaea borealis, Achlys triphylla and Adenocaulon bicolor (see Whittaker, 1960). As expected, these two sites possessed the lowest importance values for sclerophylls with Lithocarpus and Quercus chrysolepis completely absent from the immediate area at Barr Mine.

Briggs Creek's sclerophyll value was relatively high; the presence list included both mesic and xeric indicators. These conflicting data were caused by a small seepage area around which were the mesic species Chamaecyparis, Rhododendron occidentale, Woodwardia fimbriata and others. The vegetation away from the seepage area and at the other four localities was xeric or subxeric in nature.

The data agree well with Whittaker's and Emmingham's outline of the vegetational structure of the Mixed Evergreen Forest. However, both authors were able to divide the formation into several subclasses. These subclasses usually contained identical arborescent species; differentiation was based on differences in importance of the species, along with variation in species composition and/or importance of shrub and herbaceous layers. In order to test if the areas supporting Sophora could be differentiated into two or more vegetation subclasses, Braun-Blanquet's manual-visual table was constructed. Constancy values of 10 to 60 percent were used for species selection. The table was first constructed using the species list for only the undisturbed areas of each of the seven sites. However, because the species were very constant for the undisturbed areas, this analysis could not be performed using only the data from the undisturbed sites.

When the vegetational data for the undisturbed and disturbed areas were combined (see Table 6 for a species list), a separation into two population groupings was obtained based on the presence of seven species. However, two were successional species (Ribes lobbii, Rhamnus californica var. occidentalis), one was weedy (Cirsium vulgare) and another was an annual (Epilobium paniculatum) that could not have been represented late in the season. Because the only separation achieved concerned species whose presence would be governed by the nature and age of the disturbance, along with the time of year visitation took place, the twelve Sophora populations probably occur in only one broad vegetational type. Fluctuations were apparent in the sub-dominant order at several sites, but this may have been related to slight variations present within each forest or to the moisture gradient. More intensive sampling would possibly have resulted in less variability in forest co-dominant order or in possible differentiation of two community types based on a difference in importance of the species.

General vegetation in disturbed areas

The thirteen Sophora communities were visited at least once; associated species were listed if formal community measurements were not taken. All sites were highly disturbed through clearcutting and burning (Site Three and Taylor Creek), partial cutting and burning (Taylor House), mining (Upper Peavine, Briggs Creek), road construction (Squirrel Place, Upper Peavine, Lower Peavine, Soldier Creek, West Fork Taylor, New Place, Barr Mine), and through fire (Nobles

Table 6. Species associated with Sophora leachiana.

	Ba	Br	LP	NH	NP	OF	S3	SC	Sq	TC	TH	UP	WFT
<u>Acer circinatum</u> Pursh													X
<u>A. macrophyllum</u> Pursh	X							X					X
<u>Arbutus menziesii</u> Pursh	X	X	X	X	X	X	X	X	X	X	X	X	
<u>Castanopsis chrysophylla</u> (Dougl.) A. DC.				X			X		X	X	X		
<u>Chamaecyparis lawsoniana</u> Parl.		X											
<u>Cornus nuttallii</u> Aud.				X			X	X			X		X
<u>Corylus cornuta</u> Marsh var. <u>californica</u> (A. DC.) Sharp	X		X				X	X		X			X
<u>Libocedrus decurrens</u> Torr.	X	X			X			X	X	X			X
<u>Lithocarpus densiflora</u> (H. & A.) Rehd.		X	X	X	X		X	X	X	X	X	X	X
<u>Malus</u> sp.		X											
<u>Pinus lambertiana</u> Dougl.		X		X		X	X	X	X	X	X	X	
<u>P. ponderosa</u> Dougl.	X	X	X	X	X	X		X	X	X		X	
<u>Prunus emarginata</u> (Dougl.) Walpers							X						
<u>Pseudotsuga menziesii</u> (Mirb.) Franco	X	X	X	X	X	X	X	X	X	X	X	X	X
<u>Quercus chrysolepis</u> Liebm.		X	X	X	X		X	X	X	X	X	X	X
<u>Q. garryana</u> Dougl.		X		X									
<u>Q. kelloggii</u> Newb.	X	X	X	X	X	X	X	X	X	X	X	X	
<u>Salix</u> sp.	X						X						
<u>Taxus brevifolia</u> Nutt.							X		X				X
<u>Thuja plicata</u> D. Don		X											
<u>Amelanchier florida</u> Lindl.													X
<u>Arctostaphylos columbiana</u> Piper		X			X					X			
<u>A. canescens</u> Eastw.		X		X					X			X	
<u>A. parvifolia</u> How.											X		
<u>A. canescens</u> x <u>viscida</u> Parry												X	
<u>Berberis nervosa</u> Pursh.	X	X					X		X	X	X		X
<u>Ceanothus integerrimus</u> H. & A.	X	X	X	X			X		X	X	X	X	
<u>C. pumilus</u> Greene		X	X							X		X	
<u>C. velutinus</u> Dougl.										X			

Table 6 cont'd.

	Ba	Br	LP	NH	NP	OF	S3	SC	Sq	TC	TH	UP	WFT
<u>Holodiscus discolor</u> (Pursh.) Maxim.							X			X			X
<u>Osmaronia cerasiformis</u> (T.&G.) Greene	X												
<u>Linnaea borealis</u> L. var. <u>americana</u> (Forbes) Rehd.							X						
<u>Lonicera hispidula</u> Dougl. var. <u>vacillans</u> (Benth.) Gray		X	X	X			X	X	X	X	X	X	X
<u>Rhamnus californica</u> Esch. var. <u>occidentalis</u> How.		X								X			
<u>Rhododendron occidentale</u> s		X											
<u>Rhus diversiloba</u> T. & G.	X	X	X	X	X	X	X		X	X	X	X	
<u>Ribes lobbii</u> Gray		X					X						
<u>Rosa gymnocarpa</u> Nutt.			X				X	X	X		X	X	X
<u>Rubus leucodermis</u> Dougl.												X	
<u>R. parviflorus</u> Nutt.							X						
<u>R. ursinus</u> C. & S. (= <u>R. vitifolius</u> C. & S.)	X	X					X			X			
<u>Symphoricarpos albus</u> (L.) Blake	X	X	X				X	X		X	X	X	X
<u>Vaccinium ovatum</u> Pursh				X									
<u>Vitis californica</u> Benth.	X												
<u>Whipplea modesta</u> Torr.		X	X	X					X	X	X	X	X
<u>Achlys triphylla</u> (J. E. Smith) DC.	X												
<u>Adenocaulon bicolor</u> Hook.	X												X
<u>Aira caryophylla</u> L.	X	X							X	X		X	
<u>Apocynum pumilum</u> (Gray) Greene	X	X			X			X				X	
<u>Arenaria</u> sp.								X					
<u>Aster radulinus</u> Gray.	X			X	X		X	X	X				
<u>Boschniakia strobilacea</u> Gray									X				
<u>Brodiaea elegans</u> Hoov.		X											
<u>Bromus mollis</u> L.		X								X			
<u>B. sterilis</u> L.		X											
<u>B. tectorum</u> L.										X			
<u>Campanula scouleri</u> Hook	X		X					X					
<u>Cardamine</u> sp.			X									X	
<u>Carex</u> sp.	X	X							X				
<u>Caucalis microcarpa</u> H. & A.		X								X			
<u>Chimaphila umbellata</u> (L.) Nutt. var. <u>occidentalis</u> (Rydb.) Blake		X			X		X		X	X			

Table 6 cont'd.

	Ba	Br	LP	NH	NP	OF	S3	SC	Sq	TC	TH	UP	WFT
<u>Cirsium vulgare</u> (Savi) Airy-Shaw		X								X			
<u>Clarkia rhomboidea</u> Dougl.										X			
<u>Collinsia torreyi</u> Gray var. <u>latifolia</u> News.		X										X	
<u>Collomia heterophylla</u> Hook.		X	X									X	
<u>Convolvulus</u> sp.							X						
<u>Cynoglossum grande</u> Dougl.	X											X	
<u>Cynosurus echinatus</u> L.		X					X						
<u>Dicentra formosa</u> (Andr.) Walp.	X												
<u>Disporum hookeri</u> (Torr.) Britt. var. <u>trachyandrum</u> (Torr.) Q. Jones							X	X					X
<u>Dryopteris arguta</u> (Kaulf.) Watt			X										
<u>Elymus glaucus</u> Buckl.		X											
<u>Epilobium angustifolium</u> L.							X						
<u>E. minutum</u> Lindl.		X											
<u>E. paniculatum</u> Nutt.							X			X			
<u>Eriogonum nudum</u> Dougl.											X		
<u>Eriophyllum lanatum</u> (Pursh.) Forbes.											X		
<u>Fragaria vesca</u> L.	X	X	X				X			X		X	X
<u>F. virginiana</u> Duchesne												X	
<u>Festuca megalura</u> Nutt.										X			
<u>F. myuros</u> L.		X											
<u>Galium ambigium</u> Wight		X								X		X	
<u>G. andrewsii</u> Gray				X									
<u>G. aparine</u> L.										X			
<u>Gilia capitata</u> Dougl.										X	X		
<u>Godetia quadrivulnera</u> (Dougl.) Spach										X			
<u>Goodyera oblongifolia</u> Raf.							X	X	X				
<u>Habenaria</u> sp.			X						X			X	
<u>Hieracium albiflorum</u> Hook.	X			X	X		X	X	X		X	X	
<u>Hypericum perforatum</u> L.	X	X					X			X	X		X
<u>Iris chrysophylla</u> How.	X			X				X	X			X	
<u>Lactuca canadensis</u> L.	X									X			
<u>Lathyrus polyphyllus</u> Nutt.			X				X	X				X	
<u>Lepidium campestre</u> (L.) R. Br.												X	
<u>Linanthus bicolor</u> (Nutt.) Greene		X								X			

Table 6 cont'd.

	Ba	Br	LP	NH	NP	OF	S3	SC	Sq	TC	TH	UP	WFT
<u>Lomatium howellii</u> (Wats.) Jeps.		X											
<u>Lotus americanus</u> (Nutt.) Bisch.		X											
<u>Lotus crassifolius</u> (Benth.) Greene										X		X	
<u>L. purshianus</u> (Benth.) C. & C.			X									X	
<u>Lupinus micranthus</u> Dougl.		X	X		X							X	
<u>Lupinus</u> sp. (perennial)			X		X							X	
<u>Luzula campestris</u> (L.) DC.		X										X	
<u>Madia gracilis</u>			X							X	X	X	
<u>Osmorhiza chilensis</u> Hook. & Arm.	X	X				X		X					X
<u>Phleum pratense</u> L.		X											
<u>Plantago lanceolata</u> L.	X	X											
<u>Plagiobothrys</u> sp.										X			
<u>Polygala californica</u> Nutt.		X		X									
<u>Potentilla</u> sp.			X								X	X	
<u>Polystichum munitum</u> (Kaulf.) Presl	X		X	X	X		X	X	X		X	X	X
<u>Psoralea physodes</u> Dougl.							X				X	X	
<u>Pteridium aquilinum</u> (L.) Kuhn	X	X	X	X	X	X	X	X	X	X	X	X	
<u>Pterospora andromedea</u> Nutt.	X												
<u>Pyrola aphylla</u> J. E. Sm.				X						X		X	
<u>Ranunculus occidentalis</u> Nutt.		X										X	
<u>Rumex acetosella</u> L.	X									X			
<u>Sanicula bipinnatifida</u> Dougl.		X											
<u>Scutellaria epilobifolia</u> Hamilt.		X											
<u>Senecio</u> sp.	X												
<u>Sidalcea asprella</u> Greene		X											
<u>Smilacina amplexicaulis</u> Nutt.													X
<u>Stachys</u> sp.		X											
<u>Synthyris reniformis</u> (Dougl.) Benth.	X												
<u>Trientalis latifolia</u> Hook.	X		X				X	X			X	X	X
<u>Trifolium dubium</u> Sibth.		X	X								X	X	
<u>Vancouveria</u> sp.	X					X							
<u>Vicia americana</u> var. <u>truncata</u> (Nutt.) Brew.		X										X	
<u>V. sativa</u> L.	X	X			X				X		X	X	X
<u>Viola glabella</u> Nutt.			X	X								X	

Table 6 cont'd.

	Ba	Br	LP	NH	NP	OF	S3	SC	Sq	TC	TH	UP	WFT
<u>V. lobata</u> Benth.		X										X	
<u>Woodwardia fimbriata</u> J. E. Sm.		X											
<u>Xerophyllum tenax</u> (Pursh.) Nutt.				X					X	X			
<u>Zygadenus micranthus</u> Eastw.												X	

House, Briggs Creek, Upper Peavine, Lower Peavine, Squirrel Place). These areas harbor three categories of species; these divisions are very broad as a species might possess characteristics of more than one category.

A wide variety of weedy species that can colonize an ecologically diverse array of disrupted sites were represented. This category was especially important in areas that had been repeatedly disturbed. Other species present in the area with Sophora include residual species that have survived the disturbance. The majority of species in this category were represented as root or stump sprouts; Arbutus, Corylus, Lithocarpus, Quercus chrysolepis, and Q. kelloggii fit into this class.

The third division included species important in secondary succession and associated with more distinct vegetation types than weedy species. Examples of these early successional plants include Ceanothus and Arctostaphylos. These genera were usually represented only in the disturbed area itself and were not found in the adjacent, undisturbed forest. Arctostaphylos skeletons remained in the regenerating forests at several sites. Arctostaphylos and Ceanothus are fire species (Quick, 1959). The seeds of Ceanothus integerrimus germinate after exposure to high temperatures caused by fire (Quick, 1935, 1959; Quick and Quick, 1961) or high solar insolation, or by scarification of the seed coat (Cronmiller, 1959). Early successional species were rarely included in the arborescent layer; therefore tree reproduction in the disturbed sites was similar to that in the surrounding areas.

The exceptions were small areas that contained a flush of one species' saplings. Competition will probably alter the composition to the more homogeneous mixture of species represented by the remaining areas of the site. The shrub layer of the disturbed and undisturbed areas was also similar, except that the disturbed area also possessed several successional species.

The disturbed sites usually supported a dense covering of herbaceous vegetation. Because Sophora leachiana was the focus of the study, sample sites always included a large section of each Sophora colony. Therefore the data do not reflect the vegetation structure of the entire disturbed area but only the areas sampled. In association with Sophora at these different locations were such species as Pteridium aquilinum, Hypericum perforatum, and Lathyrus polyphyllus. Various grasses formed an integral part of the herbaceous layer.

Site Descriptions

Peavine Mountain Populations - Upper Peavine, Lower Peavine and New Place. Two of the three Peavine Mountain populations, Upper Peavine and Lower Peavine, occur on the southern ridge about 90 meters above Rich Gulch; Peavine Mountain Road (BLM 35-8-2) also follows the ridge. Lower Peavine begins 1.4 km west of the intersection of BLM 35-8-2 with Rd 3500. This is a large Sophora population; individuals are usually confined to the immediate roadsides but do occasionally extend back into the surrounding forest.

The Upper Peavine population is centered approximately 0.8 km farther up the road towards Peavine Mt. At this location a large cleared roadway leading to a private residence begins to the left of the Peavine Mt. Road. To the right is the large placer mine from the Old Channel Gravel Company. Sophora extends down into the southern boundary of the placer. Although two high density clusters of Sophora occur along the Peavine Mt. road, (forming the center of the Upper and Lower Peavine populations, respectively) there is no clear-cut boundary separating the populations, as patches of Sophora are found at irregular intervals connecting the two population centers. Differentiation of the two populations is based on the observation that Upper Peavine individuals lack pollen production whereas Lower Peavine individuals do make abundant pollen.

All surrounding vegetation in this Peavine Mt. area has been disturbed to a great degree. Mining was in operation at the Black Bear Mine and Old Channel Mine in the early 1900's. Other mines also existed along Rich Gulch and in the nearby vicinity. The forest shows signs of cutting as stumps are found in the area especially near the roadways. Large trees frequently have fire scars; numerous other trees appear to be root or stump sprouts. Community analysis was performed only at Lower Peavine because the Upper Peavine location was similar, yet so highly disturbed that vegetation patterns would be obscure.

The disturbed areas at Lower Peavine and Upper Peavine supported a regenerating forest of the same nature as the undisturbed

area at Lower Peavine. Dominance in the arborescent layer was shared by Pseudotsuga and Quercus kelloggii, followed by the subdominant Arbutus. Rhus and Rosa were important shrubs. Upper Peavine supported a wide variety of herbaceous members; Aira caryophylllea was very common in both disturbed areas. Sophora was the only herb in the undisturbed plot.

The third population found on Peavine Mt. is New Place, located 2.0 km past the Upper Peavine population. Sophora is represented by about 50 plants growing in the slippage area caused by a road cut along BLM 35-8-2. A dozen or so plants extend several meters into the woods. The vegetation with Sophora is very disturbed, as several large stumps and many downed logs are present. Community analysis using Poulton's index rated Arbutus and Pseudotsuga as co-dominants followed by Quercus kelloggii and Pinus ponderosa. Large trees and seedlings of all four dominant members were apparent, although the major fraction of regeneration appeared to be borne by Douglas fir and ponderosa pine. Shrubs included Arctostaphylos columbiana, Rhus diversiloba, with Lithocarpus and Quercus chrysolepis represented as shrubby individuals. Herbs were sparse but included Aster radulinus, Pteridium aquilinum and Chimaphila umbellata var. occidentalis.

Squirrel Place. Squirrel Place is located on Road 3500 at the sharp right curve about 1.6 km south of the junction with BLM 34-8-36. An abandoned dirt road intersects from the north with Rd 3500 at this point. Downslope about 61 m south of Rd 3500 is Galice Creek.

Sophora is represented by a few individuals adjacent to the southern

edge of Rd 3500 but is most common in the abandoned road at its junction with Rd 3500. Here, the forest has been completely cleared. The ground cover is still very sparse with Sophora being the dominant species. Although other herbaceous species were present in the clearing, bracken fern was the only other species represented in the plot, contributing a mere 0.5 percent of the herbaceous individuals and 0.4 percent cover. Ceanothus integerrimus individuals were present but confined to the open road area. Other shrubs included Rhus and Whipplea. Encroachment of the forest is evident in the closest quadrat to the forest, which included seedlings or saplings of Pseudotsuga, Pinus lambertiana, P. ponderosa, Arbutus, and Lithocarpus.

The surrounding forest has been disturbed to some degree as large Douglas firs (DBH approximately 120 cm) and other logs are scattered on the forest floor. Fire scars were present on several large Quercus kelloggii. The plot used to determine community vegetation was located due north of the dirt road.

The dominant for the forest was Douglas fir. Large individuals were present but the majority of individuals were younger saplings (DBH 15.24 cm). Kellogg oak, sugar pine, and Arbutus shared co-dominance as all three were present as scattered large trees (> 50 cm DBH) plus a few smaller individuals. Castanopsis, Lithocarpus, and Quercus chrysolepis furnished the lower tree strata. Rhus and Berberis were the most common shrubs; Sophora did extend far enough into the forest to be listed as the dominant herb.

Taylor House. Taylor House population is located along Rd 355 to the north side of the road about 45 meters above Taylor Creek and the private residence. The crest of the ridge is about 45 meters above the road. This area is the site of the commercial cut Taylor 02302-105C3. According to information attained from the United States Forest Service in Grants Pass, this area was a storm salvage partially cut in 1967; the slash was piled and burned that same year. The trees east of the road and "almost to the ridge top" were pruned in February of 1968. Manual weeding and release (i.e., without chemicals) was accomplished in June of 1968; further thinning occurred in January of 1971. The northern half of the partial cut has retained many trees, whereas shrubs are dominant but widely scattered in the southern half. These shrubs include Ceanothus integerrimus, Symphoricarpos albus, Rhus diversiloba and Lonicera hispidula. A three by 25 meter transect analyzed in the shrub zone yielded a total shrub cover of only 8.8 percent. One Quercus kelloggii seedling was the only tree species represented. Herbaceous vegetation included Aira caryophyllea with 28 percent cover. Sophora was abundant but did not form dense stands as the 128 individuals totaled only 4.8 percent cover. Psoralea physodes was represented in the quadrat by one individual.

Besides occurring in the shrub zone of the partial cut, Sophora is represented by scattered individuals in the upper forested area on up the ridge line; the species is not found on the other side of the ridge. Sophora also forms very thick stands lining the edge of the southern bank of the road but does not extend down the steep very grassy

southern roadside onto the private property.

The plot used to compare community structure was located to the northeast of this area before Taylor 02302-153C2 (another partial cut). The stand was not undisturbed, as fire scars were apparent on the large Douglas firs (68 and 86 cm DBH) and Arbutus was often represented as numerous root sprouts. Douglas fir is the dominant species contributing over 50 percent to each index value measured. Subdominants Quercus kelloggii and Arbutus are represented by older individuals and saplings; seedlings of Lithocarpus and Quercus chrysolepis were also present. A more varied shrub layer occurred at Taylor House than at many of the other Sophora populations; Berberis, Symphoricarpos, Whipplea, Rhus, Lonicera and Rosa were all included in the plot. Herbs were represented by Hieracium albiflorum and Polystichum munitum.

West Fork Taylor. A small population of Sophora leachiana is found just south of the junction of Rd 355 and West Fork of Taylor Creek. Here, a dirt road paralleling the West Fork a short distance leads to a 1969 clearcut and burn (Lonetree 02304-3902 and 5902). Sophora is not found in the clearcut but occurs at the junction of the dirt road with 355. The forest immediately adjacent to the stream was not cleared of vegetation. Douglas fir is the dominant species; other arborescent members include Libocedrus, Acer macrophyllum and A. circinatum, Taxus, Cornus nuttallii and Corylus. Lithocarpus and Quercus chrysolepis were represented by small individuals less than 1 m in height. Shrubs were dominated by Symphoricarpos and Lonicera and

included Rosa, Berberis and Holodiscus. Herbaceous vegetation in this riparian area were represented in part by Trientalis, Adenocaulon, Fragaria and Polystichum. Sophora exists as 21 scattered individuals in the southern edge of the forest. Another 13 are found adjacent to the dirt road. Across the logging road is a cleared area now supporting a variety of residual and weedy species including Hypericum, Achillea, Symphoricarpos and Berberis. Twenty two Sophora individuals are found at the edge of this area; the Sophora population does not cross Rd. 355.

Taylor Creek. Taylor Creek clearcut is located along Rd 355. The area is near two eastward directed ridges, resulting in southwestern, eastern, and northeastern aspects in the clear cut. Two small drainages are found in the western quarter of the area; these merge and bisect the remaining clearcut before flowing into the South Fork of Taylor Creek 73 meters below. Rd 355 cuts through the northern quarter of the clear cut. The 54 acre area was cut and burned in 1959. Douglas fir was planted in 1960, and in 1962 all 54 acres were seeded with Douglas fir and ponderosa pine. Reseedling with ponderosa pine took place in 1964. 2-4-D was sprayed on the area in April of 1966 followed by atrazine in 1969. In 1969 all 54 acres had to be replanted (species not recorded). A 1970 survey showed 24 acres satisfactorily stocked, 8 acres unsatisfactorily stocked and 22 acres nonstocked. By 1971 only 6 acres were classified as unsatisfactorily stocked with the remaining 48 acres satisfactorily stocked (although a 1971 diagram labels the 6 acres as nonstocked). In 1975 site preparation followed by replanting took place on 8 acres. These replanted

acres were fertilized by hand in winter of 1976 with 600 lbs/acre of 27-12-0.

Sophora leachiana is found in the northern section of the clearcut above 355 and along the road's edge. Thick patches of the species occur along the roadside by the more northern drainage and extend below the road between the two drainage areas. Sophora's abundance in these areas ranges from very dense stands to more dispersed colonies. No Sophora is found on the southwest slope below the road, nor does the species occur on the northeast facing slope. The species is present to the ridge line of the southwest facing slope but is not found on the other side of the ridge.

Ceanothus integerrimus was an important species associated with Sophora; a 25 x 3 meter quadrat placed north of 355 yielded 20 individuals and 35 percent cover for this species. Other shrubs included Rhus, Whipplea and Holodiscus. Sophora totaled 718 individuals (28 percent cover). Lotus crassifolius and Caucalis microcarpa were other important forbs. Other regions of this section of the clearcut included vast areas composed of Ceanothus integerrimus with a very dense understory of pure Bromus tectorum stands.

The stand used to determine the vegetation before clearcutting was located above the northwest corner of the clearcut approximately 15 meters from the crest of the ridge. Fire scars were apparent on the older trees. Once again, Pseudotsuga was dominant; Pinus lambertiana and Quercus kelloggii were subdominants present at large individuals and young saplings. Arbutus was important although seedlings were not

of sufficient abundance to be included in the study plot. Quercus chrysolepis and Lithocarpus attained definite tree status and were conspicuous members of the understory. Rhus was the sole shrub. No herbs were included in the study plot although Chimaphila umbellata was present in the forest.

Barr Mine. Barr Mine population is located adjacent to the northwest boundary of the Barr Mine property in Briggs Valley along Rd 355. The population may be reached by following Taylor Camp Trail 1138 south from Big Pine Campground, or the road through Barr Mine indicated at its intersection with Rd 3603 by a sign stating "Trail No. 1146 $\frac{1}{4}$ mile". The Sophora population is located just northeast of Dutchy Creek. Sophora is found in one patch along the road and extends back through the forest into several clearings. Numerous stumps are present although the area does not appear to have been commercially logged. Several commercial partial cuts are found near this location along the Taylor Camp Trail.

The plot used to sample the Sophora community was located in the cleared meadow. Numerous stumps were present; Corylus, Pseudotsuga, and Quercus kelloggii were represented by root sprouts. Small shrubs were very common and included Symphoricarpos, Rubus, Ceanothus integerrimus, and Berberis. Herbaceous vegetation was abundant and included many species. Bracken fern was the dominant with 42 percent abundance and 25 percent cover, followed by Hypericum (22 percent abundance, 2.0 percent cover) and Sophora (14 percent abundance and 1.5 percent cover).

The community analysis plot was located in the forest north-east of the Sophora population. This section of the forest appeared to be relatively free of disturbance. Douglas fir was dominant, contributing over 50 percent of all three measured parameters, and all age classes were represented. Quercus kelloggii, Pinus ponderosa and Arbutus were subdominants. Young plants of all species were noted although no ponderosa pine seedlings were included within the plot. Shrubs and herbaceous members were sparse; Rubus ursinus and Fragaria vesca were the most important species in their respective categories. This is the only location in which Lithocarpus and Quercus chrysolepis were not represented. Both species were present in other areas of Briggs Valley, such as near Big Pine Campground. Here, the forest had matured into an old growth, fire scarred Douglas fir and ponderosa pine forest.

Site Three. Site Three is located along 355 about 1.6 km south of the junction with 3693 and 1.6 km north of 3694. This clearcut (Waterdog 02309-68C2, 76C2, and 77C2) is bisected by Rd 355 running the length of the eastern quarter of the clearcut and by a dirt road leading to Elkhorn Mine, paralleling 355 in the western quarter. Drainage patterns flow into Briggs Creek located near the southern end of the area. The aspect to the north of the drainage is south-east; to the south the aspect varies from northwest to flat. Sophora grows in the southwest corner of the clearcut and patches extend northeast along the Elkhorn mine dirt road for approximately three fourths the length of the clearcut. The 34 acres were clearcut in

1963 and burned in 1965. Douglas fir was planted in March of 1968. In 1970 eight acres were stocked satisfactorily; 26 were unsatisfactorily stocked. By the following year 20 acres were classed as satisfactory and 14 as nonstocked. In 1972 27 acres were satisfactory; 7 were nonstocked. Three pounds of 2,4,5-T in 7.5 gallons of water per acre was sprayed in the southern half of the clearcut in September of 1972. Four acres were dishpanned (4' x 4' areas cleared of vegetation to reduce competition) in 1972; in February, 1973, these acres were planted with ponderosa pine. A fall of 1973 survey yielded 31 satisfactorily stocked vs. three unsatisfactorily stocked, however records show that 14 acres underwent further site preparation and replanting, with 20 acres subjected to spraying as well. Fifteen acres were sprayed by helicopter in April of 1974 with three pounds of 2,4-D in 0.5 gallons oil and 9.5 gallons water per acre. The location of these 15 acres were indicated on the records only by the note "just above road"; therefore the exact spray area cannot be determined.

The Sophora community was sampled at the southwest end of the clearcut. Sophora was abundant in a small, highly disturbed area adjacent to the Elkhorn Mine road. Because only a minimum amount of information regarding work accomplished on a site is recorded, it is difficult to determine what was done to this small more disturbed area. However, this area was included in the 1972 2,4,5-T spraying and is near or possibly included in a dispan. The area sampled supported high diversity, as ten tree species were represented in the

plot with additional species recorded in the adjacent area. Most of the representation was by seedlings. A wide variety of shrubs and herbs were also present. Rubus parviflorus was the dominant shrub (44 percent abundance, 9 percent cover); Pteridium was the dominant herb (44 percent abundance, 12 percent cover) followed by Sophora (25 percent abundance, 2 percent cover).

An additional plot was placed upslope from the western boundary of the clearcut approximately three fourths the way to the ridge top. This area did show disturbance signs. Fire scars were present on Arbutus and Douglas fir; downed trees were numerous, a shallow pit and dirt pile were found near the plot. Douglas fir was dominant; Quercus kelloggii and Corylus shared subdominance, while Quercus chrysolepis and Lithocarpus formed the understory. Arbutus was widely scattered through the forest and was not included within the plot.

Shrub and herbaceous cover was very sparse. Sophora was present with a low frequency throughout this forest to the ridge top.

Soldier Creek. The Soldier Creek population may be reached by following Rd 3600 from the Illinois River Road. Sophora is found in scattered small patches in the road cuts climbing the south side of a ridge, with the most vigorous growth on the crest of the ridge before Soldier Creek is reached. Briggs Creek runs about 50 meters below the north side of the ridge. The private residences at Oak Flat near this location have run a water line beginning at the brook at the southern base of the ridge. Sophora is found in numerous, small patches along this water line and occasionally into adjacent disturbed places

within the forest. The crest of the ridge where Sophora is most abundant is a very disturbed region, as parts of the area have been cleared with a camp located nearby; cutting has occurred within the forest. Douglas fir was by far the most dominant species with an important value of 73 percent, followed by Quercus kelloggii. Lithocarpus seedlings were numerous. Shrubs included small individuals of Symphoricarpos and Rosa; no Rhus was present. A large number of herbaceous species are present of which Sophora was most numerous.

Briggs Creek. The Briggs Creek population is centered in a level area at the start of the Illinois River Trail 1163. This flat area is bordered on the east by Briggs Creek 15 meters below and on the southwest by the Illinois River 50 meters down. The population begins after the Briggs Creek crossing and extends to where the trail crosses Panther Creek about 40 meters away. Sophora is not found on the other side of Panther Creek. The area where Sophora occurs is the former location of Briggs Creek Mine which was active in the early 1900's. The forest has been cut, cleared and burned. Old mining equipment, wagons and old buildings are common along the trail. Sophora is very abundant in the clearings as well as in the regenerating, young forest. This disturbed site now supports almost pure stands of Douglas fir as well as other localities where Quercus kelloggii is the most important species followed by Pinus ponderosa. Selective cutting could possibly account for this difference in vegetation types. Rhus is the dominant shrub species with Rubus ursinus and Rhamnus also of importance. Rhododendrons are mostly

confined to wetter drainage areas but are scattered elsewhere in the forest. Arctostaphylos, Lithocarpus, and Quercus chrysolepis are important. A wide variety of herbaceous species are present of which Sophora and grasses are most prevalent.

Community structure analysis was done in the forest north of the Illinois River trail. The plot was located towards the end of the flat area before the land began to rise. Douglas fir was dominant; ponderosa pine, Quercus chrysolepis, Q. kelloggii, and Pinus lambertiana were also important. Only Rhamnus, Rhus, and Lonicera were representing the shrub layer; there were no herbaceous species included within the plot.

Oak Flat. An additional population of Sophora is found along the Illinois River Road 3504 connecting Oak Flat and the Briggs Creek campground. The population begins about 1.2 km before the campground is reached and is composed of small patches of individuals found along the roadsides or in nearby more disturbed areas of the adjacent forest. The population continues almost to the campground. The forest shows signs of disturbance including fire scars, stumps, and dirt piles. Although no formal measurements were taken, Arbutus, Quercus kelloggii, Pinus lambertiana and ponderosa pine seemed to be very important community members represented by large trees as well as saplings. Douglas fir was prevalent and was well represented by younger individuals but not as larger individuals. Pteridium and Rhus formed the majority of the other vegetative layers associated with Sophora.

Nobles House. This population occurs along the Illinois River trail just east of Clear Creek about 150 meters above the Illinois River. The site is an old burn; fire scars were seen on ponderosa pine and Arctostaphylos growing at the ridge crest about 30 meters above the trail. Charred logs are still on the forest floor. There is no evidence of cutting and the U.S.F.S. report that no commercial cutting has ever been done in this or nearby areas. Sophora is located along the path and at the ridge top. Scattered individuals are found through the forest connecting these two higher density areas. Sophora also occurs in a slippage area caused by the trail on the northwest side of the ridge. Only a very few individuals were found in the unburned forest at this location.

Douglas fir was dominant followed by Quercus kelloggii. Lithocarpus and Quercus chrysolepis were very important members of the community as their relative abundance values indicate. Rhus was the most important shrub. Numerous herbs were found in the plot; Sophora was the dominant species.

Other possible localities.

Various roadsides in the Peavine Mt. area and Briggs Valley area were surveyed for possible Sophora populations. Several additional clearcuts in the Taylor Creek drainage were searched for the species. There are several reported localities for Sophora that were explored, but the plant was not found. These reports suffered from vague locations which hindered the chances of finding the populations. These reports include:

"Galice-Rand Ranger Station Trail, Curry Co., Oregon" Lilla Leach
4343, 6/18/33.

"Galice Rand Ranger Station, Almeda, Curry Co., Oregon" Lilla Leach
4893, 6/16/38.

(Rand is about 4.8 km north of Galice on the Rogue River; it is in Josephine, not Curry, County.)

"Store Gulch Guard Station. Along the Illinois River, 7 miles west of Selma, Oregon." Albert N. Steward, 5/30/57.

Population Structure of Sophora leachiana

Phenology

Sophora leachiana is a highly localized endemic species found only in the thirteen areas discussed above. However, at the sites where Sophora does occur, it is often of such high abundance that the species ranks as the dominant herbaceous member of the community. Sophora spreads by a vigorous, branched rhizome system that travels about 5-8 cm below the soil. Aerial shoots arise from the nodes of the rhizome in the area of the previous season's growth as well as prior seasons. Determination could not be made as to any maximum age beyond which that area of the rhizome would fail to produce aerial shoots. Lack of obvious annual growth rings made it impossible to age the rhizome. The majority of shoots surface in the spring and early summer; rhizome growth appears to be concentrated through summer or autumn. An occasional aerial shoot does develop in summer especially if the population has been subject to any kind of antagonist that has

destroyed a large number of existing ramets. The species dies back to the rhizomes in the fall.

Initial bud-break and aerial shoot development occur in the early spring. Most Sophora populations appeared to resume growth at about the same time, although the populations were not visited when bud break was occurring. However, assuming that flowering will take place only after a set number of days following bud break, differences in the stage of the flowering cycle present at each site would reflect a difference in vegetative shoot initiation. Populations of Sophora visited in April, 1976 and 1977, showed only slight differences in stage of flowering represented. Barr Mine population was an exception, because in April, 1977, aerial shoots were just developing for this population when all other Sophora populations visited were in full bloom. Two factors account for this discrepancy: Barr Mine is at the highest elevation (658 meters) of all Sophora populations, but this elevation differs from Taylor Creek (which was in full bloom in April) by only 50 meters. More importantly, Barr Mine is located in the basin of Briggs Valley. Cold air tends to settle in a valley resulting in warmer temperatures higher up the slopes; the colder temperatures probably caused a later bud-break date for the Sophora.

Several Sophora individuals, representing Briggs Creek, Upper Peavine, Lower Peavine and Squirrel Place populations, were transplanted in April, 1976, to the OSU Experimental Farm at Corvallis, Oregon. Two individuals, representing Upper Peavine and Briggs Creek

were potted and grown in the OSU greenhouse; they were vernalized outdoors at Corvallis. Bud break for most individuals corresponded to the first warm spring days of the season in the first week of April, 1977. However, the two individuals representing Squirrel Place did not resume active growth until the last week of April. The parent population, visited in May, 1977, did not appear to exhibit a delayed bud break compared with other populations. However, it is possible that the Experimental Farm individuals were from a clone that was physiologically programmed to respond only later in the season. At Squirrel Place it was observed that both flowering and nonflowering ramets located in open, sunny areas, did not surface all at once but continued to develop over a period of perhaps two weeks.

Aerial shoots of Sophora stand about three dm tall and include about a dozen horizontally held leaves. Axillary branches can develop on flowering shoots or if damage occurs to the apical meristem of vegetative ramets. Sophora exhibits a characteristic distinction of sun leaves versus shade leaves, with shade leaflets being longer and wider. Shoots developing in the shade appeared to be taller than their clonal counterparts located in more sunny areas. Further difference occurred in the initiation and senescence of sun and shade ramets, as bud break and development commenced earlier in the sun. The initial stages of senescence of sun-grown shoots, as indicated by a pale green or yellow coloration, was apparent by August in 1976 and 1977 whereas shaded ramets were still green and appeared healthy.

Sophora is most commonly found in sunny areas and the species exhibits several morphological adaptations to hot, dry environments. The upper epidermis of the leaflets is composed of large cells, but not noticeable thick walled as described for other xeromorphic Sophora species (Northington, Morey and Van Devender, 1977). A thick cuticle surrounds the upper and the lower epidermis. Lower epidermal cells are also enlarged, suggesting modification for water storage (Northington et al., 1977). The stomates are sunken and restricted to the lower epidermis.

Sophora and other species, including desert legumes (Daubenmire and Charter, 1942), possess a peculiar morphological adaptation to the hot dry climate. The leaflets are able to fold upward in high insolation until they are arranged edgewise to the incoming radiation. In legumes, pulvini at the base of each leaflet are probably responsible for the folding movements, whereas certain nonleguminous xeromorphic species permanently maintain their leaves in a vertical position. All angles of leaflet position have been observed in Sophora leachiana, including a completely vertical orientation, with the subopposite leaflets in contact with one another, observed on an August day when the temperature was over 37.5°C. Daubenmire and Charter (1942) and Daubenmire (1974) suggest that in some species initiation of moisture stress is most likely responsible for the upward movements of leaflets; in other species, high light intensity is the causal agent (Daubenmire and Charter, 1942; Oppenheimer, 1960; Grime, 1966). If the soil moisture content is above the wilting point, transpiration rates in the

latter species appear to be closely related to the strength of illumination (Daubenmire and Charter, 1942). Vertical orientation minimizes the solar insolation absorbed per unit leaf area, thus decreasing the heat load. Temperatures of a vertically held leaf can be several degrees lower than a horizontally positioned leaf. Treshaw (1970) reports that leaves oriented 10 degrees away from perpendicular to the incoming light will have a 15 percent heat load reduction, while a greater than 70 degree orientation will result in negligible heat absorption. A decrease in temperature will allow a reduction in transpiration rates; further control of transpiration is provided by the close contact of the leaflets which can shield one half the leaf surface from direct air contact (Daubenmire, 1974). This response appears to be associated with each leaflet rather than with an entire aerial shoot, as leaflets in the sun could be elevated while those on the same shoot in the shade could remain horizontal.

Sophora also exhibits nyctinastic leaflet movement, whereby the leaflets droop down in darkness. This "sleep movement" occurs when Sophora individuals are placed in darkness for sufficient time periods. Studies with Mimosa pudica and other legumes (Fondeville et al., 1966; Koukkari and Hillman, 1968; see also Galston and Davies, 1970) show that nyctinasty of leaves or leaflets is a phytochrome response, centered in the pulvinules, and influenced by diurnal rhythms. The adaptational benefits of this response has been subject to much speculation but remains experimentally unexplained (Schwintzer, 1971).

Sophora leachiana possesses nitrogen fixing nodules on its roots. Sections of roots bearing nodules were collected in the field and placed in moist glass vials. Acetylene reductase assays were run 48 hours later by Dr. Karel Schubert of Oregon State University. Despite their age, the nodules performed well, with a fixation rate of 140 nmoles N fixed per mg fresh weight. The nodules of Sophora probably contribute an important amount of nitrogen available for plant use. However, the nodules are either not abundant or are too fragile to be collected in the field in any quantity. In an attempt to collect more nodules for a field rerun of the acetylene assay, no nodules were found despite a two hour search.

Community Interaction of Sophora leachiana

The question of what specific environmental factors govern the microhabitat requirements of Sophora leachiana was not addressed in detail in this study. An understanding of population dynamics is also difficult because one cannot distinguish between different clones, and time was not available for lengthy demographic analysis. However, various conclusions of environmental preferences and population structure of Sophora leachiana can be suggested based on data obtained and observations of the populations.

Stands of Sophora are most common on open areas where the plants are exposed to abundant sunlight. However, the species is not restricted to sunny sites. Lower Peavine data and Briggs Creek observations show that quite dense stands can extend into lightly forested areas (areas with less than about 75 percent tree cover) that are adjacent to the

population centers in the open disturbed portions of these sites. Three hundred and five individuals (12 percent cover) were in a 70 percent forested region at Lower Peavine as opposed to 184 individuals (5.6 percent cover) in an equal sized area adjacent to the roadway. If Sophora is found in a heavily shaded area (>75 percent cover); the density of aerial shoots was usually much less than that present in the sunny area. The vegetation of several sites included more open areas interspersed in a forested region. At these locations, widely spaced individuals present in the forest connected the higher density Sophora found in the clearings. At Site Three, Taylor Creek and Taylor House, Sophora extended from the commercial cut areas with abundant Sophora on up to the ridge line as widely dispersed aerial shoots.

Several of the thirteen populations were located in mesic areas. However, Sophora was not found in the most mesic habitats at the sites but was always concentrated in the drier locations. Sophora was found in subxeric vegetation at Briggs Creek and did not extend close to the seepage area. Site Three and Barr Mine populations included Sophora ramets under the forest canopy, but the majority of individuals were found in the cut-over, drier open areas. Sophora avoided the mesic drainage areas at both locations. West Fork Taylor supported a riparian forest; however, Sophora was centered in the cleared meadow adjacent to the roadway paralleling the stream.

Production of aerial shoots from the nodes year after year rather than shoot formation only at the rhizome ends or only for one season allows a dense stand of aerial shoots to develop. No evidence

of clonal senescence was noted, although a merging of two clonal territories may hide evidence of senescence. In several locations, most notably Taylor Creek, Sophora virtually blanketed the ground. Average measured density at Taylor Creek was 9.5 individuals per square meter, with the highest value of 29 individuals per square meter. Measurements were not taken in the thickest Sophora stands, so 29 individuals per square meter is not a reflection of the maximum density of Sophora.

Other species, most notably grasses, might be able to compete effectively with Sophora in certain areas of each site. Taylor Creek and Briggs Creek were characterized by a combination of thick, pure stands of grasses without Sophora alternating with high density Sophora areas. Grasses were not excluded from the areas with Sophora, but were of a much lower density. By late August, all grasses are dead but still may present a barrier to rhizome penetration and aerial shoot development. At Taylor Creek, Sophora was found in the stands of tall Bromus tectorum where the two colonies came in contact with one another. Here, Sophora appeared to be the weaker species, as only widely scattered individuals were present. However, it could not be determined if Sophora just did not have a chance to spread to the dense grassy areas or if the grass was actually serving to exclude Sophora. Studies with Lespedeza, an eastern North American rhizomatous legume, show that its species do form dense stands in disturbed areas. However, Lespedeza is outcompeted by invading perennial grasses and various shrubs and saplings (Clewell, 1966). A different situation exists for

Hieracium floribundum. This stoloniferous composite exhibits a zonation pattern of patch development with younger more widespread individuals occurring at the margins of a dense patch; a negative correlation exists between Hieracium individuals and grass abundance. However, because the dense rosettes were able to outshade other species and vegetative reproduction with stolons was highly successful, Thomas and Dale (1974) concluded that the density of grass was not limiting the growth of Hieracium floribundum. Based on these contrasting examples, positive statements as to the effective competition of Sophora leachiana with other species can only be made after several years of field study.

The U.S.D.A. Forest Service considers Sophora leachiana to be a very serious competitor to conifers. Gabel (1975) reports that Sophora became a severe problem in the Taylor Creek drainage broadcast burn areas and contributed to the death of previously established plantations on the reforestation sites. However, I have found that Sophora only occupied the northern quarter of the Taylor Creek clearcut and was absent in neighboring clearcut and burn areas. Based on Forest Service reports, these clearcuts had to be reseeded or replanted several times before seedling establishment was successful. Therefore, Sophora may be a competitor with conifers seedlings but it could not be a major factor preventing establishment at all Taylor Creek sites.

Disease and Predation

Predators and disease are important factors influencing the ecology of any plant. These two aspects were studied to a limited extent. A rust was the only conspicuous disease; insect predators included thrips, with spittlebugs and grasshoppers being of only minor importance. A moth whose life cycle appears to be tied with Sophora leachiana was of major importance.

The rust was identified as Uromyces hylinalus Peck. This genus is not restricted to the Fabaceae, but legumes do serve as a major host (Arthur, 1934; Sampson and Western, 1954). Uromyces hylinalus is a well known disease of S. nuttalliana and has been found to infect this legume in virtually its entire range within the United States (Farlow and Seymour, 1891; Arthur, 1934). Infections of Uromyces hylinalus on S. leachiana were usually not severe, although the rust was present at every location. Infection of individual ramets ranged from patches of cinnamon brown spores dotting only several leaves, to a complete covering of spores over the entire aerial sprout. Death of the ramet would result at this stage. Although no measurements were taken, it appeared that once a ramet was infected, it would be quickly covered with the fungal growth. Tallies of the number of rust-infected individuals were compiled at four locations and are presented in Table 7. Never were vast areas decimated by the fungus; other Sophora populations where no formal tally was kept possessed only a low number of rust-infected plants. The incidence of rust appeared to show a slight increase at the close of the season; this would correlate

Table 7. Infestation of rust and insects in populations of Sophora leachiana.

	Date Sampled	Percent infected by rust	Percent infested by moth larvae	Average damage inflicted by larvae
LP (shade)	5/30/76	-	16/50 = 32%	-
LP (sun)	5/30/76	-	46/100 = 46%*	-
UP	5/30/76	-	27/100 = 27%**	-
Br	6/27/76	24/999 = 2.4%	-	-
LP (sun)	6/28/76	22/184 = 12%	38/184 = 21%	-
LP (shade)	6/28/76	32/305 = 10%	7/305 = 2%	-
TC	6/28/76	64/718 = 9%	-	-
TH	6/28/76	-	17/128 = 13%	-
Sq	6/29/76	-	189/467 = 40%	-
Up	6/29/76	5/622 = 0.8%	61/622 = 10%	-
S3	8/23/76	-	166/216 = 77%	46%
Ba	8/23/76	-	61/183 = 33%	10%

- = not calculated

* = reflects 39 vegetative ramets and seven fertile ramets in a total of 82 sterile and 18 fertile ramets.

** = eighteen of 74 vegetative ramets; three of 26 fertile ramets; plus four flowering ramets also with thrips, two sterile shoots also with thrips. Thrip infestation alone involved 19 flowering and four sterile shoots. All flowering ramets and 50 sterile shoots were infested by larvae and/or thrips.

with observations that increased susceptibility to disease occurs with approaching senescence (Hutchings and Barkham, 1976).

Small thrips (Thripidae) were very numerous in the flowers of Sophora in 1976. The heaviest infestation occurred in the Peavine Mountain populations (Upper and Lower Peavine) with the thrips' presence also noted at Briggs Creek. The thrips were identified as Odontothrips sp. by K. O'Neill of the U.S. Department of Agriculture. A specific epithet could not be assigned because species differentiation is based on characteristics of the male and the parthenogenic reproduction of the insects produced only females. They possibly represent an undescribed species.

These thrips were very common on the flowers and only rarely were encountered on the vegetative parts. A survey of 100 randomly selected ramets in the sunny roadside at Upper Peavine revealed 26 fertile ramets of which 23 were thrip-infested. Only six vegetative ramets were found to be infested. No determination was made of the number of thrips present per inflorescence but in May, 1976, they were very numerous. Thrips were present in 1977, but at a much lower density. Thrips scrape the succulent lining of flowers. They have caused up to 50 percent reduced seed yield in alfalfa and other species (Bohart and Koerber in Kozlowski, 1972). They can severely damage the flower and cause loss of blossoms (Wheeler and Hill, 1957); thrips may have been major contributors to the large percent of blossoms dropped prematurely in 1976, although blossom shedding can be due to a wide variety of other influences. Thrips were not seen past the blooming period.

The most interesting predator was a small moth. In early phases of the blooming period these moths can be quite numerous in dense stands of Sophora. The moths usually rest on or underneath the leaflets of Sophora. When disturbed they fly but rarely land on the ground or on any plant other than Sophora. No larva of the moths were found on associated vegetation. Although further work is needed, it appears that the moth may be restricted to Sophora leachiana. Restriction of an insect to a specific plant or very narrow range of host plants is not uncommon (Wilson, 1964, Janzen, 1970, and Andres and Goeden, 1971, as in Fitz, 1972).

The larvae would spin together several of the upper leaves of Sophora, including the inflorescence on flowering ramets. These 'larvariums' were easily seen; counting the total larvariums in a set number of plants furnished a good approximation of the extent of infestation in a population. Although the adult moth was not seen past the blooming period nor the larvae past June, the larvariums were retained throughout the summer and measurements could be taken at any time. The infestation rate varied from locality to locality, ranging from two percent to 77 percent (Table 7). The average damage at three sites, as indicated by the amount of plant contained in the larvariums, was five percent (not shown on table), ten percent and 46 percent.

Infestation by moth larvae appeared to occur with equal intensity in sun vs. shade ramets. Even though a sun vs. shade study conducted at Lower Peavine in late June, 1976, did show a difference (21 percent vs. two percent), data collected late May, 1976, showed no real

difference (46 percent vs. 32 percent). Flowering vs. nonflowering ramet infestation was sampled at Upper and Lower Peavine. Data revealed 39 percent fertile ramet infestation vs. 47 percent sterile ramets infected at Lower Peavine; with 31 percent vs. 27 percent and 27 percent vs. 24 percent, respectively for two counts made at Upper Peavine. Because the percentages of fertile and sterile ramet infestation are approximately the same within all three samples, one may tentatively conclude that infestation of ramets is random; there is no selection of flowering ramets over non-flowering individuals. Further data from 50 shade ramets at Lower Peavine showed 32 percent infestation in this nonflowering area.

More intensive measurements involving the effect of predators on the inflorescences was conducted at Lower Peavine in late May, 1976. Floral damage was mainly due to larvae; however, despite Upper Peavine data which showed only six percent of the 100 ramets infected with both thrips and larvae (as opposed to 21 percent and 23 percent ramets damaged by larvae and thrips alone, respectively), thrip induced damage causing floral dehiscence was probably an additional main contributor.

Of the 26 inflorescences surveyed, 62 percent did show damage. These 16 inflorescences sported a total of 339 flowers of which 114 (34 percent) were destroyed. The average percent damage on an infected inflorescence was 44 percent. Recalculating the data to include all 26 racemes yields 20 percent of the total flowers destroyed with an average percent damage per inflorescence at 27 percent.

Based on the data presented above, the moth and thrips have an obvious negative impact on seed set. Actual measurements of seed destruction (as outlined by Fitz, 1972; or Green and Palmblad, 1975) could not be calculated because the number of seeds per healthy, normal raceme is not known.

The actual extent of damage caused by the larvariums is not known. It may be less than suggested by the high infestation rate because leaves in the larvariums usually remained green throughout the growing season.

Herbivory by higher animals appears to play a very minor role, if any; no evidence of browsing by ungulates was observed. Other Sophoras are usually protected from extensive direct herbivore attack by the toxic compounds in their foliage (Kingsbury, 1964). Foliage compounds toxic to mammals can also be harmful to insects (Fraenkel, 1959); many perennial plants which occur in large dense stands like Sophora are chemically protected from a wide range of insect predators (Feeny, 1975). If Sophora leachiana does contain these protective compounds, the moth would have had to adapt to Sophora, an event which would have assured the moth of a competition-free food supply as long as Sophora remained in the community. Coevolutionary events like this are not rare in plant-insect relations (Feeny, 1975). However, greenhouse specimens of Sophora provide contrasting evidence for wide-scale predator protection, as all rametes were heavily infected with spider mites the summer of 1976 and whiteflies (family Aleyrodidae) in 1977.

Successful reproduction is of prime importance as it influences not only the distribution and survival but also the evolution of a species. Sexual reproduction of *Sophora leachiana* was studied in hopes of quantifying the success of the process along with an estimate of the impact reproduction has as a factor limiting the distribution of the species. Because broad topics are most efficiently covered by concentrating on their various fractions, numerous studies were initiated involving all phases of the reproductive process.

Pollen grain formation was followed beginning with the pollen mother cell and continuing through meiosis and development of the grain, concluding with stainability and germination in vitro of the mature grains. Floral development and morphology in relation to pollinator adaptations were noted. Field and lab crosses were performed within and between populations to test for compatibility. Reproductive potential, as indicated by the percentage of fertile shoots and the reproductive success signaled by mature seed development was followed through the course of one season. Germination tests and the effect of heat on embryo viability were studied. Aborted seeds as well as mature seeds were studied for embryo development and anatomy.

Chromosome Numbers and Meiotic Cytology

Chromosome counts were obtained from only three populations - Lower Peavine, Taylor Creek and Briggs Creek. The remaining populations with the exception of Upper Peavine could not be visited at the correct time for chromosome study. Chromosome counts for Upper

Peavine could not be obtained because this population lacks mature pollen; squashes performed with anthers at various stages of development showed that pollen mother cells are formed, but these abort before entering meiosis. Counts from Lower Peavine individuals revealed a tetraploid level of $n = 18$. Briggs Creek and Taylor Creek individuals were hexaploid, with $n = 27$. For ease of presentation cytological observations will be discussed separately for the tetraploid and hexaploid populations.

Tetraploids. The tetraploid count of $n = 18$ was obtained from pollen mother cells entering metaphase I. At metaphase I these 36 chromosomes were paired as bivalents in 76 percent of the 26 pollen mother cells (PMCs) examined. One quadravalent and 16II occurred in 19.2 percent of the metaphase spreads; whereas one spread showed 16 bivalents, two univalents that possibly represented a just divided bivalent, and two additional univalents. No trivalents were observed in any of the spreads.

Anaphase I usually appeared normal, as very seldom were lagging bivalents or other abnormalities observed. Disjunction patterns for the different chromosomes pairing relationships could not be determined, but chromosome counts could be obtained in both daughter nuclei of 21 PMCs. These counts revealed a disjunction of 16-20, 17-19 and 17-19 chromosomes to the respective daughter nuclei in three PMCs (14.5 percent); the remaining 18 PMCs had a normal 18-18 distribution. Metaphase II appeared normal in 117 out of 134 (87 percent) randomly selected PMCs. Spreads were considered normal if no observable

abnormalities existed; this criterion had to be adopted because in a majority of these spreads (85 percent) the exact chromosome count for a daughter nucleus could not be determined. Visible abnormalities included chromatin bridges (with and without an evident fragment) between the two daughter nuclei and lost chromosomes, i.e., chromosome material that is no longer associated with the remainder of the nucleus.

Anaphase II was studied in 147 PMCs and in 92.5 percent there were no visible abnormalities. One PMC contained only three nuclei of approximately equal size; two contained five daughter nuclei. Seven PMCs contained one micronucleus in addition to four daughter nuclei; one contained two micronuclei. All observed PMCs in telephase contained four developing pollen grains. One spread was characterized by abnormalities in 27 percent of the PMCs. The PMCs in telophase II were forming four grains of equal size; however most of the nuclei had either decomposed (i.e., no observable nucleus in the grain) or had undergone fragmentation, with up to four fragments in a grain. Sometimes two grains in the tetrad would have one nucleus per grain, but these would be of unequal size. This could have been due to unequal distribution at the second division but most likely was due to fragmentation of one or both nuclei, followed by decomposition of some of the fragments.

Hexaploids. Hexaploid counts of $n = 27$, $2n = 54$ at Briggs Creek and Taylor Creek were based on spreads of metaphase I, anaphase I, metaphase II and mitosis in anther filament tissue. Metaphase I in the

hexaploids was characterized by the presence of univalents, bivalents, trivalents, and quadrivalents, with quintivalents or sexivalents occurring in several of the spreads. Table 8 summarizes the analyzed metaphase spreads for both hexaploid populations. Univalents appeared as small, highly contracted spheroidal or rod-shaped bodies in contrast to the larger more complex outline of paired chromosomes. These univalents were very characteristic of hexaploid spreads, as only one PMC in all observed spreads lacked them. The average number of univalents per PMC was calculated in four spreads, yielding values of 7.2, 5.9, 4.9, and 3.5 univalents per PMC. It must be noted that these are minimum values, representing only the univalents that were readily apparent in the PMCs. Because the complete chromosomal configurations could usually not be determined, some of the univalents may have been overlooked. In those cells in which chromosomal pairing relations could be determined, it was noticed that univalents typically did not align on the metaphase plate but remained scattered near the plate and in the polar regions of the cells. In many instances, the univalents did not appear to be randomly distributed with respect to one another but would be in close proximity to another univalent.

Anaphase I was also irregular, as analysis of two spreads revealed 0 percent and 11 percent of the cells appearing normal at this stage. Bridge formations between the two daughter nuclei were frequent, but the most common irregularity was the presence of lagging chromosomes. There were usually several pairs of homologues still

Table 8. Chromosomal configurations at metaphase I in hexaploid individuals of Sophora leachiana.

Location of individual*	I	II	III	IV	V	VI
T	8	17	4	-	-	-
T	9	19	1	1	-	-
T	6	13	4	1	-	1
T	8	15	4	1	-	-
Br	2	15	3	2	1	-
Br	6	13	4	1	-	1
Br	8	15	4	1	-	-
Br	12	16	2	1	-	-
Br	6	15	3	1	1	-
Br	8	12	3	2	1	-
Br	4	17	4	1	-	-
Br	8	8	3	1	1	2
Br	7	12	6	-	1	-
Br	12	18	2	-	-	-
Br	17	17	1	-	-	-
Br	8	18	-	1	-	1
Br	9	13	5	1	-	-

*T and Br refers to Taylor Creek and Briggs Creek, respectively.
Each line represents one PMC.

remaining in the region of the metaphase plate; in most instances these homologues appeared to separate from each other but the chromosomes would not migrate to the poles or would migrate very slowly. Disjunction patterns of the different chromosomal pairing relations could not be determined, but in some instances chromatin material connected a lagging chromosome to one that had been incorporated into a daughter nucleus.

Micronuclei were often apparent in late anaphase I. That these micronuclei were formed from lagging chromosomes and not from univalents is suggested by the low number of micronuclei present in the PMCs as well as the fact that micronuclei were usually located between the daughter nuclei in the region of the metaphase plate rather than in the polar regions. As further evidence, several micronuclei were seen in metaphase II configurations although none were observed in cells entering anaphase II. Probably univalents were included in a daughter nucleus or became diffuse and lost in the cytoplasm. There were five PMCs in which it was possible to count all the chromosomes in each daughter nucleus. In two of these cells a normal 27:27 distribution at anaphase I had occurred, whereas two others showed a 29:25 disjunction, and a fifth PMC had a 24:30 disjunction. These PMCs suggest that univalents can be included in a daughter nucleus and that the disjunction can sometimes be normal at least with respect to the number of chromosomes.

Early anaphase II showed lagging chromosomes commonly present between the daughter nuclei. The chromosomal material most likely

represented chromatids that separated from their sister but failed to migrate to the poles or were doing so at a slower rate than the remaining chromosomes. This assumption is indicated by the shape of the lagging material and by the fact that the laggards typically existed in pairs. Late anaphase II indicated that many laggards were not included in a daughter nucleus but formed micronuclei within the PMC. Analysis of three spreads from Briggs Creek showed the following composition:

1. 21.7 percent of the PMC had four nuclei plus one or more micronuclei.
18.8 percent were unreduced dyads, of which 2.9 percent also contained a micronucleus.
9.4 percent had three nuclei, of which 1.4 also had one micronucleus.
50.0 percent (69 of 138) appeared normal.
2. 44.5 percent had four nuclei, but also one or more micronuclei.
3.2 percent had three nuclei, of which 1.08 percent also contained one or more micronuclei.
52.1 percent (48 of 98) appeared normal.
3. 42.6 percent had four nuclei plus one or more micronuclei.
1.3 percent had only two nuclei.
4.0 percent had three nuclei plus one or more micronuclei.
52.0 percent (39 of 75) appeared normal.

Telophase II observations (Table 9) revealed that the micronuclei were often still evident in the maturing sporad. Usually these micronuclei were included within one of the four developing pollen grains; however, occasionally these micronuclei were enclosed within their own cytoplasm. The number of PMCs containing these microcytes per spread was usually fairly low, although three squashes from a Briggs Creek individual showed a very high frequency of polyads rather than tetrads. One of these squashes had only 13.0 percent tetrad formation and the remaining 87.0 percent PMCs contained from one to six microcytes. Other spreads were characterized by as much as 21.9 percent dyad formation. Taylor Creek individuals averaged 51.3 percent normal appearing PMCs; Briggs Creek individuals averaged 53.2 percent.

Pollen Stainability

Data on pollen stainability, measured with aniline blue in lactophenol, are presented in Table 10 for the tetraploid and hexaploid populations. A very wide range in stainability (47-99.5 percent; 20.5-96.9 percent) was characteristic for each of the two individuals analyzed from the tetraploid population. This variability existed between different flowers of the same individual and between different anthers in the same flower, and it was also evident between different halves of the same anther. On several slides examined for stainability, several anthers from both individuals possessed numerous very large, deeply staining pollen grains. These most likely represented the products of unreduced dyads, or perhaps grains formed from

Table 9. Observations of newly formed microsporads in hexaploids. Data presented as actual number of PMCs followed by percentage. The numbers separated by a slash refer to number of sporads with normal appearing nuclei/number of abnormal (micronuclei present); percentage calculated from total of both.

Population and Individual	Monads	Dyads	Triads	Tetrads				
				Normal	Unequal sized nuclei	One micro-nucleus	Two micro-nuclei	More than two micro-nuclei
TC2			1(0.3%)	300 (99.7%)	tetrads			
TC2				107 (89.0%)	tetrads			
TC3				95 (88.0%)	tetrads			
TC1				68(66%)		25(24%)	10(10%)	
TC1				53(40%)		34(26%)	29(22%)	17(13%)
Br3	1 (1%)	41/3(26%)	9(5%)	106(63%)	3(2%)	1(1%)		
Br3		3(2%)	3(2%)	129(75%)	3(2%)	17(10%)	2(1%)	5(3%)
Br2		15/2(8%)	8/3(5%)	114(52%)		20(9%)	5(2%)	1(0.5%)
Br2		18/3(10%)	7/5(6%)	143(69%)	2(1%)	8(4%)		
Br2				51(51%)	2(2%)	14(14%)		
Br2				16(11%)		3(2%)		
Br2			0/1(1%)	22(20%)	7(6%)	8(7%)	2(2%)	1(1%)
Br2			0/1(1%)	32(28%)		6(5%)	1(1%)	
Br4		8/1(8%)	1(1%)	73(64%)		11(10%)		
Br4		10/1(6%)	6(4%)	130(76%)	1(1%)	7(4%)	1(1%)	
Br4		22/1(22%)	4/2(6%)	53(51%)		9(9%)	1(1%)	

Table 9 (continued).

	Pentads	Sexads	Septads	Octads	Nonads	Decads
TC2						
TC2	13(11%)					
TC3	12(12%)	1(1%)				
TC1						
TC1						
<hr/>						
Br3	5(3%)					
Br3	8/1(5%)	1(1%)				
Br2	46/3(22%)	3(1%)				
Br2	17/2(9%)	2(1%)				
Br2	24/2(26%)	8(8%)				
Br2	41/6(32%)	50/3(38%)	20(14%)	3(2%)	1(1%)	1(1%)
Br2	30/12(37%)	21/2(20%)	7(6%)	1/1(2%)		
Br2	32/4(32%)	23/1(21%)	10/1(10%)	1(1%)	1(1%)	
Br4	14/3(15%)	3(3%)				
Br4	10/3(7%)	1(1%)				
Br4	10/1(11%)	2(2%)				

Table 10. Pollen Stainability

Lower Peavine Individual #1

	<u>Total Number of Grains</u>	<u>Percent Stainable Pollen</u>
Flower #1	716	50.1
	618	62.9
	844	70.0
	837	80.0
	641	89.2
	813	90.5
	667	91.5
	632	96.0
	<u>603</u>	<u>99.5</u>
Subtotal and Mean	6371	80.6 \pm 16.7
Mixed Flowers	1155	47.0
	903	65.6
	4014	75.8 1/2 anther a
	4032	80.2 1/2 anther a
	688	86.6
	3847	76.6 1/2 anther b
	<u>3451</u>	<u>90.0 1/2 anther b</u>
Total and Grand Mean 24,461		78.5 \pm 15.6
Range		47.0 - 99.5

Table 10. (Continued)

Lower Peavine Individual #2

	<u>Total Number of Grains</u>	<u>Percent Stainable Pollen</u>
Flower #1	3250	53.4 1/2 anther a
	3188	70.3 1/2 anther a
	<u>944</u>	<u>62.5</u>
Subtotal and Mean	7382	62.0 <u>+ 8.5</u>
Flower #2	1164	20.5
	745	32.2
	729	39.0
	579	43.0
	764	55.1
	525	60.4
	585	62.7
	682	69.9
	<u>773</u>	<u>71.2</u>
Subtotal and Mean	6546	48.0 <u>+ 17.7</u>
Mixed Flowers	1103	28.5
	1211	36.8
	704	53.8
	630	54.5
	644	57.0
	597	58.6
	724	60.9
	647	96.9
	3291	56.4
	<u>4320</u>	<u>73.3</u>
Total & Grand Mean 27,799		57.5 <u>+ 17.1</u>
Range		20.5 - 96.9

Table 10. (Continued)

	<u>Total Number of Grains</u>	<u>Percent Stainable Pollen</u>
Briggs Creek Individual #1		
Flower #1	373	83.9
	458	85.4
	499	90.8
	3839	94.9
	3797	95.2
	3596	95.5
	423	95.5
	<u>2751</u>	<u>95.6</u>
	15,790	95.4 \pm 4.9
Flower #2	488	82.8
	636	86.5
	610	89.8
	480	90.0
	714	91.0
	710	95.8
	<u>465</u>	<u>96.8</u>
Subtotal and Mean	4103	90.5 \pm 4.9
Mixed Flowers	2198	79.2
	511	84.9
	592	86.0
	514	88.1
	451	89.6
	538	90.3
	3361	90.8
	529	93.2
	487	93.2
	498	94.0
	835	94.7
	804	94.8
	384	95.0
	477	95.1
	543	95.4
	3440	95.8
	572	96.2
	369	96.2
	3171	98.0
	<u>3019</u>	<u>98.4</u>
Total and Grand Mean	43,186	93.2 \pm 4.8
Range		79.2 - 98.4

Table 10. (Continued)

	<u>Total Number of Grains</u>	<u>Percent Pollen Stainability</u>
Taylor Creek Individual #1	296	96.2
	555	96.6
	562	96.6
	986	97.7
	<u>1001</u>	<u>98.2</u>
Subtotal and Mean	3400	97.2 \pm 0.8
Taylor Creek Individual #2	468	81.6
	956	87.3
	292	88.7
	368	94.3
	<u>504</u>	<u>95.4</u>
Subtotal and Mean	2588	89.0 \pm 5.6
Taylor Creek Individual #3	343	91.8
	697	92.7
	452	93.1
	417	94.0
	446	94.6
	467	94.7
	1286	95.0
	1012	95.2
	558	95.5
	1030	95.8
	507	95.9
	442	95.9
	613	95.9
	698	96.0
	606	96.0
	347	96.5
	416	97.1
	458	97.6
	<u>404</u>	<u>97.3</u>
Subtotal and Mean	11,199	95.6 \pm 1.5
Taylor Creek Individual #4	1027	95.6
	<u>742</u>	<u>96.9</u>
Subtotal and Mean	1769	97.6 \pm 0.29

Table 10. (Continued)

	<u>Total Number of Grains</u>	<u>Percent Stainable Pollen</u>
Taylor Creek Individual #5	349	91.4
	316	95.9
	538	96.5
Subtotal and Mean	1203	94.8 ± 2.8
Taylor Creek Individual #6	812	87.0
	824	90.9
	633	91.1
	661	92.7
	884	93.2
	526	93.7
	479	94.6
	688	95.0
	515	95.3
	779	95.4
	1422	95.5
	901	95.7
	770	96.2
	652	96.5
	600	96.8
	612	97.0
Subtotal and Mean	11,760	93.9 ± 2.7
Total and Grand Mean	31,635	95.5 ± 3.1
Range		81.6 - 98.3

the failure of both divisions. One spread was highly abnormal, with both viable and inviable pollen grains present in many different sizes.

The hexaploid populations also showed variation in stainability although the range was less than in the tetraploid population. Taylor Creek's range was 1.79 - 18.37 percent unstainable grains; while Briggs Creek ranged from 1.6 - 20.74 percent. The mean for all individuals at each population was 5.31 percent and 6.73 percent respectively. Several spreads from Briggs Creek possessed dyads in addition to grains formed from tetrads. Inviably microcytes were frequent in some spreads. In squashes used to determine pollen-ovule (P/O) ratios, these microcytes were tallied, but were not included in the P/O determination or in the stainability measurements. The number of microcytes present was used to calculate the expected number of sporads containing a microcyte. These results are presented in Table 11.

Aperture pattern in mature grains was most easily observed in anther squash preparations used for chromosome determinations. Tetraploid populations usually possessed tricolporate pollen grains; however, tetracolporate grains were often observed as well. Hexaploid grains were occasionally tri- or tetracolporate, but the majority of grains possessed 5, 6, 7, or 8 germ pores scattered randomly over the grain. Small microcytes present in several spreads had only two germ pores. With increasing ploidy level, the number of germ pores commonly increases over the tricolporate diploid condition (Funke, 1956).

Table 11. Estimates of Percent Polyad Formation

Total Grains per Anther Half	Number of Microcytes	Total Number of Sporads	Estimated Number of Polyads	Percent Polyads	Percent Stainable Pollen
3440	555	860	370	43.0	95.8
3171	320	792.75	213.3	26.9	98.0
3015	369	753.75	246	32.6	98.4
2198*	225				79.3
3797	411	949.25	274	28.9	95.3
3596	820	899	546.6	60.8	95.5

* This spread contained a large number of unreduced gametes, therefore number of sporads and percent polyads cannot be estimated.

Total number of sporads = total grains divided by four.

Estimated number of polyads = number of microcytes divided by 1.5 microcytes per polyad. This ratio was calculated from those spreads with a large percentage of polyad formation (Table 9).

Percent Polyads = estimated number of polyads divided by total number of sporads.

Data from one individual from the hexaploid Briggs Creek population.

Pollen Germination in Vitro

Pollen germination data are presented in Table 12. F distribution analyses comparing within population values and among population values are listed in Table 13. Altering the sucrose concentration did not significantly ($\alpha = 0.05$) influence the percent germination of pollen within each population. There was also no significant difference between each of the four tested populations with respect to the germination values in the 10 percent sucrose solutions.

A significant difference did exist between the germination values in the 20 percent and also the 30 percent sucrose solutions. F analysis showed that the average percent germination of Squirrel Place pollen in the 20 percent sucrose medium was significantly different ($\alpha = 0.05$) from the remaining three populations' averages. The germination response in the 30 percent solution was much more varied between populations, as only Taylor Creek and Lower Peavine values were not significantly different from one another.

Combining the three data sets for each population resulted in no true difference between Taylor Creek and Lower Peavine; however, Briggs Creek and Squirrel Place are significantly different from each other and from the two former populations. Analysis of length of pollen tube growth (Table 14) showed no true difference within each population with respect to the sucrose concentration or as compared with one another. The average pollen tube length is fairly short; pollen usually does not grow long tubes in liquid media, but does produce tubes of more normal length on agar media (Brewbaker and

Table 12. Pollen Germination in Vitro

Lower Peavine Population

A	B	C	D	E	F	G	H	I
10%	1121	26.39	3.83	6.06	3.30	13.2	16.5	2.8
20%	148	31.06	10.13	6.75	5.40	8.78	14.18	2.0
30%	77	42.84	28.57	6.49	2.59	5.19	7.78	1.0
10%	110	38.17	10.90	10.00	7.27	10.00	17.27	2.3
20%	206	49.98	7.76	4.85	13.59	23.78	37.37	3.26
30%	117	41.0	15.38	4.27	6.83	14.52	21.35	3.36
10%	261	41.37	24.90	8.81	7.66	0.0	7.66	-
20%	121	41.30	10.74	4.95	23.14	2.47	25.61	3.0
30%	124	41.11	8.06	5.64	11.29	16.12	27.41	4.1
10%	74	41.88	0.0	13.51	22.97	5.40	28.37	1.62
20%	12	33.33	0.0	0.0	25.0	8.33	33.33	2.0
30%	9	11.11	0.0	0.0	0.0	11.11	11.11	7.0

	Average of C	Average of H	Average of I
Anther 1	33.43	12.82	1.93
Anther 2	43.05	25.33	2.97

Table 12. (Continued)

	Average of C	Average of H	Average of I
anther 3	41.26	20.22	2.36
anther 4	28.77	24.27	3.54
10% sol'n	36.95	17.45	2.24
20% sol'n	38.91	27.62	2.56
30% sol'n	34.01	16.91	3.86
overall	36.62	20.66	2.94

A - The concentration of sucrose in the nutrient media

B - Total number of grains per nutrient drop

C - Sum of columns D,E,F, and G. Represents the percentage of grains that exhibited any indication of germination.

D - The percentage of grains that were swollen.

E - The percentage of grains whose pollen tubes were less than the diameter of the grain.

F - The percentage of grains whose pollen tubes were greater in length than the grain diameter, but possessed any of several abnormalities.

G - The percentage of grains possessing good pollen tubes of a length greater than the diameter of the grain.

H - Sum of columns F and G; the percentage of grains considered to have germinated.

I - The average length of the pollen tubes expressed as X diameter of the grain. Calculated from the grains in group 5 (column G) only.

Table 12. (Continued)

Briggs Creek

A	B	C	D	E	F	G	H	I
10%	21	57.13	4.76	42.85	4.76	4.76	9.52	1.0
20%	329	57.73	5.16	7.29	27.35	17.93	45.28	3.63
30%	284	50.68	1.05	5.98	18.30	25.35	43.65	5.53
10%	121	62.79	0.82	7.45	34.71	19.83	54.54	2.81
20%	70	64.26	1.42	4.28	37.14	21.42	58.56	3.46
30%	184	58.14	1.63	3.26	24.45	28.8	53.25	7.49
10%	101	47.52	15.84	19.80	8.91	2.97	11.88	2.00
20%	49	51.00	-	10.20	22.44	18.36	40.80	3.91
30%	125	38.40	3.20	0.80	17.60	16.80	34.40	4.61
10%	132	65.89	2.27	6.81	17.42	39.39	56.81	5.87
20%	120	40.81	14.16	5.83	11.66	9.16	20.82	2.27
30%	122	49.97	2.45	3.27	11.47	32.78	44.25	3.11
		Average of C		Average of H		Average of I		
	anther 1	55.18		32.81		3.38		
	anther 2	61.73		55.45		4.58		

Table 12. (Continued)

Briggs Creek

	Average of C	Average of H	Average of I
anther 3	45.64	29.02	3.50
anther 4	52.22	40.62	3.75
10% sol'n	58.33	33.18	2.92
20 sol'n	53.45	41.36	3.31
30 sol'n	49.29	43.88	5.18
overall	53.69	39.47	3.80

Table 12. (Continued)

Taylor Creek

A	B	C	D	E	F	G	H	I
10%	11	54.54	0.00	45.45	0.00	9.09	9.09	2.50
20%	13	69.15	38.46	7.69	23.00	0.00	23.00	-
30%	12	74.98	33.33	16.66	8.33	16.66	24.99	2.25
10%	66	24.23	1.51	12.12	1.51	9.09	10.60	6.00
20%	81	44.42	0.00	7.40	16.04	20.98	37.02	2.80
30%	145	50.32	0.68	6.89	18.62	24.13	42.75	3.11
10%	99	25.25	0.00	4.04	17.17	4.04	21.21	2.75
20%	133	40.59	14.28	4.51	17.29	4.51	21.80	3.41
30%	108	18.50	0.92	1.95	13.88	1.85	15.73	7.70
10%	102	44.11	0.98	6.86	33.33	2.94	36.27	1.83
20%	131	54.95	3.81	2.29	44.27	4.58	48.85	2.79
30%	164	40.22	6.09	11.58	17.07	5.48	22.55	4.33
10%	201	33.32	9.95	7.96	12.93	2.48	15.41	3.00
20%	104	46.13	2.88	4.80	33.65	4.80	38.65	5.10
30%	26	30.76	0.00	19.23	3.84	7.69	11.53	6.25

Table 12. (Continued)

Taylor Creek

	Average of C	Average of H	Average of I
anther 1	66.22	19.02	2.37
anther 2	39.65	30.12	3.97
anther 3	28.11	19.58	4.62
anther 4	46.62	35.89	2.98
anther 5	36.73	21.79	4.78
10% sol'n	36.29	18.51	3.21
20% sol'n	51.04	33.82	3.52
30% sol'n	42.95	23.51	6.00
overall	43.42	25.28	3.84

Table 12. (Continued)

Squirrel Place

A	B	C	D	E	F	G	H	I
10%	210	38.08	2.38	7.61	24.76	3.33	28.09	2.07
20%	40	60.00	2.50	10.00	30.00	17.50	47.50	2.07
30%	63	65.06	0.00	6.34	19.04	39.68	58.72	8.70
10%	286	41.58	0.69	2.79	33.21	4.89	38.10	2.35
20%	198	78.75	0.00	2.02	42.90	33.83	76.73	6.39
30%	271	84.49	0.00	0.00	53.50	30.99	84.49	7.47
10%	77	74.01	0.00	2.59	55.84	15.58	71.42	4.625
20%	132	68.93	0.00	0.00	46.21	22.72	68.93	10.13
30%	95	72.61	0.00	10.52	44.20	17.89	62.09	3.70
10%	113	66.65	0.00	1.17	62.83	2.65	65.48	1.66
20%	96	93.74	0.00	2.08	66.66	25.00	91.66	5.52
30%	226	92.46	0.00	2.21	69.46	20.79	90.25	6.82
		Average of C		Average of H		Average of I		
anther 1		54.38		44.77		4.28		
anther 2		68.27		66.44		5.40		

Table 12. (Continued)

Squirrel Place

	Average of C	Average of H	Average of I
anther 3	71.85	67.48	6.15
anther 4	84.28	82.46	4.66
10% sol'n	55.08	50.77	2.67
20% sol'n	75.35	71.20	6.02
30% sol'n	78.65	73.83	6.67
overall	69.69	65.29	5.12

Table 13. F Distribution Analysis for Germination in Vitro

Comparisons in 10 percent sucrose medium.

Populations	T, Sq, Br, Lp
Sample F	3.26
Critical F ($\alpha= 0.05$)	3.41
df	(3,13)
Significant?	No

As no significant difference existed,
further tests are unnecessary

Table 13. (Continued)

Comparisons in 20 percent Sucrose Medium Populations used in individual tests						
	T, Sq, Br, Lp	T, Sq, Br	T, Lp, Br	T, BR	T, Lp	T, Sq
Sample F	7.66	7.346	1.211	0.70	0.71	14.15
Critical F	3.41	4.10	4.10	5.59	5.59	5.59
($\alpha= 0.05$)						
df	(3,31)	(2,10)	(2,10)	(1,7)	(1,7)	(1,7)
Significant?	Yes	Yes	No	No	No	Yes
	Br, Lp	Sq, Lp	Sq, Br			
Sample F	2.167	17.158	6.053			
Critical F	5.99	5.99	5.99			
($\alpha= 0.05$)						
df	(1,6)	(1,6)	(1,6)			
Significant?	No	Yes	Yes			

Table 13. (Continued)

Comparisons in 30 percent Sucrose Medium

	Populations used in individual tests					
	T, Sq, Br, Lp		T, Br, Lp	T, Sq, Br	T, Sq, Lp	Br, Sq, Lp
Sample F	20.07		7.989	18.779	25.312	24.904
Critical F ($\alpha= 0.06$)	3.41		4.10	4.10	4.10	4.26
Degrees of freedom	(3,13)		(2,10)	(2,10)	(2,10)	(2,9)
Significant?	Yes		Yes	Yes	Yes	Yes
	T, Sq	T, Br	Br, Lp	Sq, Lp	T, Lp	Sq, Br
Sample F	29.756	8.55	20.55	39.09	0.82	11.64
Critical F ($\alpha= 0.05$)	5.59	5.59	5.99	5.99	5.59	5.99
Df	(1,7)	(1,7)	(1,6)	(1,6)	(1,7)	(1,6)
Significant?	Yes	Yes	Yes	Yes	No	Yes

Table 13. (Continued)

Comparisons of Populations using all Data from each Population

Populations	T, Sq, Br, Lp	T, Br, Lp	T, Sq, Br	Br, T	Br, Lp	Sq, Br
Sample F	21.66	6.524	19.91	6.244	10.98	11.64
Critical F ($\alpha = 0.05$)	2.80	3.27	3.27	4.24	4.30	4.30
Degrees of freedom	(3,47)	(2,36)	(2,36)	(1,25)	(1,22)	(1,22)
Significant?	Yes	Yes	Yes	Yes	Yes	Yes

Populations	Lp, Sq	T, Sq	T, Lp
Sample F	48.427	40.714	1.0933
Critical F ($\alpha = 0.05$)	4.30	4.24	4.24
Degrees of freedom	(1,22)	(1,25)	(1,25)
Significant?	Yes	Yes	No

Table 13. (Continued)

Comparisons within a Population of the Effect of a Change in
Sucrose Concentration

	Lower Peavine	Taylor Creek	Squirrel Place	Briggs Creek
Sample F	1.69	2.31	1.86	0.38
Critical F ($\alpha = 0.05$)	4.26	3.88	4.26	4.26
df	(2,9)	(2,12)	(2,9)	(2,9)
Significant?	No	No	No	No

Table 14. F DISTRIBUTION ANALYSIS OF MEAN POLLEN TUBE LENGTH IN VITRO

Comparisons Among Populations Within Each Sucrose Concentration

	10 percent sol'n	20 percent sol'n	30 percent sol'n
	Sq, Br, T, Lp	Sq, Br, T, Lp	Sq, Br, T, Lp
Sample F	0.257	2.786	1.16
Critical F ($\alpha= 0.05$)	3.49	3.49	3.41
df	(3,12)	(3,12)	(3,13)
Significant?	No	No	No

Comparisons Among Populations Using all Data

Sample F	2.199
Critical F ($\alpha= 0.05$)	2.82
df	(3,45)
Significant?	No

Table 14. (Continued)

Comparisons Within a Population of the Effect of a Change in
Sucrose Concentration

	Taylor Creek	Squirrel Place	Briggs Creek	Lower Peavine
Sample F	1.014	3.22	2.11	1.07
Critical F ($\alpha = 0.05$)	3.98	4.26	4.26	4.46
df	(2,11)	(2,9)	(2,9)	(2,8)
Significant?	No	No	No	No

Majumder, 1961). The average percentage of grains that exhibited any sign of germination was also significantly different when all populations were compared ($F = 14.92$; Critical $F (\alpha = 0.05; 3,47 \text{ df}) = 2.80$).

Pollen behavior in vitro is usually highly variable and is influenced by a wide variety of factors; the age of the pollen, the vigor and genotype of the parent, and the duration of temperature and humidity conditions following anthesis are all important (Brewbaker and Majumder, 1961). The well known pollen mass effect in which a greater percent germination is achieved with higher densities of pollen grains should not be an important variable in this test, because Brewbaker and Kwack's (1963) medium is specifically designed to overcome the mass dependence and allow small numbers of grains to germinate alone.

A large difference in the average percent germination between populations was obtained, the range being 20.66 - 65.29 percent. Although the lowest percent viability that would still insure normal seed set must be determined for each species, a 40 percent or better viability is usually considered necessary (Stanley and Linskens, 1974). Positive conclusions cannot be formed as to whether these variations were due to the different genotypes of each population or were merely a reflection of outside influences upon the anthers tested. Because such large variability existed in the products of meiosis and in pollen stainability, the germination values might be expected to exhibit a wide range in viability from anther to anther and from individual to individual. In order to characterize the pollen germination capacity

of an entire population, extensive replicates should be performed using a large number of individuals from each population.

Flower Structure and Pollinator Activity

Sophora leachiana possesses a terminal raceme of (10) 20-50 (60) creamy pale yellow papilionaceous flowers 10-15 mm long. As with many other Fabaceae (Faegri and van der Pijl, 1971) the flowers appear to be protandrous; they possess a simple valvular type of tripping mechanism (Wheeler and Hill, 1957). Although the floral development is similar to that described by Urban (1934) for Sophora tetraptera, the necessary details for Sophora leachiana will be presented in this section.

As the flower bud opens, the banner, wings and keel protrude first, while the immature stamens and pistil remain tightly invested by the calyx. Gradually the corolla elongates as the calyx expands into a gibbous, bell shaped structure. During this process, the stamens and pistil are maturing and elongating. Although the length of time involved in flower maturation could not be studied, corolla elongation appeared to be a rather slow event, since as many as three whorls at a time in the inflorescence could be in this stage of development. The banner of S. leachiana is a very rigid, tough, almost linear structure 10 mm long, with only the terminal 4 mm reflexed and petal like in texture. The mature flower never opens fully, as the wings and keel are always in close contact with one another. This results in a tube-like corolla despite the fact that all petals are free. The corolla is almost fully developed before or soon after

the first anthers dehisce; however, at this time the thin-textured banner tip often begins to turn brown.

The top two or three stamens are the first to dehisce. At this stage the pistil is shorter than the stamens by approximately 2 mm and all stamens are about the same length. After the top stamens dehisce, the lower stamens appear to lengthen. This is actually due to differential growth of the receptacle, with more elongation occurring on the lower side, as well as to the fact that the upper part of the filaments of these top anthers has started to turn brown and shrink. By the time that about half the anthers are fully dehisced, ovary elongation has taken place positioning the stigma at about the same level as the anthers. When all anthers have dehisced, the stigma is usually placed about 1-2 mm above the stamens. After or during the time that the last anthers are dehiscing, nectar begins to be secreted at the base of the ovary and to collect in a cup-like depression formed by the differential growth of the receptacle. Sophora leachiana's top two filaments are not placed side by side but are positioned about 1.5 mm apart and bend slightly away from one another before coming together. This creates a physical gap giving an insect access to the nectar. By the time that nectar production occurs, the exerted portions of all corolla members have usually begun to dry and brown, and the flower changes from a horizontally held position to a nodding position.

The pollinators of Sophora leachiana are bumblebees (cf. S. flavescens; Knuth, 1908). Several individuals were observed visiting

Sophora flowers at Upper Peavine, Lower Peavine, Taylor Creek, and Briggs Creek. The one individual collected was identified as a worker of Bombus vosnesenskii; this species is very common throughout the interior valleys and mountains of Western Oregon and California. It is also one of the earliest species to fly, with the queens emerging from hibernation as early as March 6, followed by the workers on April 17 and males on May 12 (Stephen, 1957). These dates effectively overlap Sophora's blooming period of the end of April through May. It must be emphasized that even though only Bombus vosnesenskii was collected, other bumblebees probably visit Sophora leachiana as well. However, it is believed that the only effective pollinators of Sophora leachiana are members of the genus Bombus. Honeybees were observed at the flowers at Taylor Creek and Briggs Creek; however, these bees are only nectar thieves. Honeybees fly directly to the opening on the side of the flower between the calyx and the carina where they have access to the nectar. Bombus was the sole observed pollinating insect; furthermore, certain characteristics of the flowers suggest that Sophora leachiana has become specifically adapted to this pollinator.

The large tightly packed terminal inflorescence is in itself an adaptation to bumblebee pollination (Wheeler and Hill, 1957). The exertion of the corolla from the calyx long before the anthers dehisce probably serves the purpose of flag flowers which visually attract the bees attention. The creamy pale yellow flower color is also a good attractant to bumblebees (Macior, 1974).

The individual flowers themselves also show adaptations to bumblebees. These include modification of the banner into the very rigid structure, which serves as a landing platform and allows the bee to get a secure grip on the flower as well as acting as support for the bee's head to press against as it goes after the nectar (Knuth, 1908). The closed corolla is also an adaptation to bumblebees (Faegri et al., 1971), as only a large bee will be strong enough to push aside the petals to get into the flower.

Sophora leachiana possesses what Wheeler and Hill refer to as a simple valvular type of tripping mechanism; the stamens and pistil project from the keel as long as pressure from the bee continues. When a bumblebee alights on the flower the weight of its body forces the keel to bend down. The more flexible stamens move with the keel for a ways before breaking out of the keel and returning to their original position; thus the bumblebee will first contact the more rigid pistil before being dusted with pollen from that flower. When the bumblebee moves on to another flower, the sexual column returns to its original position inside the keel. If the bee has just come from a flower of a different clone, it could effect outcrossing for that flower. It must be noted that based on observations in both field and laboratory, it appears that the stigma becomes dusted with its own anthers' pollen usually only if that flower had been manipulated by a bee. Careful cutting away of the banner, wings and keel without disturbing the sexual column, and observation of the stigma with a dissecting microscope, usually showed an absence of

pollen grains on the stigma. Many papilionaceous protandrous flowers do not automatically self pollinate as in most cases the pollen lands on the style rather than the stigma (Gray, 1889). A ring of trichomes found encircling the stigma may offer further protection in preventing a transfer of pollen from the neighboring anthers (Knuth, 1908; Clewell, 1966). Thus it appears that Sophora leachiana may have difficulty self-pollinating in the absence of a Bombus visitor.

In keeping with general observations on bumblebee behavior reported by Faegri and van der Pijl (1971), the bumblebees seen on Sophora leachiana did tend to land towards the lower part of the inflorescence and work their way up the raceme. However, in order for Bombus sp. to receive nectar, only flowers with brown corollas must be visited. This is atypical of the usual method of visual attraction used by many flowers, as a "fresh" appearance of the corolla, especially the banner of legumes, serves as an attractant to the bee. Likewise bees normally learn to avoid browning corollas because they usually indicate no nectar rewards due to prior pollination of the stigma or due to the age of the flower (Wheeler and Hill, 1957). It was noted that the flowers of Sophora leachiana possess a slight fragrance. Although the initiation of odor production in relation to the stage of flower development could not be determined, if the intensity of odor is stronger in the older, nectar-secreting flowers, the odor could be serving as an important signal to the bee. It is known that members of Bombus do not forage exclusively for nectar but will also gather pollen. Furthermore, bumblebees must individually learn how to manipulate any floral mechanism, including learning

which flowers are offering rewards. One member of Bombus vosnesenskii was observed on several inflorescences at the Upper Peavine location. This worker would begin at the base of the inflorescence, then climb its way up the inflorescence far above the nectar secreting flowers all the way to the newly opened buds. This individual appeared to be just exploring the inflorescence; because the plants of the Upper Peavine location produce no pollen, this could not have been the object of the search.

Despite four days' field work by the author during the blooming season, only about ten bumblebees were observed visiting Sophora leachiana. The weather was partly at fault, as scattered showers occurred all four days. However, at Upper Peavine, numerous Bombus individuals were seen on Lathyrus polyphyllus, but only three visited Sophora leachiana. Due to the low number of pollinators that were observed, a complete analysis of pollinator behavior was not attempted. However, Bombus usually limited its foraging activities to those Sophora individuals found at the edge of a colony, or to those occurring in a relatively small open stand. Bumblebees were never seen in the interior of a densely flowering stand of Sophora leachiana.

Pollen-Ovule Ratios

An evolutionary change from xenogamy to autogamy in many plant species has resulted in decreased energy cost per flower through a decrease in flower size and in the amount of pollen produced per flower. Cruden (1977) was able to correlate the ratio of the pollen grains produced in a flower per the number of ovules in that flower

(pollen-ovule ratio, or P/O) with the breeding system. Five categories ranging from cleistogamy to xenogamy, each with their respective P/O ratio, were defined, with the P/O ratio increasing logarithmically from group to group.

The flower's structural adaptation to the breeding system is summarized in an outcrossing index (OCI) (Cruden, 1977). The diameter of the flower, and spatial and temporal relationships between the stigma and anthers determine the OCI. The index values increase from zero to five with increasing xenogamy.

The breeding system, therefore also the P/O ratio, has been correlated with the habitat occupied by the species. Autogamous or cleistogamous individuals are usually early successional or weedy species whereas late successional species tend towards xenogamy. The former habitats are characterized by unpredictable pollinators; late successional, usually stable habitats have dependable pollinators.

Sophora leachiana's average pollen-ovule falls well into Cruden's xenogamous category (Table 15). The outcrossing index of five also is evidence favoring xenogamy. Sophora's P/O ratios show differing values due to the variation in amount of pollen produced from anther to anther or even between halves of the same anther. The lower values of total grains per anther reflect the production of unreduced spores as well as tetrad formation by the PMCs.

Table 15. Pollen-Ovule Ratios.

Population	Total Grains per Half Anther	Total Grains per Anther	Pollen-Ovule Ratio	Log P/O
Br	3797, 3596	7393	12321	4.09
Br	3440, 2198*	5638	11276	4.052
Br	3171, 3105	6276	12552	4.098
LP	3250, 3188	6438	10730	4.03
LP	4320, 3291	7611	10872	4.036
LP	3451, 3847	7298	12163	4.085
LP	4032, 4014	8046	11494	4.060
Average of Briggs Creek: P/O = 12049				4.0809
Average of Lower Peavine: P/O = 11315				4.053
Average of all values: P/O = 11682				4.067
Cruden's (1977) Xenogamous value P/O = 5859.20				3.650

*reflects a large number of unreduced spores.

Pollen-Stigma Interaction

The results of experiments on pollen-stigma interaction are presented in Table 16. For each cross the staining response of the stigma and style was recorded along with the presence and condition of any pollen grains. A potentially successful cross was taken to be one in which the stigma retained the pollen grains. As it was difficult to tell if pollen tube growth had occurred, the success of a cross could not be based on this criterion. Several observations were noted in analyzing the results.

Successful crosses only occurred in the older flowers of Sophora leachiana in which the stigma was equal to or elevated above the dehisced stamens. In no instance was pollen retained on a younger stigma. Grains adhered to the mature stigmas only if the cross was a self between flowers on the same inflorescence or between individuals from the same population. Eight out of 14 crosses (57.1 percent) performed by selfing older flowers, and two out of five (40 percent) intrapopulation crosses, successfully held the pollen. Of these, 25 percent of the selfs and 50 percent of the intrapopulation crosses held germinated grains on the stigmas. These results support the morphological evidence that flowers of Sophora leachiana are protandrous. Although further tests should be conducted, it appears that the populations of Sophora leachiana tested are not able to form compatible interpopulation crosses.

Observations were also made on the older flowers in the inflorescences used in the laboratory and field experiments (Table 17). Note that even though all pistils reported in this table were

Table 16. Pollen-Stigma Interactions

Vial #	Pollen Source	Color of stigma/ color of style tip ¹	Pollen grains
<u>Taylor Creek</u>			
T1	Br	Clear/clear	
T3	Lp	Clear/clear	
T4	Br	Clear/clear	
T2	S	Clear/clear	
T5	Sq	Clear/clear	
T6	T	Clear/clear	
T8	Lp	Clear/clear	
T17	S	Clear/clear	
T7	S	Clear/clear	
T9	Sq	Clear/clear	
* T10	S	Deep blue/deep blue	2 deep blue grains
T12	T	Light blue/clear	
T11	Br	Clear/clear	
T16	S	Light blue/clear	
T14	S	Light blue/clear	
T18	Sq	Light blue/clear	
T15	Br	Light blue/clear	
T19	S	Blue/Light blue	2 deep blue grains
<u>Briggs Creek</u>			
Br1	T	Clear/clear	
Br2	Lp	Clear/clear	
Br3	Sq	Clear/clear	
Br4	T	Clear/clear	
Br5	Lp	Clear/clear	
Br17	Br	Clear/clear	
Br6	Lp	Clear/clear	
Br8	S	Clear/clear	
Br9	S	Bluish/clear	
Br18	Br	Bluish/clear	
Br10	T	Bluish/clear	
* Br19	Br	Bluish/clear	1 blue grain
Br12	Sq	Bluish/clear	
Br13	Lp	Bluish/clear	
Br14	S	Deep blue/deep blue	5 deep blue grains

*This line separates the immature stigmas from the mature, receptive stigmas. The line was drawn based on flower morphology at the time the crosses were performed.

Table 16. (Continued)

Squirrel Place

Sq2	T	Clear/clear	
Sq3	Br	Pale blue/clear	
Sq6	S	Clear/clear	
Sq5	T	Light blue/clear	
Sq9	Sq	Clear/clear	
Sq10	T	Pale blue/clear	
Sq1	Lp	Light blue/clear	
Sq4	Lp	Light blue/clear	
Sq15	S	Deep blue/blue	3 grains; 2 germ tubes
Sq12	Lp	Bluish/clear	
Sq11	S	Bluish/clear	
Sq16	Sq	Clear/clear	
Sq14	Br	Clear/clear	
Sq18	S	Deep blue/blue	(no grains)
Sq17	S+Br	Blue center/clear	
Sq19	S+T	Deep blue/deep blue	2 deep blue grains

Lower Peavine

Lp1	Sq	Clear/clear	
Lp2	T	Clear/clear	
Lp3	Br	Clear/clear	
Lp4	T	Clear/clear	
Lp5	Sq	Clear/clear	
Lp6	Br	Light blue/clear	
Lp7	Lp	Clear/clear	
Lp8	Br	Pale blue/pale blue	
Lp10	T	Pale blue/pale blue	
Lp9	S	Light blue/clear	1 blue grain
Lp11	S	Deep blue/deep blue	numerous grains w/tubes
Lp12	Lp	Pale blue/clear	
Lp13	Sq	Clear/clear	
Lp14	S	Clear/clear	
Lp15	S	Blue/clear	1 blue grain
Lp16	Lp	Deep blue/deep blue	numerous grains w/tubes

Table 16. (Continued)

Upper PeavineInflorescence #1

Up2	T	Light blue/light blue
Up3	Br	Clear/clear
Up4	Lp	Light blue/clear
Up7	Br	Light blue/light blue
Up5	T	Light blue/clear
Up6	Br	Blue/light blue

Inflorescence #2

Up9	Lp	Light blue/clear
Up10	T	Blue/blue

Total Populations:

	Sq	Lp	Br	T	Up	Total
Selfed						
*successful	2	3	1	2	-	8
*unsuccessful	3	1	0	2	-	6
Intrapopulation						
*successful	0	1	1	0	-	2
*unsuccessful	1	1	0	1	-	3
Interpopulation						
*successful	0	0	0	0	0	0
*unsuccessful	4	3	2	3	8	20

*Results based only on crosses using receptive stigmas, not on those using young nonreceptive stigmas.

¹Staining reaction with analine blue (Nair and Narashimhan, 1963).

Table 17. Analysis of Receptive Stigmas for Natural Pollination.

	<u>Condition of Stigma/Condition of Style Tip</u>						Number of stigmas w/germinated grains
	<u>Light blue or clear/clear</u>		<u>Blue/blue</u>		<u>Dark blue/dark blue</u>		
	Without grains	With grains	Without grains	With grains	Without grains	With grains	
Lp17	-	-	-	-	-	5	3
Lp18	-	-	-	-	-	12	12
Up11	11	-	1	-	3	-	-
Up12	8	-	-	-	2	1	1
Up1	3	-	-	-	3	2	1
Up2	-	-	-	-	5	3	1
Br	8	1	-	-	-	-	-
T1	8	-	3	-	2	4	2
T2	2	-	-	-	2	6	5
Lpfruits	-	-	-	-	-	5	5
Brfruits	-	-	-	-	-	1	1
Total	40	1	4	0	17	39	31

Table 17. (Continued)

Lp17 - lower flower of the inflorescence used in lab crosses.

Lp18 - flowers with browning styles below the Lp17 flowers.

Up11 - lower flowers of inflorescence #1 used in the lab crosses.

Up12 - lower flowers of inflorescence #2 used in the lab crosses.

Up1 - flowers with brown stigmas and styles collected in the field.

Up2 - flowers with brown stigmas and styles collected in the field.

Br - lower flowers from the inflorescence used in the lab.

T1 - lower flowers from the inflorescence used in the lab.

T2 - lower flowers collected in the field.

from mature flowers with all or nearly all dehisced stamens, only 40/101 (39.6 percent) had pollen grains. This may indicate that self pollination does not occur spontaneously (or occurs only sporadically) but is effected by visiting insects. Since these flowers were all older flowers, their stigma should have been receptive to pollen if selfing had occurred. Developing fruits collected at Lower Peavine and Briggs Creek all had numerous grains with tubes entrapped on the stigmas.

Extensive checks of flowers at Upper Peavine did not reveal any pollen production. Nonetheless, six out of 42 (14.2 percent) pistils from Upper Peavine contained pollen grains. These grains probably were transported from the nearby Lower Peavine population by insects. Even so, pollen transfer between the populations was not extensive; only 18 grains of six stigmas were present, and only five of these grains (including three large unreduced spores) did germinate. If the pollen was indeed from Lower Peavine, these two populations may have the potential for crossing successfully. On the other hand, if the pollen came from sporadic production at Upper Peavine, these results indicate that pollen transfer can occur and that intrapopulation grains can germinate on the stigma.

Large unreduced microspores, probably from dyads, were seen on stigmas of Briggs Creek and Lower Peavine, as well as Upper Peavine. Such spores had already been noted in Briggs Creek and Lower Peavine populations during meiotic and pollen stainability studies. Only one unreduced spore was present on a Briggs Creek stigma; this large grain was stainable but had not germinated. Lower Peavine stigmas

held three large grains, all stainable, and two possessed germ tubes.

Color reactions of the stigmas and styles following clearing and staining are given in Table 16. In nearly all cases, stigmas to which pollen grains adhered retained the dye and were blue or deep blue, while clear (destained) stigmas were devoid of pollen. If the stigma was stained, its style was blue or deep blue as well. A similar correlation was found in pistils collected in nature (Table 17). To explain the relationship between color reaction and successful pollination, two hypotheses were considered. One is that placing compatible pollen on receptive stigmas effects a change that can be detected by the staining reaction. The other is that some innate characteristic of receptive stigmas itself, independent of compatible pollination, causes the staining reaction. In order to test if a correlation existed between pollen grain retention and blue dye retention, a multinomial distribution contingency table was constructed and analyzed using Chi Square. The resulting test failed to support a random occurrence of these events. Therefore, the correlation between retained pollen and blue coloration, which occurred only in intrapopulation crosses was probably caused by a differential response of the stigmas favoring intrapopulation pollen.

In summary, the artificial crosses and the pistils analyzed for natural pollination suggest that Sophora leachiana is protandrous. The species appears to be self-compatible in that intrapopulation and selfed pollen grains, including unreduced dyads, are retained and do germinate on the stigma. Interpopulation crosses are not compatible,

at least among the individuals used in this series of experiments. Natural pollination studies show that an insect visitor (Bombus sp.) is helpful in pollination, because self-pollination is not automatic as the flowers mature. Finally, although more work should be done to offer further support, these results suggest that retention of the blue dye could be used as a convenient indication of cross compatibility in Sophora leachiana.

Artificial Field Crosses

The results of the field crosses performed in the spring of 1977 are in Table 18. Note that the only crosses yielding even partial fruit development were at Briggs Creek. All young fruits had swollen ovules inside which suggests that successful fertilization did occur.

In individual 2Br several ovaries began development following pollination by Taylor Creek. Only slight development took place before abortion, as the ovaries only lengthened to 9mm as compared with an average of 5.8mm (5.5 - 7.0mm) long for the undeveloped ovaries. The selfed flowers in this cross did not show any development.

Some flowers on shoot 4Br had partially developed fruits. Pollen from Lower Peavine was supplied to the stigma, but the stamens were first allowed to self the flower. Other flowers were emasculated and pollinated with Lower Peavine pollen; in these instances the flower was not allowed to self. Partial fruit development with fruits averaging 17mm in length occurred in 14 flowers; all 14 were from the initially selfed flowers and not from the emasculated and crossed flowers.

Table 18. Field Crosses.

Upper Peavine

- | | | |
|-----|---|-----------|
| 1Up | - Nine flowers crossed with Taylor Creek. The remaining flowers left alone to check for prior pollination or selfing. | No fruits |
| 2Up | - Eight flowers crossed with Taylor Creek. | No fruits |
| 3Up | - Eight flowers crossed with Taylor Creek. | No fruits |

Taylor Creek

- | | | |
|----|--|--|
| 1T | - Five flowers selfed. | No fruits; possible mechanical damage. |
| 2T | - Five flowers selfed. | No fruits; mechanical damage. |
| 3T | - Six flowers crossed with different individuals. | Could not locate. |
| 4T | - Eight flowers with different individual. | No fruit. |
| 5T | - Six flowers crossed with different individual; lower flowers manually tripped. | No fruit. |
| 6T | - Five flowers crossed with different individuals; five flowers selfed. | No fruits; bag knocked off plant. |
| 7T | - Inflorescence bagged; flowers not manually tripped. | No fruits; possible mechanical damage |
| 8T | - Ten flowers crossed with different shoot on same rhizome. | Mechanical damage. |

Table 18. (Continued)

Briggs Creek

- | | | |
|-----|--|---|
| 1Br | - Nine flowers crossed with Taylor Creek. | Plant died. |
| 2Br | - Seven flowers crossed with Taylor Creek; lower buds manually tripped. Six flowers on second inflorescence crossed with Taylor Creek; lower flowers manually tripped; upper buds on this and other inflorescence not tripped. | Three swollen ovaries in Taylor cross. |
| 3Br | - Ten flowers crossed with Lower Peavine. | No fruits. |
| 4Br | - Thirteen flowers crossed with Lower Peavine after selfing; seven flowers crossed with Lower Peavine after emasculating. Other flowers on this and other inflorescence allowed to self. | Fourteen fruits underwent some development after selfing. |
| 5Br | - Six flowers crossed with a different Briggs Creek individual; lower flower dehisced but not manually tripped; upper flowers not tripped. | Two partial fruits developed in Briggs cross. |

Inflorescence 5Br was crossed with another individual from Briggs Creek. Two out of these six flowers did undergo partial development; these two fruits were 20 mm and 11mm long. Several of the remaining flowers had dehisced anthers but they were not manually tripped; no partial fruit development took place.

Two factors introduced error into the experiment. Mechanical damage interfered with the results of several crosses and there is a high probability that almost all crosses were affected to some degree. The three individuals which had partial fruit development were also the three individuals in which the cheesecloth bag was still securely held up away from the inflorescence. In all other crosses the bag had become disarrayed and was in direct contact with the inflorescence.

The second factor is the protandrous condition of Sophora leachiana. When this experiment was performed in the field, the timing of stigma receptivity had not definitely been established. Therefore several of these crosses may have been performed on stigmas that were too young, although emphasis was placed on using the older stigmas of flowers in which careful cutting away the petals and dehisced stamens did not cause the flower to self.

These crosses show that intrapopulation crosses and selfs can lead to successful fertilization and at least partial fruit development. Furthermore, the two hexaploid populations, Briggs Creek and Taylor Creek have the potential for successful fertilization, even though the results of the pollen-stigma studies suggested otherwise.

Reproductive Success of *Sophora leachiana*

The reproductive success of *Sophora leachiana*, as measured by the various stages leading to mature seed set in a population, is summarized in Table 19. The percent of flowering individuals could be determined for six populations. The remaining populations were visited at the end of the summer and in addition showed insect damage. This combination made it too difficult to judge the presence or absence of an inflorescence rachis.

Flowering of *Sophora leachiana* occurred almost exclusively in those areas exposed to full sun and seldom took place in locations even lightly shaded. Flowering at Nobles House did not occur in the area of the forest with a southern exposure but did take place in the section facing north-northwest where the plants were exposed to direct light as a result of a break in the forest canopy. Further support for this observation comes from two transects analyzed at Lower Peavine. One in full sun at the shoulder of the road yielded 34 flowering individuals out of 184 (18.47 percent). The second transect was in a stand of *S. leachiana* located in the interior of the forest and receiving light shade (about 50 percent cover). No flowering occurred in any of the 305 individuals present in the area. In calculating the percent flowering individuals for the populations (Table 19), areas of the population in locations not conducive to flowering were removed from the estimate. The percent flowering appears to be rather low; however, it must be recalled that the shoots are not separate individuals but are part of one or more large clones.

Table 19. Reproductive Success of Sophora leachiana

Population	Shoots	Inflorescences	Fruits when area was sampled	Developing Seeds	Mature Seeds
Up (1977)	189	38	0	0	0
¹ Th (1976)	128	34	11	11	0
² Lp (1976)	184	34	12	18	3
Up (1976)	355	16	0	0	0
¹ Sq (1976)	467	45	13	23	5
² Br (1976)	946	62	9	4	0
² Tc (1976)	718	39	4	3	0

Site Three - (plot area) No fruits in 1976, 1977; area visited too late to determine flowering. Fruits at other locations in this area in 1977.

Barr Mine - No fruits in 1976, 1977; area visited too late to determine flowering.

Soldier Creek - No fruits 1976; area visited too late to determine flowering.

Nobles House - Flowered in sun in 1976; no fruits.

New Place - Flowered 1977; no fruits.

Oak Flat - Flowered 1976, 1977; no fruits.

Table 19. (Continued)

	Individuals per m ²	Percent flowering individuals	Fruits per flower ³	Maturing seed per flower	Fruits per inflorescence	Maturing seed per inflorescence
Up (1977)	1.512	20.10	0.0	0.0	0.0	0.0
Th	1.700	26.56	0.0129	0.0129	0.3235	0.3235
Lp	2.450	18.47	0.0141	0.0211	0.3529	0.5294
Up (1976)	4.730	4.50	0.0	0.0	0.0	0.0
Sq	6.220	9.63	0.0115	0.0204	0.2880	0.5110
Br	6.300	6.55	0.0058	0.00258	0.1451	0.0645
Tc	9.57	5.43	0.0041	0.00307	0.1025	0.0769

¹Flowered 1977, but no fruits.

²Flowered and fruited 1977.

³The number of flowers per inflorescence was taken to be 25. This was based on a survey of young inflorescences at Lower Peavine and is probably a conservative estimate.

The percent fruit set was based on an average of 25 flowers per inflorescence. The fruit set for this species is extremely low, as the majority of the flowers drop after anthesis. It must be mentioned that in 1976, when much of the data were obtained, the populations were subject to heavy moth infestation which claimed many flowers. Thrips, which scrape the succulent lining of the flowers, were also numerous. These insects seemed to take a large toll of flowers, but their exact impact on fruit set cannot be determined.

Some ovaries began development only to abort at a later stage before maturity. Analysis of these swollen and lengthened ovaries showed that one or more ovules were also enlarged, signifying that fertilization and partial development had taken place. Fruits that aborted later in development contained aborted ovules at virtually all stages of maturation. This implies that fruit development is triggered only by initiation of development of a fertilized ovule and is not a response to pollination alone.

The calculation of total fruit set is based on fruits remaining on the plant in June. Therefore this figure does not reflect the ovaries which began development but aborted and dropped before the stand was sampled. However, if an ovary developed sufficiently to reach about twice the average length, it appeared to be retained on the rachis. Hence, fruit observations in late June probably reflect a large part of the total fruit set involving those fruits past a certain developmental stage.

The total seed set given in column four, Table 19, represents developing seeds present as a bulge in the wall of the young fruit.

However, not all of these seeds reached maturity. The final seed set for the area (column five, Table 19) as compared with the initial seed set reflects the number of these developing seeds which aborted towards the end of their maturation.

Various hypotheses are possible concerning the data collected in 1976 and 1977. There appears to be a correlation between the density of the population (expressed as individuals per square meter) and the percentage of flowering individuals. A higher density was usually correlated with a reduction in flowering as compared with less populous stands. An exception to this general rule were the Upper Peavine values for 1976.

Less populous areas also appear to have a stronger probability of setting fruits and undergoing at least partial development than higher density areas, although this was subject to perhaps even more variation than the flowering intensity vs. density correlation. However, field observations of final seed set does appear to support this hypothesis.

The fruit and seed collected in August of 1976 (Table 20, next section) represent extensive searching of many thousands of individuals throughout a large area of the population. Informal observations made during these searches suggested that a correlation exists between seed set and position of the individual with respect to the remaining colony and surrounding vegetation. Seed set was higher at the edges of a large patch rather than within the interior of the colony. Specifically, seed set was highest in those places that were adjacent to any area

relatively free of competition. At Briggs Creek, mature fruits were most commonly found on individuals next to the path or at the edge of the colony. For example, one patch of 114 individuals of Sophora leachiana was searched for mature seed. No check on percent of flowering was done for the whole colony, but fruit and seed development were restricted to a narrow (approximately 0.66m x 2m) strip adjacent to the path at the edge of the colony. Seventeen of the 27 individual (62.96 percent) present in this area flowered; ten of these 17 (58.82 percent) possessed some fruits and seeds, the fruit set being 0.235 per flower or 0.5882 per inflorescence. The fruits of five of these individuals contained good seeds; there were six mature seeds produced by these individuals for an average of 0.0141 mature seeds per flower (0.3529 seeds per inflorescence). Other seeding individuals at Briggs Creek were noted, although they did not occur together with as high a frequency as illustrated above; these individuals were also adjacent to the trail and/or at the edge of a colony.

The Taylor Creek and Site Three locations had seed set very strongly correlated with areas around old stumps, especially those located along the road at Site Three. No seeds were found at Site Three in 1976; however, only the area immediately surrounding the plot was carefully searched. The area that yielded seeds in 1977 was not checked in 1976. The plot area was checked for seed in 1977 but none were found. The mature fruits that were found at Site Three occurred on individuals adjacent to the road or more commonly in highly disturbed, less populated areas around old stumps along the road.

At Taylor Creek the higher seed set around stumps was noted in 1976 as well as in 1977. Very few mature fruits were seen in the dense stands of Sophora located in the southern half of the clearcut. The seeds collected in 1976, and noted in 1977, were found in the less populated areas farther up the slope, on individuals next to old stumps or to shrubs of Rhus and Ceanothus. Mature seed was also found on individuals next to downed logs, either at the edge of a Sophora colony or in the interior of a dense stand. In these searches for seeds at the populations visited, every effort was made to check all areas of the colony rather than to present a bias for the areas adjacent to a disturbance or at the edge of the colony.

Seed Morphology and Anatomy

The external appearance of the mature seed of Sophora leachiana is very similar to that of S. nuttalliana. Both are elliptical, attenuate at the apex, and yellow to light brown with a darker line marking the raphe. Sophora nuttalliana's seeds are about five by three mm (Rudd, 1972) whereas S. leachiana's range from this size to six by four mm. Germinable seeds of S. leachiana can possess concavities of varying extent and depth rather than being completely plump.

The mature embryo of S. leachiana is bright yellow, with a short straight radicle. The plumule is relatively undeveloped, the embryonic leaves not being visibly differentiated. Food storage in the cotyledons is in the form of several starch grains per cell (cf. S. tomentosa L., Corner, 1976).

The anatomy of the mature seed of S. leachiana is typical of those found in the Fabaceae and is similar to S. tomentosa (Corner, 1976). The seed is "hard", that is, impervious to water and able to retain viability for long periods. As with other legumes (Watson, 1948), S. leachiana also produces a small number of water-permeable seeds. The testa of S. leachiana is composed of a cuticle-covered outer palisade layer composed of a single row of tall, narrow macrosclereids. Within this palisade layer is the linea lucida, the light line. This lighter band running horizontally through the cells is believed to account for the impervious nature of the seed coat (Esau, 1967). The mesophyll or subepidermal layer below the palisade is composed of large, lacunose parenchyma with an outer layer of smaller cells slightly differentiated into hourglass cells. Small, round, pigment-containing bodies are found in the parenchyma furnishing color to the seed coat. Below this layer is a nonpigmented parenchyma representing the remains of the inner integument. In the mature seed, both parenchyma layers are crushed and collapsed to a total thickness less than the palisade layer; however, when wet, each layer expands to about equal thickness with the palisade. This observation conflicts with Corner's (1951) report that it is the palisade layer which swells with water.

The inner cuticle, a cuticle of double thickness located between the nucellus and the inner integument (Esau, 1967), persists in the mature seed as a casing around the embryo. Removing the testa from the embryo sometimes also served to remove this layer; however, it frequently

persisted around the dissected embryo. All endosperm is consumed by the embryo during development.

The hilum of Sophora leachiana is covered in part by a rim-aril, a vestige of a once prominent aril (Corner, 1976). The hilum itself is composed of the palisade and a second layer termed the counter palisade. A median groove (hilar fissure) provides an opening through the palisade layers. Below the median groove is the tracheid bar composed of short, reticulately pitted tracheids. Under the palisade and surrounding the tracheid bar are closely packed, very thick walled cells with the thickening occurring primarily in the walls perpendicular to the hilum. Corner (1976) noted this tissue in S. tomentosa; Reeve (1946a, 1946b) reports similar cells to be derivatives of the mesophyll's hourglass cells.

The hilum of hard seeds function in gas and water exchange. The hilum has a valvular action; it opens in low humidity, allowing the seed to reduce its water content, and closes in higher humidities, thus preventing the seed from absorbing water. Therefore, hard seeds usually have moisture contents equal to the lowest relative humidity to which they have been exposed. The opening and closing is regulated physically by a balance of moisture tension between the palisade and counter palisade layers. When swelling of the counter palisade layer occurs, the hilum closes, with the boundaries of the hilar fissure first contacting one another at the light line (Hyde, 1954).

Seed Variation in Natural Populations

A tally of seeds collected in August, 1976, is presented in Table 20. These figures represent most of the final seed set within six populations; no mature fruits were seen in the remaining seven areas. All fruits containing mature seeds were collected. Most but not all fruits in an arrested young stage of development were gathered. Classifying seeds into one of the eight categories outlined previously showed that well over half the fertilized ovules abort in the early stages of development. The rate of abortion sharply declines past this point. Only 25 percent of the fertilized ovules reached maturity.

The figures mentioned above have two sources of error. Not every fruit in which all ovules aborted at a young developmental stage was collected, therefore the true number of ovules aborted early in development is not known. Coupled with this is the fact that the smallest ovules (0.5mm x 0.25mm) were always considered to have been unfertilized. However, this size category may have also included those fertilized ovules that were quickly aborted before significant growth had occurred. If the true numbers of early aborted ovules were known, the percentage of early abortion would be higher and the percentage of seeds reaching maturity would be reduced.

The original tally was kept to indicate each fruits' contents, although data from all fruits were combined for presentation. Ovules within one fruit usually aborted at different developmental stages. A tally was also kept for the number of fungus-infected seeds. Percent infection was zero percent at West Fork Taylor, one percent at Lower

Table 20. Fruit and Seed Variation in Six Populations of Sophora leachiana.

	Total	Percent of Total	Briggs Creek	Lower Peavine	Squirrel Place	Taylor Creek	Taylor House	West Fork Taylor
Fruits Sampled								
Number of fruits			20	39	55	244	15	1
Fruits/fertile shoot			1	2.1	3	4	1	1
Unfertilized Ovules	591		27	28	29	505	1	1
Aborted Seeds	517	75	20(83%)	63(77%)	86(81%)	333(72%)	12(86%)	3(75%)
Group 1	145	21	4	10	11	107	10	3
Group 2	221	32	9	30	53	127	2	0
Group 3	55	8	1	1	12	41	0	0
Group 4	46	6.6	3	8	9	26	0	0
Group 5-6*	50	7.25	3	14	1	32	0	0
Mature Seeds	173	25	4(17%)	19(23%)	20(19%)	127(28%)	2(14%)	1(25%)
Group 7	61	8.8	4	7	5	44	1	0
Group 8								
yellow testa	104	15	0	10	15	77	1	1
brown testa	8	1	0	2	0	6	0	0
Total Seeds	690		24	82	106	460	14	4

* See Materials and Methods for reason of combining these classes.

Peavine, seven percent at Taylor House, nine percent at Taylor Creek, 21 percent at Briggs Creek and 25 percent at Squirrel Place. Infestation occurred with equal frequency in Groups 2, 3, 4, and the combined Groups 5 and 6. Only one Group 7 seed was infected; a tally was not kept for Group 1 seeds because fungal detection was too difficult on the very small aborted ovules. Infected and noninfected seeds were found in the same pod. The mold probably does not influence seed abortion and limits its attack to aborted seeds.

Aborted Seeds

Analysis of aborted seeds yielded several interesting results. Embryos isolated from seeds in the same size category sometimes varied 100 percent in length. Therefore, the size of the seed was not determined by embryo size. Isolated embryos were sufficiently mature to possess at least young cotyledons. The embryos were usually well formed, although several possessed cotyledons of unequal size. All isolated embryos from seeds of Group 6 or smaller appeared starved, in that the cells lacked stored food and were highly vacuolate. A Group 4 embryo did have some food reserves in the upper radicle region, but only a very limited amount in localized areas of the cotyledons. Embryos were usually firm, although as shown in the following section, this does not automatically signal a viable embryo. One Group 3 embryo did possess green cotyledons following 24 hours imbibition and exposure to light. Thus, some of these embryos may still be viable, but save for Group 7 and 8 none possessed the extensive food reserves necessary for germination.

In the remaining categories of seed size the embryo was too small to attempt isolation, therefore the entire seed was microtomed. Because preservation in FAA took place about four months after the seed was aborted, the tissues were difficult to section without tearing, and interpretation of aborted seeds was complicated by the shriveled nature of some tissues. Satisfactory sections from seeds revealed embryos in developmental stages ranging from small globular embryos to those with cotyledons developing. Leguminous endosperms are nuclear during early development, later usually becoming cellular at least in the micropyle region of the embryo sac (Anahtaswamy, 1951). Sophora's endosperm appeared to begin cell wall formation in the late globular embryo stage. However this tissue was always very starved and in disarray, therefore conclusive statements can not be made. The nucellus tissue surrounding the embryo sac was usually a single layer of small, regular cells. The inner cuticle was often prominent.

Sections of one Group 2 seed are of special interest. The embryo was in the heart-shaped stage of early cotyledon differentiation; the endosperm was composed of collapsed cells. The nucellar tissue was composed of greatly enlarged cells in the area immediately surrounding the radicle region and the dorsal side of the embryo. Enlarged cells were also found near the chalazal end of the embryo sac. In addition, the inner epidermis of the integument appeared to have changed to an integumentary tapetum composed of enlarged, densely cytoplasmic cells oriented perpendicular to the surface of the embryo (Esau, 1967). Hyperplasia of the nucellar cells or inner integument

is a characteristic of somatoplastic sterility (Cooper and Brink, 1940b). In this developmental pathway, the maternal tissue enlarges sufficiently to interfere with the transfer of nutrients between the embryo sac and the vascular bundle. This interference leads to abortion of the embryo. Somatoplastic sterility has been known to cause abortion in interspecific crosses as well as in inbreeding. Medicago sativa ovules abort after self-fertilization for this reason (Cooper and Brink, 1940a, 1940b). Other characteristics of somatoplastic sterility include failure of the vascular bundle to differentiate completely along with limited growth of the endosperm. Whether these occurred in this seed could not be determined. It must be mentioned that suspensors of legumes can undergo massive endoreduplication up to the 4096 ploidy level with an increase in cell volume of about 3000 times over the normal diploid cells (Nagl, 1962). It is unlikely that the cells in the Sophora sections are suspensor cells, as they are positioned around one complete side of the embryo rather than the expected suspensor position at the radicle only. Further evidence is the placement of the enlarged layer directly adjacent to the inner cuticle, suggesting that it was indeed the nucellus layer.

Abnormalities in Mature Seeds

Differences in mature embryo structure were evident in the Group 7 and Group 8 seeds used in this study and in the following viability study. A very common variation was the presence of extra lines or grooves along the cotyledons which gave the appearance of there being more than two cotyledons. Three cotyledons symmetrically

placed around the embryo were observed in only one individual, however. Placement of cotyledons also varied among the embryos. Normal embryos possessed two equal sized cotyledons symmetrically positioned on either side around the radicle. Many pairs of cotyledons were unequal in size, and many were placed off-center to the line of symmetry produced by the radicle or were positioned normally but twisted so that the tips of the cotyledons deviated as much as 45° from the plane of symmetry. One individual had two equal cotyledons whose placement was 90° with respect to the typical cotyledon position. There was no correlation between placement or size relations of cotyledons and viability of the embryo.

Twin seedlings were found in several instances. Sections of a Group 7 seed showed two mature embryos each with densely cytoplasmic radicle cells and starch filled cotyledon cells. One twin was thinner and shorter than the other, they were placed parallel to one another but their respective planes of symmetry were perpendicular. There was no physical connection between the embryos. Additional twins found in viability studies included a second embryo in much the same position as the above twin. In this instance, the twin was in the same plane of symmetry as the larger embryo although the primary embryo's cotyledons twisted 45° . The third example from Group 7 had one embryo at the apex of the other. The only slightly smaller lower embryo's radicle was tucked between the lower halves of the cotyledons of the upper embryo. Both embryos of this twin were fully viable; the former twin exhibited some staining but was considered inviable after 70° followed by an 80°C heat treatment.

One embryo sectioned from Group 3 represented conjoined twins, with fusion occurring throughout most of the hypocotyl region. The radicle possessed a bifid apex; the plumule did not appear to be bifid although distinction was difficult due to the embryonic nature of the shoot tip even in a mature embryo. There were three cotyledons; these were not symmetrically positioned around the embryo axis but were all placed side by side. Conjoined embryos can develop from two sources--cleavage of one embryo or fusion of two embryos into one. Cleavage of the initial embryo will form two separate embryos if division occurs in the early developmental stages. Division at a much later stage of development will yield a common hypocotyl with bifid radicles and plumules (Randall and Rick, 1945). Conjunction of two embryos into one is not uncommon. Multicotyledonous embryos have often been attributed to fusion of two embryos (Maheshwari and Chopra, 1955).

The extra embryos in a polyembryonic seed can arise from a variety of sources. More than two embryo sacs can be present in an ovule. Embryos can be borne from the nucellus layer, integument, antipodals, synergids or the suspensor. Studies with other legume species have shown cleavage polyembryony to be responsible for twin formation in Trifolium and Medicago (Skovsted, 1939, in Webber, 1940; Greenshields, 1951, in Maheshwari, 1963). Medicago can also form two embryo sacs within one ovule (Skovsted, 1939, in Webber, 1940). Synergids can develop into embryos with or without fertilization in Phaseolus vulgaris (Belikova, 1952, in Maheshwari, 1963); nucellar

embryos have been found in Trifolium pratense (Fedortschuk, 1944, in Maheshwari, 1963).

As with any physiological process, polyembryony is influenced by a variety of factors. Genetic controls are well known. Polyembryony is usually a recessive trait controlled by one or more genes (Kappert, 1933, Leroy, 1947, in Maheshwari, 1963). Atabekova (1957, in Maheshwari, 1963) reports that different races of several species of Lupinus have genes governing not only polyembryony but also regulating the degree of embryo fasciation. A hybrid condition is believed to increase the incidence of polyembryony (Martin and Watt, 1964; Maheshwari, 1963). Environmental conditions also influence polyembryony; for example, the frequency of nucellar embryos produced in Citrus decreases with a reduced food supply. It is not possible to state the source of polyembryony of S. leachiana. Extensive anatomical sections of the developing ovules often coupled with genetic characteristics of the twins must be studied before the origin of secondary embryos are known.

Seed Germination Studies

Germination of seeds of Sophora leachiana is epigeal. The hypocotyl hook usually emerged from the soil before straightening; however, in some instances straightening took place below ground and the cotyledons were first to emerge. The yellow cotyledons were held never more than one cm from the soil; they became upright an average of 2.5 days after the hypocotyl hook became evident. The cotyledons had separated and were beginning to green by the fifth day. Visible

signs of shoot development occurred by the ninth day. The first leaf is not compound but is oval-elliptic and approximately 14mm x 12mm. The second leaf and often the third is trifoliate with one pair of opposite lateral leaflets and a larger terminal leaflet. The next leaf possesses five leaflets (two pairs of lateral leaflets with one terminal leaflet) and the next has seven leaflets. The stems, petioles and rachillas are clothed with short, soft, white hairs. This pubescence continues on the lower epidermis of the leaflets, is conspicuous as a fringe around the leaf, but is more sparse on the upper leaflet surface. The stem below the cotyledons quickly develops a covering of dark brown bark.

By the end of two months' growth, the number of leaves per plant ranged from two to five. The height varied from 2.5 cm to 8.9 cm, averaging 5.25 cm. As the differences in height indicate, seedlings varied in vigor and rate of growth. The most robust individual possessed green cotyledons and obvious shoot development two days after the hypocotyl emerged from the soil. At the end of two months it was the tallest individual by one cm and possessed five leaves. In contrast, three seedlings took 23 days or more for shoot formation to become apparent.

Some variations encountered in seedling growth could have been due to improper watering. The flats were first allowed to stand in shallow water. This plus the presence of a glass plate on top of the flats, kept the soil extremely moist at all times. The first seeds to show visible signs of germination were those that were on

the surface of the soil (even though all seeds were buried approximately 1.3 cm deep, several seeds had become displaced to the surface). Radicles of germinated seeds did not grow into this wet medium but remained at or above the soil. The flats were then drained of excess water and allowed to dry several days; further watering was done from above. With improved soil aeration and drainage, the radicles of affected seedlings grew into the soil, but a few individuals had to be replanted. Once the radicles were in the soil, shoot development commenced.

A second problem occurred with two seedlings due to mechanical cracking of the seed coat. Artificial scarification has been known to cause abnormal germination and seedling development. In these cases, the seedlings' radicles stayed inside the seed coat and could not penetrate the soil. These seedlings were not vigorous, wilted readily, and died before or shortly after the first leaf developed.

Germination occurred quickly after the stratified seeds were placed in the greenhouse. Radicle elongation was evident within 24 hours in those seeds that had been displaced to the soil surface. Hypocotyls became visible the third day in several seeds that remained buried. Germination commenced an average of seven and a half days after the end of stratification, with the longest period being 19 days. Of the twelve seeds tested from Group 7, seven (58.3 percent) germinated. The germination percentage of the seeds in Group 8 was also 58.3 percent, the individual results of the three flats being five out of twelve (41.66 percent), seven out of twelve (58.3 percent), and nine out of twelve (75.00 percent).

Seedling survivorship was high (23 out of 28, or 82.14 percent) with three seedlings dying in Group 8 and two in Group 7. One seedling from Group 8 died due to manual scarification damage, one underwent slight radicle emergence but no further development, while the third seedling remained for over a week with the hypocotyl hook above the soil but never raised the cotyledons. One Group 7 individual perished due to scarification damage and the other underwent only slight radicle elongation. Since two of the seedlings died as a result of pretreatment and not from natural causes, the actual seedling survivorship was 25/28 or 89.28 percent.

Effects of Heat on Embryo Viability

The results of the viability studies following heat treatment are presented in Table 21. Several observations can be summarized.

Out of 59 seeds soaked in dH_2O , seven (11.8 percent) imbibed without treatment. All seven were from Group 7; six embryos were nonviable, the seventh seed was placed in soil from Site Three and germinated one month later. Four of the nonviable embryos were abnormal. One embryo possessed three cotyledons, one did not have a plumule, and the remaining two (even though 5mm long) had failed to undergo differentiation or had differentiated abnormally.

Scarified seeds of Group 7 and 8 with no heat treatment contained both viable and nonviable embryos. Therefore the heat treatment results must be interpreted with this in mind.

Table 21. Effects of Heat on Embryo Viability.

Final Treatment	Prior treatment	Manually scarified	Group number	Number of seeds	Viable
no treatment		yes	8	3	2 no; 1 yes
no treatment		yes	7	2	yes (includes twin embryos)
no treatment		no	7	1	no
no treatment		no	7	1	yes, germinated
no treatment		no	7	5	no
60°C	none	yes	8	1	no
70°C	none	no	8	1	no
70°C	none	no	7	2	no (?); no (no rxn)
80°C	none	yes	8	1	yes
90°C	none	yes	8	1	no
58°C	58°C	yes	7	2	yes
70°C	60°C	2 yes, 1 no	7	3	yes
70°C	70°C	yes	7	2	yes
80°C	70°C	yes	7	2	yes; yes (?) twin embryos
90°C	80°C	no	7	1	no (no rxn)
90°C	80°C	yes	7	2	yes
100°C	80,2x	yes	7	1	no (no rxn)

Heat treatment caused imbibition to occur in some seeds. Other seeds imbibed following the second heat treatment, whereas still others did not imbibe but had to be scarified before the viability test could be run. Five seeds, four from Group 7 and one from Group 8, did imbibe as a result of heat treatment alone. Of these only one from Group 7 was viable. The Group 8 embryo turned bright red in tetrazolium chloride, except for a patch of tissue at the junction of the radicle and the cotyledons. This dead tissue was extensive enough that it would have prevented proper germination of the seed.

From those seeds that did not imbibe despite the heat treatments, both viable and nonviable embryos were obtained. The fact that two out of four seeds tested at 90°C were viable shows that embryos of Sophora leachiana can survive high heat.

Positive conclusions as to the effect of heat on seeds of Sophora leachiana are difficult to make, because both viable and nonviable embryos were found in untreated seeds and because such a low number of seeds could be tested. Evidence does suggest that seeds of Sophora exhibit varying plasticity in the controls governing imbibition. It is not unusual for a species with hard seeds to produce a low percentage of seeds that imbibe without treatment. Based on these tests, heat treatment can cause changes in the seed coat which allow imbibition to occur; furthermore the embryos can withstand high heat below the boiling point without loss of viability.

The actual range of temperatures conducive to germination of Sophora was not measured, but work with other legumes yield values of

50°C to 90°C with maximum germination between 70°C to 80°C (Martin et al., 1975). Temperatures within the 50°C to 90°C range are usually found within the first three centimeters of soil during a light slash burn, between 2.5 cm to 7.6 cm of soil under medium slash and below 7.6 cm under a heavy slash burn (Ahlgren et al., 1960; Gratkowski, 1962). Solar radiation alone can raise surface temperatures to 65°C or 73°C and can trigger the seed germination of fire-species (Silen, 1960; Gratkowski, 1962). Soil temperatures decrease with increasing depth. Sophora's large seeds probably allow successful emergence and seedling establishment from a depth of several centimeters. The varying responses to heat controlling viability and imbibition, coupled with different depth of burial in the soil could insure that at least a proportion of seeds received the correct treatment to trigger germination. Plasticity in germination responses allowing seeds to respond to slightly different environmental conditions is of definite value to a species in that it usually insures survival of some if not all seedlings (Mayer and Poljakoff-Mayber, 1963).

DISCUSSION

Sophora leachiana is an ancient, highly localized endemic of the Siskiyou Mountains in southwestern Oregon. The genus Sophora is considered to be a Tertiary relic (Gray, in Stevens, 1948). Whether Sophora entered North America from the north or from the south has not been established, but most authors favor a northern entrance. The herbaceous Sophoras of Asia and North America follow a distribution similar to species of Crepis, a well studied composite believed to have entered North America over the Siberian-Alaskan land bridge during the late Miocene, Pliocene and early Pleistocene (Babcock and Stebbins, 1938). Western North American species with Asiatic affinities are thought to have migrated to North America over the land bridge (Potbury, 1937; Detling, 1968). Fossils of Sophora species are known from the late Oligocene and early Miocene from the west Cascade Range and from the Eocene in Alaska and California (Potbury, 1937; Hu and Chaney, 1940; Peck et al., 1964), although the true identity of one fossil has been questioned (Chaney, 1944). The genus is considered to be a member of the Arcto-Tertiary Geoflora and one of many genera that are temperate to warm temperate isolates of tropical groups (Axelrod, 1958). However, Stebbins and Major (1965) consider many semi-xeric warm temperate or subtropical types to be associated with the Madro-Tertiary flora and to have migrated over the land bridge from Asia in small semi-arid areas within the Arcto-Tertiary flora.

Sophora leachiana most likely possessed a wider distribution in the past but has become restricted to the Siskiyou Mountains as a

result of extensive climatic changes, competition, biotype depletion, and perhaps other factors. The other herbaceous Sophoras are found in open, often dry habitats, much like those of S. leachiana. The leaflet morphology, leaflet movements to avoid high insolation, and the dependence of flowering on adequate sunlight points to a relatively xeric adaptation. The Siskiyou support permanent open areas on peridotite and serpentine. However, legumes rarely grow on serpentine soils because the nitrogen fixing bacteria in their nodules appear to be inhibited by them (White, 1971). Sophora instead requires the non-serpentine habitats occupied by the Pseudotsuga-sclerophyll community. The only way Sophora can survive in this forested area is to act as a primary colonizer within the Pseudotsuga-sclerophyll forest.

Sophora leachiana may be distributed throughout most of the Taylor Creek, Galice Creek and Briggs Creek watersheds. Fires should have been more frequent there before present day fire-control measures, thus Sophora may have been able to spread widely by vegetative reproduction. Sophora's ability to enter forested regions surrounding disturbed sites could allow it to spread from one burned area to another if the burns are in close proximity and the intervening forest is not especially dense. Rhizomes are considered to be an effective method of surviving a fire (Stebbins, 1950; Oppenheimer, 1960); however, because Sophora probably in time dies out in heavily forested areas, the species must rely on seeds or on vegetative introduction to re-establish after a burn. Hard seeds of legumes are long-lived, and Sophora's should be no exception. Sophora's appearance in disturbed

areas today is probably due to seed germination triggered by high temperatures of fire, solar insolation or scarification during road construction or logging. However, Sophora still can be introduced into new areas. Despite extensive mining and other disturbances at Briggs Creek since the early 1900's, the species first appeared in the area about 15 years ago (Mansfield, 1976, personal communication).

The species' present day restriction to south or west slopes could be due to more abundant blooming and seed set in such areas. Although no Sophora population is currently restricted to a north slope, various populations do extend onto north slopes and into the shaded forest surrounding clearcut areas. Thus, the species is probably not vegetatively excluded from open north- or east-facing areas, although it may strongly prefer more southern exposures.

Sophora's occupation of newly opened areas classifies the species as a primary colonizer. Early successional species usually produce numerous, lightweight seeds easily dispersed throughout the forest community. Studies of other forested regions have shown that these lightweight seeds are ubiquitous throughout the forest duff and soil (Quick, 1956). However, as with many legumes and with other species adapted to open communities in dry areas (Stebbins, 1950), the seeds of Sophora are large and possess no special means of dispersal. Their possible poisonous nature should preclude distribution by rodents. However, S. leachiana's fruits are indehiscent, therefore the fruit itself must be considered as the dispersal form. These fruits can float on water for two or three days. Water dispersed seeds are not

uncommon in the genus Sophora (Guppy, 1912; Sykes and Godley, 1968). Sophora tetraptera in Southern Chile, considered by Sykes and Godley (1968) as a race of S. microphylla, produces buoyant seeds capable of remaining afloat for several months, allowing this streamside species to disperse over waterways (Urban, 1934). Sophora leachiana also follows a distribution adjacent to or near streams along three drainages. However, it must be mentioned that disturbance from logging and road construction also follows waterways. If fruits of Sophora are truly water dispersed, flooding of the present streams could result in transportation to new locations at or above the normal river boundary. Periodic floods do occur in this area (U.S. Weather Bureau, 1962). Because the seeds themselves are not buoyant, dispersion will take place only as long as the fruits are intact. As already mentioned, S. tetraptera possesses buoyant fruits and seeds.

Drainages do not always keep the same course, and past waterways are sometimes indicated by gravel deposits. Lower Peavine, Squirrel Place and the Briggs Creek populations are located adjacent to old channel gravel deposits. The old streambed now lies 152 - 823 meters above the present stream courses (Diller, 1914; Wells et al., 1949) and estimations of their age range from Cretaceous or Eocene (Josephine Co., 1952) to Pleistocene (Wells et al., 1949). If one stream did flow through this area, it would explain how Sophora jumped from the Taylor Creek-Galice Creek to the Briggs Creek watershed. However, these present day drainages are separated by a distance of only 0.80 km over an elevational change of 73 meters. Vegetative spread today

between the three drainages would be very possible. Migration to the drainages southeast and northwest of the present distribution would involve crossing ridges averaging 1219 meters. If Sophora is vegetatively excluded from higher elevations this could possibly explain why the species has spread out of these drainages only along the low elevations of the Illinois River to the Nobles House population. However, why the species is restricted to such a small area within the Siskiyou is not known. The area in question is next to the environmentally distinct Rogue River valley and the Eastern province of the Siskiyou (Waring, 1969). Therefore some special ecological balance may be operating in this area that promotes the growth of Sophora leachiana.

Sophora leachiana is most likely an autotetraploid. That the chromosomal complement is not of hybrid origin is supported by the occasional formation of quadrivalents in the tetraploid and the higher multivalent configurations observed in the hexaploid populations. Depending on the degree of similarity of the parental chromosome complements, an allotetraploid will pair only as bivalents; quadrivalents may be formed if the homology between the different genomes is great. Quadrivalents in allotetraploids can also signal translocation heterozygosity which arises by structural exchanges between two nonhomologous chromosomes. Theoretically, an autotetraploid is capable of forming all quadrivalents within a cell, although this is seldom encountered (Morrison and Rajhathy, 1960, in Estes, 1969). The fact that tetraploid Sophora forms zero or occasionally one quadrivalent can be due to several reasons. Sophora leachiana's

chromosomes are very small, and small chromosomes may have fewer chiasmata (Darlington, 1937; Stebbins, 1971), therefore quadrivalent formation rarely occurs. Because quadrivalent formation is often accompanied by abnormal segregation which reduces fertility, selection will favor genes governing the pairing relations allowing a cell to form regular bivalents rather than quadrivalents. This "diploidization" of tetraploids is widespread and usually results in increased fertility (Darlington, 1937).

The hexaploids could theoretically form all hexavalents; however, this would also be very unlikely. Besides their small size, the high number involved would make it difficult for the chromosomes to find all their pairing partners (Dawson, 1962). Univalents can arise because of failure of initial associations at zygotene and pachytene or through desynapsis and failure of chiasma formation (Dawson, 1962; Thomas and Rajhathy, in Estes, 1971). The univalents present within the hexaploids were usually in close proximity to another univalent, suggesting one of the latter two modes of formation. Desynapsis is controlled by a recessive gene, although polygenes are in operation in some species (Tease and Jones, 1976). Sophora leachiana may be an autotetraploid; however, verification will depend on more intensive cytological and morphological studies of the herbaceous Sophoras possibly coupled with artificial crosses between the species (Stebbins, 1950).

Evolution of these polyploid levels could have followed several routes. Spontaneous chromosome doubling of a shoot of a diploid

(Darlington, 1937) or the union of two unreduced gametes from a diploid would form an autotetraploid. The hexaploid could have arisen directly from tetraploids, by the functioning of an unreduced gamete. The tetraploid and especially the hexaploid populations are known to produce unreduced spores with sometimes quite high frequencies. This could initiate still higher polyploid levels.

Autotetraploids are characterized by a reduced fertility compared with their parent diploids. Meiotic abnormalities such as formation and irregular segregation of multivalents, lagging chromosomes and various irregularities at later stages of meiosis are important causes of sterility (Sparrow et al., 1942; Stebbins, 1950; Darlington, 1956). High sterility in the induced autotetraploid Lactuca sativa was due to undeveloped ovules or abortion of megasporogenesis coupled with failure of pollen germination and pollen tube growth caused by partial self-incompatibility (Einset, 1944). Sterility of other species has been blamed not on meiotic features but on specific genes or gene combinations influencing the physiology of the individual (Randolph, 1941 in Stebbins, 1950; Einset, 1944).

Pollen stainability in Sophora tetraploids averaged only 78 and 58 percent. Tetraploid meiosis did include unequal segregation which would cause chromosome duplication and deficiencies. Quite possibly some of the aborted grains were those with unbalanced genomes; although direct evidence is lacking, this has been mentioned as a prime factor triggering pollen abortion in other tetraploids (Estes, 1971).

Environmental factors are well known causes of pollen unstainability

(Clewell, 1966); however, the percent pollen abortion can also be hereditary (Rotar, 1962). All hexaploid Sophora plants had a high percent stainable pollen, despite their aberrant meiosis. Polyads of microspores were frequently seen in these plants; therefore, their pollen grains were often aneuploid, yet they retained their stainability due, perhaps, to the higher ploidy level (Darlington, 1937).

Sophora leachiana's very low seed set is probably due to a combination of factors, including environmental effects. Environmental stresses often make plants drop fruits or abort ovules, with only the most vigorous individuals if any, setting seed. Competition between the ovules, along with environmental influences and the irregularities of polyembryonic ovules sometimes result in 50 percent aborted ovules in red clover and 80 percent in sweet clover (Martin and Watt, 1934). Lack of proper nutrition, drought, competition, premature defoliation by insects or disease, or any factor which limits photosynthetic production have been hypothesized to explain ovule abortion (Garner, 1951; Elmore, 1955; Wheeler and Hill, 1957; Stiles and Cocking, 1969). Furthermore, a plant will rarely concentrate its photosynthate in both vegetative and sexual reproduction, although exceptions are known (Thomas and Dale, 1975). Sophora would not be expected to concentrate energy into vigorous fruiting and vigorous rhizome production as well.

The lack of fruit set at Upper Peavine is due to failure of microsporogenesis, possible failure of megasporogenesis, or inadequate pollen transfer from Lower Peavine. The other sterile Sophora populations could not be visited during flowering, therefore it is not known

if their plants also failed to initiate microsporogenesis. Most of these sterile populations were small, or the ramets were noticeably damaged by predators when the sites were visited in August, 1976.

Sophora leachiana is xenogamous, as indicated by its high pollen-ovule ratio, its protandry, and the low frequency of spontaneous selfing. This dependency on pollinators could contribute to the low frequency of initial seed set. Pollinators on Sophora were infrequently observed, although they were often common on surrounding vegetation. The individual flowers appear to be well adapted to Bombus pollinators. Nectar thieves working through the gap between the carina and the keel may make the flower less attractive to pollinators; however, work with other species has shown that this may in fact increase seed set, as the pollinators must visit more flowers to get the same rewards (Price, 1975).

Because the type of self-incompatibility is usually constant in a given family, Sophora probably exhibits gametophytic self-incompatibility (GSI), if any. Polyploidy can interfere with GSI. If a diploid is strongly self-incompatible, then an increase in ploidy level will not change the incompatibility response. However, if the diploid has some self-compatibility, this is usually greatly increased in the autotetraploid (Lewis, 1945; Stebbins, 1950). There are several accounts of partial self-incompatible autotetraploids derived from fully self-compatible diploids (Einset, 1944, 1947). Gametophytic incompatibility is governed by one locus, although control in some species is by two loci that complement each other (Lewis, 1956).

Possession of like alleles by the stigma and pollen usually prevents incompatible pollen tube growth in the style, but inhibition of pollen tubes can also occur in the ovary (Cooper and Brink, 1940b); occasionally incompatible grains are inhibited from germinating on the stigma (Cohen and Leffel, 1964; Heslop-Harrison, 1975). Incompatible crosses can also fail at any stage of development, including abortion of the embryo (Brink and Cooper, 1940; Thompson, 1940; Wardlaw, 1955).

Pollen-stigma interactions were studied in Sophora to test if incompatibility operates at this stage. However, because the blue stain was retained by the maternal tissue as well as by the pollen tubes, detection of in vivo growth was not possible. In several selfed flowers some grains did show sufficient germination to allow the cytoplasm to migrate from grain to tube. This, plus the fact that some selfed field crosses began ovule and fruit development, confirmed that at least some selfed grains are able to effect fertilization. In my experiments pollen was retained on stigmas only after selfing or crossing within a population (perhaps a single clone). That at least the hexaploid populations can effect fertilization was indicated by the field crosses. No explanation can be offered for Sophora's seeming preference for self-pollen; however, a similar preference has been described for Nicotiana (Eghiazarjan, 1962), a genus which usually exhibits full or partial self-incompatibility. Alleles are known that allow for self-fertilization while maintaining self-incompatibility with other alleles.

Only indirect evidence can be offered that self-pollinated Sophora can set fully mature seed, because no mature seeds resulted from the

controlled field crosses. West Fork Taylor was a very small population and probably represented only one clone. In 1976 this population did set a mature fruit containing one mature seed and three aborted seeds. The mature seed was probably the product of a self. The nearest known population of Sophora is at Taylor Creek, 0.8 km away.

The aborted seeds themselves provided further clues. In all cases the embryo appeared starved but was well formed. Aborted embryos commonly can be isolated and matured in artificial culture (Rietsema et al., 1955; Wardlaw, 1955). However, the endosperm of Sophora seeds was usually disorganized. Endosperm failure is a widespread cause of embryo abortion (Thompson, 1940; Cooper and Brink, 1944; Maheshwari, 1963; Maheshwari and Rangaswamy, 1965; Siddiqui and Farooq, 1965). Endosperm of an incompatible cross usually lags behind normal development (Brink and Cooper, 1940); in those species which have cellular endosperm it is slow to become cellular, if it does so at all (Cooper and Brink, 1944; Ganesan et al., 1957; Weaver, 1958). Reciprocal differences in crosses between individuals of different ploidy levels are common and suggest that an altered balance of chromosomes between the endosperm and maternal tissue contributes to endosperm failure (Ledingham, 1940; Thompson, 1940). Duplications and deficiencies within the endosperm and embryo could possibly cause failure at various stages of development, due to an imbalance with the maternal tissue or a lack of the necessary genes to continue proper development. Endosperm failure can be coupled with overdevelopment of the maternal tissue. This defines somatoplastic sterility (Cooper and Brink, 1940b).

Somatoplastic sterility can occur at any stage in the maturation of the embryo after an incompatible cross following selfing, as well as after interspecific crosses (Brink and Cooper, 1940; Cooper and Brink, 1940a; Thompson, 1940; Allard, 1960).

Self-incompatibility is often not 100 percent effective in preventing mature seed after selfing. The setting of some seed in an incompatible cross is referred to as partial self-compatibility or pseudocompatibility. Some authors distinguish between the two terms (Stout, 1938; Townsend, 1971) although they never fully define the distinction. Based on their reports, partial self-compatibility can vary between individuals; pseudocompatibility is also genetic but heavily influenced by the environment. Modifying factors include season and temperature (Townsend, 1965), soil moisture, age of the flower, reduced vigor, and randomly segregating modifier genes (Leffel, 1975). The upper limits of seed-set can approach self-fertility.

The effect of aneuploidy on gamete fertility and zygotic viability varies greatly between species, ploidy level, and the type and number of chromosomes involved. Aneuploid conditions at the diploid and triploid level are known but are not common; deficiencies are usually rarely viable but one or two extra chromosomes can be tolerated. Aneuploidy is usually passed through the egg rather than through the pollen. Aneuploid zygotes in triploids are eliminated by failure of active growth or failure in competition with normal ovules (Darlington, 1937). Einset (1947) studied reproduction in highly sterile aneuploid forms (lacking one chromosome or with one, two, or three extra ones)

of the induced autotetraploid Lactuca sativa. Increased sterility over the balanced autotetraploid could not be determined because pollen abortion, megasporogenesis failure and other factors all appeared equal. No zygotic abortion occurred. Selfed aneuploids produced 75 percent aneuploids; selfed euploids produced 20 percent. Higher ploidy levels appear to be able to tolerate aneuploid conditions without loss of viability or without as great an upset in genetic balance because of the large number of homologues present (Strickberger, 1968).

Aneuploidy probably does contribute to seed abortion in Sophora leachiana, although its exact effect cannot be estimated. However, that seed abortion was primarily not due to aneuploidy can be deduced from several factors. The prime causes of an autotetraploids' increased pollen abortion compared with a diploid are meiotic irregularities. Therefore, stainable pollen in tetraploids has a greater chance of being euploid than aneuploid. Meiosis in the hexaploids was sometimes 100 percent abnormal, which should lead to a very high incidence of aneuploid gametes and in turn a high percent of aneuploid embryos. Although hexaploids can tolerate aneuploidy better than tetraploids, one would still expect a greater percentage of embryo abortion in the hexaploids if aneuploidy was the chief factor triggering abortion. However, the percent abortions at the hexaploid populations Taylor Creek and Briggs Creek are 72 percent and 83 percent respectively, which agree well with the tetraploid Lower Peavine value of 77 percent abortion of all counted fertilized ovules. All populations which set any seed also had abortion rates within these ranges (81 percent for

Squirrel Place, 86 percent for Taylor House, 75 percent for West Fork Taylor). If aneuploidy was the chief factor triggering abortion, a constant percent abortion value would not be expected for both 4x and 6x populations. Therefore seed abortion is determined by a physiological process that is constant between populations and between ploidy levels; aneuploidy cannot be the controlling factor in Sophora.

The most likely cause of seed abortion in Sophora leachiana is self-incompatibility. This could be gametophytic incompatibility per se or an inbreeding effect. The inbreeding effect is usually explained by the bringing together of deleterious recessive genes in the homozygous condition; crossing failure due to incompatibility exhibits many of the same symptoms, and distinction between the two is difficult (Cooper and Brink, 1940a). Selfed alfalfa also aborts for these reasons, and the anatomy of the aborted tissue is similar to that seen in Sophora. Outcrossed embryos can also abort but with a much lower frequency. Because the percent abortion rates of Sophora seeds were constant for all areas, environmentally influenced pseudo-compatibility was probably not operating. Instead, partial self-incompatibility would be the physiological process that could account for widespread embryo abortion, with a certain percentage of crosses succeeding.

Mature fruit-set seen in August was not random but was concentrated at the edges of the clone or adjacent to stumps, roads, paths, or in isolated individuals. Differential pollinator activity could account for the nonrandom distribution. If pollinator activity is nonrandom,

then the ramets in the interior of the clone might not initiate fruit development. Patterns of initial fruit-set within a clone could not be studied, therefore it is not known whether many fruits start development in the interior of the clone only to abort later. However, failure of fertilization or immediate abortion of fertile ovules in the interior of the clone, before fruit development could be commenced, would mimic nonrandom pollination. Environmental or physiological factors might then allow partial self-compatibility to operate in those edge areas more conducive to seed set. The observed average reproductive success in these sites was 21 percent mature seeds, based on the total of fertilized ovules. This is obviously a tentative outline of the possible cause of low reproductive success and nonrandom distribution of mature seeds. The problem will not be fully answered until extensive checks are followed throughout the entire blooming and fruiting season.

Self-incompatible autotetraploids are rarely found in nature. If two autotetraploids arise in a diploid population, they must cross inter se and not with the diploids if the tetraploid line is to survive. The amount of sterility between the tetraploids would be inversely related to the number of S-alleles present in the tetraploid population. A newly made self-incompatible autotetraploid has two options for its survival. One would be to break down the self-incompatibility by selection of polygenes controlling the strength of the incompatibility reaction, changing from partial self-compatibility to full self-compatibility (Mather, 1943). The other option is for the plant to rely on vegetative reproduction (Lewis, 1943). Sophora leachiana may be selecting

for self-compatibility; however, if the necessary alleles are not already present in the populations, the species must depend on chance mutation.

Judging from the small total area occupied by the species and the vigorous vegetative reproduction, Sophora is probably an ancient relic, depleted in biotypes and possessing a limited gene pool. Current seed production may be adequate for the species to persist in the limited areas it now occupies; however, the low seed-set strongly limits the spread of the species. As with certain other self-incompatible polyploids, S. leachiana could not survive without its vigorous rhizome production.

The future of this species is precarious. It exists in only a small area, comprising a limited number of populations some of which are completely seed-sterile. Flowering can be sparse and fruiting essentially nil even in genetically fertile populations. Forest management practices that would destroy its vegetative clones in habitats favorable for seed production, could push the species towards extinction. It is unlikely Sophora leachiana has the biological resources, as a species, to survive the usual chemical and mechanical control methods used to manage the widespread, vigorous and weedy fire-adapted brush species of southwestern Oregon.

SUMMARY

Sophora leachiana is known from thirteen populations in a 29 by 6.4 km area in the Siskiyou Mountains of southwestern Oregon. Twelve populations occur in the Galice Creek, Taylor Creek and Briggs Creek watersheds; one occurs along the Illinois River 3.2 km past Briggs Creek. Sophora acts as a primary colonizer of areas disturbed through fire, mining and road construction. The surrounding forest includes Pseudotsuga menziesii as the dominant, with Quercus kelloggii, Pinus lambertiana or P. ponderosa, Arbutus menziesii, Lithocarpus densiflora and Quercus chrysolepis as co-dominants. Rhus diversiloba, Ceanothus integerrimus and Rosa gymnocarpa are important shrub species. Sophora is usually the dominant herbaceous species at its population sites.

Most populations occur on south or west slopes. The plant exhibits adaptations to this summer-dry area, including xeromorphic leaflet anatomy, leaflet movements to avoid high insolation, and flowering that depends strictly on adequate sunlight. Sophora has very vigorous rhizomes which allow clones of the species to spread extensively throughout open areas.

Chromosomes analysis in three areas showed one tetraploid ($n = 18$) and two hexaploid ($n = 27$) populations. One population was characterized by failure of the pollen mother cells to enter meiosis; in this clone no pollen was produced and fruit development failed. The tetraploid is probably an autotetraploid, although meiosis was characterized by formation of bivalents, occasionally quadrivalents did occur. Hexaploids have variable and irregular meiosis characterized by

univalents and multivalent formation up to hexavalents. Pollen grains vary in size, and often more than four grains are formed by a single mother cell.

The papilionaceous, racemose flowers bloom in April and May. Bombus is the only effective pollinator; however, even though the nectar-producing flowers appear to be well adapted to the bumblebees, the activity of the pollinators on Sophora is low. Xenogamy is the breeding system, as evidenced by the protandrous flowers, the occurrence of spontaneous selfing at a low frequency if at all, and the high pollen-ovule ratio of 12,000. The dependency on a single class of pollinators may limit initial seed-set.

The pollen of tetraploids exhibited a wide range in stainability, with an average of 77 percent. Despite a high frequency of polyad formation in the hexaploids, pollen stainability remained over 90 percent. Stigmas used in studies of pollen-stigma interactions showed a preference for self or intrapopulation pollen (which may be clonal). Interpopulation pollen in the hexaploids can initiate seed development, as was shown by artificial field crosses. Pollen tube growth in the style could not be observed because the maternal tissue retained the blue dye used to measure pollen-stigma compatibility.

Sophora leachiana has a low initial seed-set. The vast majority of pistils never develop past the flowering stage. An average of 79 percent of the seeds in developing fruits will abort at various stages before maturity, making the final seed set very low. The anatomy of aborted seeds suggest that the cause of failure was the endosperm.

Most embryos showed no visible abnormal development; several twin embryos in mature and aborted seeds were observed. Most likely the endosperm failure was due to self-incompatibility. Mature fruit-set was not random but was concentrated at the edges of the clones where plants were more isolated or were next to stumps and logs. Partial self-compatibility, coupled with differential pollinator activity, could account for this distribution. If pollinator activity is random, physiological or ecological factors may favor partial self-compatibility in the areas of the clone where seed set was observed.

Sophora leachiana does have vigorous asexual reproduction, but because the species eventually dies out as the forest matures, it must depend on seeds in order to persist in an area. The seeds are "hard" and are able to survive the heat of brush fires. They are probably long-lived, but their germination averaged only 58 percent when tested. Seeds are triggered to germinate in open areas probably by the heat of fires or solar insolation, or by scarification during logging or road construction.

Sophora leachiana is probably a Tertiary relic, depleted in biotypes and possessing a restricted gene pool. Its ability to evolve towards self-compatibility is limited, although this advance would greatly increase its reproduction by seeds. Current seed production may be adequate for continuance in the small area Sophora now occupies, but it does not allow for expansion of the species' range. An increase in range through rhizomal vegetative reproduction may be hindered by modern curtailment of fires coupled with possible ecological exclusion

at higher elevations. The seeds themselves possess no special means of dispersal aside from the possibility that the indehiscent fruits are buoyant in water. Forest clear-cuts are a favorable habitat for the growth and flowering of S. leachana. However, forest management practices that would destroy the vegetative clones and hence end seed reproduction in these sites would probably lead to the extinction of the species.

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