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# THE MISTLETOES

# A LITERATURE REVIEW

by Lake S. Gill and Frank G. Hawksworth Rocky Mountain Forest and Range Experiment Station Forest Service



Grawth Dhicogh Agricultural Progress

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For sale by the Superintendent of Documents, U.S. Government Printing Office Washington 25, D.C. - Price 35 cents Striking advances have been made in recent years in the field of plant pathology, but most of these investigations have dealt with diseases caused by fungi, bacteria, or viruses. In contrast, progress toward an understanding of diseases caused by phanerogamic parasites has been relatively slow. Dodder (*Cuscuta* spp.) and broom rape (*Orobanche* spp.) are well-known parasites of agricultural crops and are serious pests in certain localities. The recent introduction of witchweed (*Striga* sp.) a potentially serious pest for corn-growing areas, into the United States (Gariss and Wells 1956) emphasizes the need for more knowledge of phanerogamic parasites.

The mistletoes, because of their unusual growth habits, have been the object of curiosity for thousands of years. Not until the present century, however, has their role as damaging pests to forest, park, orchard, and ornamental trees become apparent. The mistletoes are most abundant in tropical areas, but they are also widely distributed in the temperate zone. The peak of destructiveness of this family seems to be reached in western North America where several species of the highly parasitic dwarfmistletoes (*Arceuthobium* spp.) occur. However, there are numerous reports indicating that various mistletoes are serious pests in many countries throughout the world.

This is the first general review paper on the Loranthaceae. The only prior contribution along this line was a partially annotated bibliography of about 100 articles on various mistletoes (Sanzen-Baker 1938).

This review was prompted by a deep and continuing interest in the pathological significance of Arceuthobium in the western United States. Our researches in this field have resulted in the development of an extensive annotated bibliography of the mistletoes in general with particular emphasis on their role as damaging agents. Some 800 out of more than 3,100 accumulated references on the Loranthaceae have been included here in support of the discussion of what seemed to us to cover the major facets of interest and importance about mistletocs. To some readers the discussions may seem skewed on the economic or phytopathological ends. Many important references have been deliberately omitted because they are cited and discussed in subsequent papers that are listed here; a few have been inadvertently overlooked; and a small number will have appeared since the manuscript was completed in March 1960. Anonymous contributions, annual reports of Government agencies, floras, and textbooks have been cited only where they were needed to support a specific point that was not adequately covered in more acceptable sources.

It is hoped that this compilation of the world literature on the mistletoes will facilitate future investigations in this field.

Obviously an undertaking such as this involves the help of many people. We sincerely appreciate the assistance we have had from the inception of the manuscript to its release in print. Those who have reviewed all or parts of the manuscript and have given us the benefit of many constructive suggestions are Mr. C. G. Greenham and Mr. A. G. Brown of Commonwealth Scientific and Industrial Research Organization, Australia; Dr. Martin M. Cummings, Veterans Administration, Washington, D.C.; Professor A. W. Galston, Yale University; Mr. W. L. Baker, Dr. S. F. Blake, Dr. T. S. Buchanan, Dr. E. L. Little, Mr. J. A. Stevenson, and Dr. W. W. Wagener, all of the U.S. Department of Agriculture. We also wish to express our appreciation for the valuable assistance on the bibliography that has been given by Mrs. Mona F. Nickerson of the Rocky Mountain Forest and Range Experiment Station and by the staffs of the libraries at Colorado State University, the U.S. Department of Agriculture, and the National Medical Library.

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# THE MISTLETOES; A LITERATURE REVIEW

by Lake S. Gill and Frank G. Hawksworth, Rocky Mountain Forest and Range Experiment Station,<sup>3</sup> Forest Service

# Taxonomy of the Mistletoe Family (Loranthaceae)

## THE FAMILY AS A WHOLE

The mistletoes are members of the family Loranthaceae which includes about 36 genera with some 1,300 named species or forms. Most of these are perennial evergreens parasitic on the stems and branches of trees or shrubs. The prefarred hosts are woody dicots or gymnosperms but occasionally succulents (Engler and Krause 1908; Marloth and Drege 1915; Reiche 1907), monocots (Arens 1912; Rizzini 1951; Young 1947), and parasites from other families (Dutt 1950) are attacked. Parasitism within the family is common (Brown 1918; Trelease 1916). Viscum often parasitizes Loranthus (Burkill 1906; Ezekiel 1935). Cases of triple parasitism have been reported (Fischer 1926; Greenham and Brown 1957; Rao 1938), and autoparasitism within a species is not uncommon (Blakely 1922-28; Curtiss 1878; Muller 1908; Zaborski 1929).

A small number are terrestrial shrubs or trees growing in the tropics. Of these, Nuytsia floribunda (Labill) R. Br. and Atkinsonia ligustrina (A. Cunn.) F. Muell. are known to be root parasites leaving only the several species of Gaiadendron G. Don of South and Central America as possible autophytes. Considering the morphological similarities between A. ligustrina and Gaiadendron it would not be surprising if this genus also proved to be parasitic (McKee 1952; Menzies and McKee 1959).

The myriad nonterrestrial species may be loosely regarded as "mistletoes," a word with conflicting opinions about its derivation (Clute 1940; Funk and Wagnalls 1950; Lustner 1936; Tubeuf 1923). In gross appearance they may range from showy perfectflowered outgrowths that virtually supplant the normal crown of their host tree to tufts of small leafless shoots with inconspicuous unisexual flowers.

 $<sup>^{1}</sup>$  Central headquarters at Fort Collins in cooperation with Colorado State University.

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Whereas most mistletoes are tropical, the name is perhaps more closely associated with Viscum album and Phoradendron flavescens, the common mistletoes of Europe and the United States respectively. Both plants are similar in form and habit and are prized for their pearly white berries that ripen during the Christmas season. They were classified as two species of Viscum until Nuttall (1847) differentiated the New World genus. V. album exhibits two host races on conifers and one on hardwoods. One or more of these races occurs throughout Europe from about the latitude of Stockholm southward to the Mediterranean. This mistletoe is absent in Ireland and the northern half of Great Britain. P. flavescens is transcontinental in the United States; it reaches northward to southern New Jersey in the east and to northern Oregon in the west. It is found only on angiosperms but exhibits several geographic variations. It reaches into Mexico but does not occur in Canada.

There are three other well-known mistletoes in Europe. Viscum cruciatum is a red-berried species found in the Mediterranean countries, commonly on olive. Loranthus europaeus Jacq. (Hyphear europaeum Danser) is found in the south central part of the continent on hardwoods, particularly oak. It is often parasitized by V. album. Arceuthobium oxycedri is an unccnspicuous leafiess mistletoe found principally on juniper along the Mediterranean coast.

In North America there are five morphologically distinct species of Arceuthobium. Four of these, including one with several host forms, cause extensive damage to commercial softwoods from central Manitoba westward in Canada and southward into the Rocky Mountain and Pacific Slope States of the U.S.A. and Mexico. An eastern species, primarily on black spruce, extends from the North Atlantic Coast westward into Ontario and the Lake States. Several distinct species of *Phoradendron* occur on the continent. These are concentrated in the far west where both leafy and leafless types are found on conifers and hardwoods. The leafless species on conifers, particularly Cupresseae, are sometimes confused with Arceuthobium (Gill 1953a; Gill and Bedwell 1949).

Engler and Krause (1935) give the most recent worldwide systematic treatment of the family, which follows rather closely the principles developed by Van Tieghem (1894a). However, there have been a number of thorough and detailed studies of the family in circumscribed geographic areas. Danser (1929, 1931, 1933, 1935a, 1935b, 1936, 1940, 1941) has made exhaustive revisions of the Old World, Malayasian, Philippine. Indian, and Australian species. His work generally supersedes the earlier treatments of the Australasian forms by Blakely (1922–28), the Philippine forms by Merrill (1909), the Indo-Chinese forms by Lecomte (1914, 1915) and the Indian forms by Parker (1924). Balle (1944, 1954, 1955, 1956) has made critical revisions of the African species. Rizzini (1950b, 1952a, 1952b) and others (Abbiatti 1943, 1946; Conill 1953; Krause 1922) have treated the South American species and there have been isolated contributions on the Central American and Mexican forms (Standley 1920-26; Standley and Record 1936; Woodson and Schery 1940, 1941; Yuncker 1938, 1940). The forms in the French Antilles have been described by Stehle (1953-54).

An outstanding character of the Loranthaceae is the absence of true ovules; this is discussed further on page 8.

#### THE SUBFAMILIES

DeCandolle (1830) divided the family into two groups based on the presence or absence of a subfloral bract or calyculus. These groups are generally recognized today as the subfamilies Loranthoideae and Viscoideae. Some botanists advocate family rank for each (Maheshwari et al. 1957) and Van Tieghem (1895b) believed that the genus *Arcenthobium* (Viscoideae) warranted classification as a separate family between the Santalaceae and Loranthaceae. The calyculus is invariably present in the Loranthoideae but also occurs in a few Viscoideae. A more distinguishing character is the position of vascular tissues of the fruit; these are internal to the viscin layer in the Loranthoideae; external in the Viscoideae.

The Loranthoideae are extremely complicated from the taxonomic standpoint. Much controversy has centered about the genus Loranthus, which had some 200 species assigned to it by 1830. DeCandolle arranged these into four sections. Between 1893 and 1911, Van Tieghem broke Loranthus into a score or more genera in an incomplete treatment that was not generally accepted by taxonomists but which nevertheless outlined useful systematic principles. The more recent works of Danser (1929, 1931, 1933) are now generally regarded as the authority for the Loranthoideae. Danser (1933) states that the only genus that can be legitimately called Loranthus is the Tropical American genus Psittacanthus. His nomenclature has not been consistently followed in this review: rather the binomials used by the various authors where work is cited are usually given. The synonymy for Old World species is easily traced in Danser's Nomenclators (Danser 1929, 1933).

The systematics of the Viscoideae are relatively uncomplicated. Its genera are few and fairly well defined. The largest is *Phoradendron* to which Trelease (1916) assigned 240 species prior to subsequent emendations of his monograph (Trelease 1927, 1928– 29, 1935). Fosberg (1941) recently grouped or proposed varietal rank for several of Trelease's North American species and Wiens (1956) has evaluated the systematic criteria for the genus. The South American species *P. fragile* Urb. (Rizzini 1950a) and the North American *P. flavescens* (Pursh) Nutt. have been treated in detail (Bray 1910; York 1909). It has recently been proposed that the name of the latter species be changed to *P. scrotinum* (Raf.) M. C. Johnston because of an error by Pursh in referring to *Viscum flavens* as *V. flavescens* (Johnston 1957). Trelease (1916, p. 23), who was aware of Pursh's mistake, did not regard this technicality as a basis for adopting the Rafinesque species. A smaller but nevertheless widespread genus is *Viscum*, which has been revised by Danser (1941). *V. album* has been monographed by Tubeuf (1923) and is the subject of many contributions to the botanical literature. A third genus *Arceuthobium* M. Bieb. (*Razoumofskya* Hoffman) has been the subject of several taxonomic treatments (Gill 1935; Kuijt 1955, 1960a, 1960b; Tubeuf 1919). The genus *Korthalsella* has been monographed by Danser (1937-40).

#### EVOLUTIONARY TRENDS

The great variety of species in the tropics suggests that the family originated there. According to Balle (1955), certain primitive genera of the Loranthoideae are common to Africa and Indo-Malaysia. He believes, however, that evolution has progressed along quite different lines on each continent, and further suggests that the Australasian forms are intermediate between the American and African ones. On the other hand, Danser (1929) recognizes only one intercontinental genus in the Loranthoideae, namely, the typically American *Phrygilanthus*, a few species of which occur in Australasia. These so closely resemble the species of western Mexico that they could be regarded as indicative of former land bridges (Croizat 1952). Trelease (1916) says that *Phoradendron* "may be regarded as probably of late Tertiary origin in the New World. When and where on this continent its two primary subdivisions came into existence will make a fascinating subject for future study."

Evolution in the family appears to have been mainly a process of degeneration of both vegetative and floral parts, a trend that has been considered to go hand in hand with parasitism (Bessey 1915; Bessey 1919). On that premise Arccuthobium represents the ultimate in degeneration and parasitism. It is common in the eastern and western hemispheres. Its species reach from near the equator far into the north temperate zone, are all dioecious, aphyllous, and often produce shoots no greater than an inch in length. They are also notable for their restricted host associations. Dowding (1931a) found evidence that the central cushion in the staminate flowers of A. americanum contained the vestiges of carpels, and Datta (1951) reports the occurrence of a single perfect, superior-ovaried flower of A. minutissimum, which he considered to be a reversion to a primitive form. As further evidence of degenerative evolution Chaney and Mason (1933) state that the fossil A. campylopodum found in Pleistocene asphalt beds in California has primarily 4-merous staminate flowers, whereas the living species today is predominantly 3-merous.

Evidence of a once perfect-flowered species has been found in the staminate flowers of *Viscum orientale* (Schaeppi and Steindl 1945).

# Growth and Reproduction

#### CYTOLOGY

The cytology of the mistletoes has been a relatively neglected field except for isolated contributions on a few species of Viscum (Coutinho 1957; Hiraoka 1950; Pisek 1923; Schurhoff 1922); Loranthus (Kumar and Abraham 1942; Pisek 1924); Arceuthobium (Pisek 1924); Scurrula, and Dendrophthoe (Rauch 1936). Additional cytological information is contained in many of the papers on floral morphology and embryology (page 6).

Chromosome counts of at least 22 mistletoes have been reported (table 1). There is considerable variation in both subfamilies but,

Subfamily	Species	Number of chromosomes	Reference
Loranthoideae			
	Dendrophthoe neutandra	n == 8	Rauch 1936.
	Loranthus curopacus	n = 9	Pisek 1924.
	L. longiflorus	n = 9	Kumar and
	• -		Abraham 1942.
	L. rubromaryinatus	n = 9	Pjenaar 1952.
	Phrygilanthus verticilliatus	n = 12	Schnack and
		D	Covas 1944.
	P. pageneris	$2n \approx 16$	Covas 1947.
	Psittacanthus curefolius	2n = 20	Schnack and
	1		Covas 1947.
***	Scurrula atropurpurca	n = 8	Rauch 1936.
	Struthanthus angustifolius	2n = 16	Covas 1949.
viscoldeae	Arccuthobium americanum	n = 14	Dowding 1931a.
	A. oxucedri	n = 13	Pisek 1924.
	Dendrophthory opuntoides	2n = 18 - 22	York 1913.
	D. gracile	2n = 18 - 20	York 1913.
	Karthalsella daerudii	n = 13-14	Rutishauser
		n 10-14	1935.
	K. opuntia	n = 13-14	Schaeppi and
	<b></b>		Steindl 1945.
	Phorydendron flavescens	n = 14	Baldwin and Speece 1957
	P. macrophallum	n == 10 <sup>1</sup>	Billings 1932
	P villosum	n = 10	Billings 193 <sup>n</sup>
	Tisenn album	n = 10	Pisok 1922
	V articulatum	n == 10	Ernet 19.19
	1' constallatum	n = 10.19	Schuoppi and
	s, cupiciturem	n 10-12;	Steindl 1945.
	V. orientale	n == 10	Schaeppi and
			Steindl 1945.

TABLE 1.—Chromosome numbers in the Loranthaceae

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in general, the numbers are higher in the Viscoideae (range 2n = 20 to 28) than in the Loranthoideae (range 2n = 16 to 24).

The most comprehensive study on a single species is that on *Phoradendron flavescens* by Baldwin and Speese (1957), who found no variation in chromosome numbers in 26 collections from 15 different hosts. On the basis of this work, they question the accuracy of the earlier chromosome counts in *Phoradendron* reported by Billings (1932). York (1913) observed no haploid cells in *Dendrophthora*.

#### FLOWERS

The classic studies by Griffith (1841) and Treub (1882, 1883– 85) on floral morphology and embryology in the Loranthaceae have been supplemented by other contributions (Baillon 1892; Billings 1933; Brackett 1909; Dixit 1958a, 1958b; Ernst 1942; Gjokic 1896; Heinricher 1915c; Johri et al. 1957; Löffler 1923; Maheshwari et al. 1957; Menzies 1954; Narayana 1954, 1958a, 1958b; Pisek 1924; Rauch 1936; Rizzini 1952a; Schaeppi and Steindl 1942, 1945; Singh 1952; Steindl 1935; Thoday and Johnson 1930; Van Tieghem 1869, 1893, 1894b, 1895a, 1898; York 1909, 1913). As one can readily appreciate from these and the more inclusive taxonomic accounts (Balle 1955; Blakely 1922–28; Danser 1929, 1933; Engler and Krause 1935) the variations in floral structure and development are much too involved and numerous to discuss in detail here.

In gross appearance the flowers may be hermaphroditic or unisexual (monoecious or dioecious), with or without a "corolla" or its counterpart. There is some confusion with respect to the homology of the perianth whorls with those of the conventional flower. When a "corolla" is present it is usually showy, actinomorphic, and often designed with special devices and stamen mechanisms that insure cross-pollination by nectar-seeking birds (Ali 1932; Docters 1938, 1954; Evans 1895). Unisexual flowers are inconspicuous, usually having only one series of perianth segments, often reduced to scales in the z and with sessile circular anthers in the z as in *Arccuthobium* (Dowding 1931a). A unique floral structure is the calyculus or subfloral bract which has been the subject of some controversy as to whether it is a distinct structure (Schaeppi and Steindl 1942) or actually a calyx (Maheshwari et al. 1957).

Lecomte (1926) describes a calyptra on certain species of *Viscum* in Madagascar which he interprets as a protective device against wind.

#### POLLINATION

Most students of the Loranthaceae now believe that pollination is accomplished with the aid of animals. In the showy-flowered Loranthoideae, birds are undoubtedly the principals, particularly the sunbirds (Nectariniidae) and the mistletoe birds or flower peckers (Dicaeidae) (Ali 1932; Docters 1954; Fries 1903). Specialized floral structures and mechanics of the stamens suggest that cross-pollination is the rule in this group (Ali 1932; Evans 1895).

Blakely (1922–28), who admits that birds aid in pollination, contends that selfing is the rule, otherwise there would be more evidence of hybridization among many Australian species that bloom simultaneously. A natural hybrid between *Loranthus micranthus* and *Tupeia antarctica* has been reported (Thompson 1949) and hybridization has been observed in the European species of Viscum (Heinricher 1926a).

In the small-flowered dioecious Loranthoideae and the Viscoideae, most of the morphological evidence and observations of insects favor entomophily although experimental proof is weak (Cammerloher 1921; Docters 1954; Pohl 1931; Trelease 1916; Tubeuf 1923; Werth 1923). Heinricher (1920a and b, 1922b, 1925) believed that anemophily is the rule in both Viscum and Arceuthobium but that insects may play a minor incidental role. His theories are partially supported by the experiments of Horne (1923) and Pisek (1923) who obtained mature fruits of Viscum when living shoots bearing staminate and pistillate flowers were enclosed together in bags that were believed to have excluded insects. Pisek (1923) ruled out the possibility of apogamy in Viscum but York (1913) observed it in Dendrophthora and Phoradendron.

The time of pollination varies with the species without particular reference to its climatic range. In Viscum album anthesis occurs in the spring (Tubeuf 1923). Certain species of Arceuthobium bloom in the spring, others in the fall (Datta 1956; Gill 1935). Phoradendron flavescens is fall flowering (Allard 1943; Bray 1910) while P. californicum is spring flowering (Billings 1932).

#### FRUIT

The fruit is characterized by a leathery or fleshy coat enclosing a layer of mucilaginous viscin together with parenchyma and vascular tissues. The latter may be either external or internal to the viscin layer. Viscin serves as an adhesive to attach the seed to the host and also presumably aids germination in some species by providing better moisture conditions. Detailed studies of *Viscum album* indicate that viscin consists of an inner pectic-viscin layer and an outer cellulose-viscin layer (Mangenot et al. 1948). In the passage of the seeds through birds, only the outer layer is digested and the pectic-viscin layer surrounding the seed remains essentially intact (Tomann 1906).

Certain Viscoideae, notably Arccuthobium (Gill 1935; Heinricher 1915a; Kuijt 1955) are equipped with explosive mechanisms which shoot the seeds with considerable force and thus favor local spread without the aid of animal vectors. General observations indicate that seeds may be shot for distances of 15 to more than 30 feet (Dowding 1929; Gill and Hawksworth 1954; Hawksworth 1958b; Palhinha 1942; Peirce 1905). Detailed studies on the ballistics of these seeds (Hawksworth 1959a) indicate that the normal angle of discharge is well above horizontal and that an initial velocity of about 1400 cm./sec. may be obtained. Explosive fruits also characterize the genus Korthalsella but do not develop the forces observed in Arceuthobium. For example, K. opuntia (Thunb.) Merr. (Viscum japonicum) is said to shoot its seeds for distances of about 2 feet (Sahni 1933).

#### SEEDS

The absence of true ovules has already been mentioned as a family character. The embryo sacs are formed in a mound of undifferentiated tissue at the base of the ovary often referred to as the mamelon (Maheshwari et al. 1957) or ovarian papilla (Gill 1935). This may vary from a minute outgrowth to one that virtually fills the ovarian cavity; it may be dome shaped or definitely lobed. The latter form, together with the fact that vascular elements are sometimes found in the lobes, suggests to some morphologists that the mound may represent the rudiments of carpels about a central placenta. In any case one to several embryo sacs are borne directly in the mound and in their upward development attain various heights inside the style; in some species they barely penetrate its base, in others they reach the stigma.

Normally only one "seed" is formed. It is technically a naked embryo and endosperm protected by the crushed tissues of the ovarian mound or the pericarp of the fruit or both as the case may be. These are analogous to the integuments of conventional seeds. In most cases only one of several embryo sacs develops although polyembryony is not uncommon (Maheshwari et al. 1957; Tubeuf 1923; Weir 1914). Allard (1943) discusses the possible importance of polyembryony in maintaining the dioecious mistletoes in areas where the plants are remotely spaced. This is based on the assumption that plants of both sexes may arise from different embryos within a single seed.

Seeds of the genera Loranthus and Aëtanthus are without endosperm (Danser 1933). In most genera the embryo is surrounded by a copious endosperm. In the Loranthoideae this is formed by the fusion of tissues from several embryo sacs; in the Viscoideae it is derived from a single primary endosperm nucleus (Maheshwari et al. 1957). There are two cotyledons that are frequently fused to present a monocotyledonous condition. There is always a hypocotyl, but never a true radicle; there may or may not be an epicotyl and plumule.

#### GERMINATION

Accounts of germination in the Loranthaceae indicate that the hypocotyl is well developed long before there is any manifestation of leaves (Menzies 1954). The cotyledons usually remain in the fruit attached to the endosperm where they eventually wither, although they do emerge in a few species (Docters 1954). In most species the first leaves originate either from a plumule or as secondary outgrowths from the holdfast (Menzies 1954; Tubeuf 1923; York 1909) but in *Arceuthobium* the aerial shoots are entirely secondary structures originating from the endophytic system, months or even years after its establishment (Gill 1935; Heinricher 1916a; Kuijt 1955).

In the process of establishing a new plant, the seed may often slide downward from its original landing place until it reaches a point where the forces of gravity will not disturb it while the viscin is in a moist gelatinous condition. Recently expelled seeds of Arcenthobium may slip down upright needles until they reach the fascicle base: by the same token, seeds that alight on drooping needles may slide off their tips (Roth 1959). However, driving rains sometimes wash newly lodged seeds off the twig. Fresh seeds on the upper surface of smooth stems may often slip around the sides and become permanently fastened to the lower surface. A fantastic and almost incredible method of locomotion is reported for the germinating seeds of Loranthus globosus Roxb. (Brown 1881), which, if true, permits the seedlings to virtually "walk" along a stem by alternately fastening each end to the bark and swinging the free end ahead. After several successive wettings and dryings, the viscin loses much of its hygroscopic quality and acts as a firm cement regardless of external moisture conditions.

In most species, once the seed is firmly cemented, the hypocotyl grows along the surface of the host stem; if it reaches a suitable point for invasion, it forms a holdfast, if not it will exhaust its food supply and die. The factors affecting the selection of this point are imperfectly known. Tubeuf (1923) found that *Viscum album* will not form holdfasts on smooth surfaces such as glass, and Peirce (1905) states that the germinating seeds of *Arceuthobium* will not form holdfasts on the smooth surfaces of pine needles. a fact that has been fully confirmed by our own observations. However, the earlier implications (Gill 1935; Peirce 1905) that any irregularity in the bark surface would promote holdfast formation are now open to question; there appear to be other unknown limiting factors involved in the process.

The holdfast of Viscum album according to Thoday (1951) is a domelike structure which becomes attached to the host along its rim by the secretion of a viscous substance that forms a firm airtight seal. He described papillae which form inside the dome and attach themselves to the host bark. Growth of the dome thus causes the periderm to lift until a crack forms that is large enough to admit the primary haustorium—the final outgrowth from the holdfast. He concluded that further penetration is accomplished by: (1) solvent action of enzymes secreted by the tip of the haustorium which dissolve the pectic middle lamella of host tissue including cork; (2) tissue tensions in the host phloem which tend, as cambial activity proceeds, to widen a gap once formed; and (3) growth in thickness of the haustorium itself. He found no evidence of a solvent action directly on cellulose. There is general agreement among those who have studied the process of penetration of haustoria in the Loranthaceae that both chemical and mechanical forces play a part (Cannon 1904; McLuckie 1923; Menzies 1954; York 1909). In general, young host tissues are more often invaded than old ones, although *Arceuthobium americanum* has been found invading unwounded bark of 40- to 58-year-old lodgepole pine growth (Hawksworth 1954). The bark of this host often has exposed chlorophyllaceous tissue on growth as old as 60 years.

The external factors influencing germination are not fully understood. Apparently a dormant period is not a prerequisite in most species but the process may be delayed until favorable temperature, light, and moisture conditions prevail (Heinricher 1916b; McLuckie 1923; Tubeuf 1923). There is no indication that a stimulus from a suitable host is needed for the development of the hypocotyl, though the holdfast may be absent or abortive on unnatural substrata (McLuckie 1923; Thoday 1951; Tubeuf 1923). Several Brazilian loranths were observed to be germinating on telegraph wires (Lietz 1888).

There have been a number of investigations and literature reviews on the factors affecting germination particularly of the European mistletoes (Bedel 1933-34; Crocker 1936; Funke 1939; Gardner 1921; Glimcher 1938; Heinricher 1915b; Kuijt 1955; Mayr 1928; Tubeuf 1923). From these it appears that the optimum temperature range for germination of the temperate zone species is between  $15^{\circ}$  and  $20^{\circ}$  C., although germination occurred in *Viscum album* during a month where minimum temperatures averaged  $3.8^{\circ}$  C. (Heinricher 1912). Moisture requirements vary considerably; the tropical forms usually germinate in free water. In laboratory tests high humidities favored germination in the temperate zone species but they also favored the development of molds and bacteria. *Viscum cruciatum* seeds germinated in a desiccator but rotted in saturated air (Glimcher 1938).

The classic work of Wiesner (1879, 1893) showed that light was necessary for the germination of Viscum album seeds, the minimum intensity being 4 percent of maximum Vienna sunlight (presumably about 400 foot-candles) and the optimum was about one-half maximum sunlight (presumably about 5.000 foot-candles). Heinricher (1915b) reports that Arceuthobium oxycedri seeds showed 7 percent germination after 3 months in the dark and, hence, retain their viability in darkness much longer than those of Viscum album. Percent germination for Phoradendron flavescens was about five times greater in the light than in the dark (Gardner 1921), while that for the Australian Amyema (Loranthus) miquelii was about twice as great (Coleman 1950; May 1941). Seeds of Loranthus europaeus will germinate in darkness, but the percentage is low and the tissues are disorganized (Kinzel 1920; Mayr 1928). Other species of Loranthus would not germinate in darkness (McLuckie 1923). Storage in darkness killed seeds of Viscum album after 5 weeks and briefer periods in darkness adversely affected germination (Funke 1939; Tubeuf 1923). Light from the red end of the spectrum favors germination, whereas the blue rays do not (Crocker 1936).

Several workers have shown that the hypocotyl is strongly negatively phototropic in Viscum album (Dutrochet 1837; Pitra 1861; Tubeuf 1923; Wisener 1879) and Arceuthobium spp. (Heinricher 1917a; Peirce 1905). The response mechanism is located in the tip of the hypocotyl in Loranthus celastroides (McLuckie 1923). Geotropic responses, if present at all, are also negative and much weaker (Tubeuf 1923; Wiesner 1879) and thermotropic responses have been claimed for V. album (Schnaase 1851).

A much debated question is whether passage of the seed through the alimentary tract of its avian vectors is essential for germination. Evidence points to the fact that it is not essential and that seeds of many species germinate in nature whether or not they have been evacuated from birds (York 1909). In the case of Arcenthobium vaginatum, which is regularly disseminated by an explosive force of its own fruits without the aid of animal vectors, we have observed germinating seeds in bird feces. Laboratory experiments with a few species, however, indicate that removal of the viscous pulp hastens and improves germination. Seeds of Amyema (Loranthus) miquelii do not germinate unless the fruit coat is removed by digestion or by other means (May 1941). The reasons for this have not been determined with complete satisfaction; perhaps there are inhibiting substances in the pulp (Funke 1939), perhaps the viscin tends to reduce the supply of oxygen and moisture to the embryo (Heinricher 1917b), or perhaps very high light intensities are needed to stimulate germination of seed that remain inside of the fruit. Apparently the composition of the viscin in certain species is so altered in the process of digestion, that it becomes a more favorable medium for germination and at the same time retains its adhesive qualities. In one study it was found that poorer germination took place when the pulp was washed off (Glimcher 1938),

#### STEMS

The stems may originate in three ways: (1) from an epicotyl, (2) from buds in the endophytic system, or (3) from a holdfast. The holdfast may form either as an outgrowth of the hypocotyl or as a secondary structure at the tip of stolonlike runners which originate as low branches from an established stem and follow along the surface of the host until they find a suitable point for penetration. In *Arceuthobium*, the stems arise only from adventitious buds formed on the endophytic system (Gill 1935; Heinricher 1916a; Peirce 1905) whereas in most loranths, two or more of the three possibilities may be employed.

There is wide variation in the longevity of stems. They range from the tiny, usually biennial stalks of Arceuthobium pusillum (Gill 1935), to the trunks of Dendropthoe magna that have been known to reach a diameter of 40 centimeters (Docters 1954). Branching is the rule but it varies in its order and degree. Montfort and Müller (1951) report that the growth rate of Viscum album shoots and leaves increased rapidly with age until the plants were 5 years old and then gradually declined.

The tissue structure is typical of the dicotyledons (Greguss 1945, pp. 70-71; Jungers 1937; Metcalfe and Chalk 1950) in that it normally consists of a central pith and xylem cylinder surrounded by an interfascicular cambium, a phloem, and a cortex. Notable exceptions are the terrestrial genus Nuytsia in which phloem bundles are enclosed in the wood (Danser 1933) and Arceuthobium where vascular tissue is in strands within a parenchymatous matrix. Young stems are enclosed by a heavily cutinized epidermis which is later replaced by an analagous secondary cuticular epithelium in those species where the stems function as part of the photosynthetic apparatus for their duration (Cannon 1901; Gill 1935; Tubeuf 1923; York 1909). The shoot apices of Phoradendron flavescens and Loranthus globiferus are structurally similar to autotrophic plants but somewhat reduced in size (Cutter 1955).

#### LEAVES

The leaves vary from minute scales such as are found in *Arceuthobium, Korthalsella*, and certain species of *Phoradendron, Loranthus*, and *Viscum*, to conspicuous, often articulated structures. Variation in both form and color has often been noted within a species (Metcalfe and Chalk 1950; Trelease 1916; Tubeuf 1923). In *Viscum album*, for example, leaves may vary frem ovate with a single midrib, to lobed with a forked midrib, to completely articulated dichotomous leaflets (Bugnon 1924). There are reports that some tropical loranths accommodate their leaf form and coloration to the host foliage (Hartigan 1958a). Despite this recognized variation, Lushington (1902) prepared an elaborate key for the recognition of Indian mistletoes by their leaves.

In general, the leaf structures are typical of xerophytes. The mechanisms for reducing evaporation are most highly developed in the most parasitic forms (Kamerling 1914b). Most species are rich in cholorophyll although it may be scant in the highly parasitic forms. The dull green to yellowish green cast often seen in the Viscoideae is usually caused by a heavily cutinized epidermis which masks the cholorophyll green. Stomata in *Phoradendron* appear on both sides of the leaf, are larger but less abundant than those of the host (Cannon 1901; York 1909). Cystoliths have been noted in a number of genera (Ravn 1897).

The vascular system shows no striking departures from autotrophic plants, although in some species it is weakly developed and apparently interrupted. York (1909) working with *Phoradendron flavescens* described special structures such as water storage reservoirs at the ends of traces. These were identified by groups of mucilaginous cells similar to those previously reported in *Viscum album* (Tubeuf 1923).

The leaves of *Phoradendron*, when not reduced to scales, tend to grow so that both surfaces are equally exposed to light (York 1909). In this way, both surfaces apparently receive adequate light

for photosynthesis but presumably avoid the excessive evaporation that would occur if they were directly exposed. The leaf tissues do not show marked dorsi-ventral differences; both surfaces appear to be equally efficient for photosynthesis. Further discussions of transpiration and photosynthesis are given in the section on Physiology and Parasitism.

#### THE HAUSTORIAL SYSTEM

The haustorial or absorbing system of the mistletoes has been a subject of much interest since the classic works of Solms-Laubach (1867-68, 1877) on phanerogamic parasites. Tubeuf (1923) gives a complete account of it for Viscum album and this has since been supplemented by the contributions of Tronchet and Montaut (1958) and Thoday (1951, 1956-58) who also worked with several other species of Viscoideae. The haustorial system of Arceutho-bium has been the subject of extensive studies (Cohen 1954; Heil 1923; Heinricher 1915a, 1922a, 1924; Kuijt 1960b; Shea 1957; Thoday and Johnson 1930). The North American species of Phoradendron were investigated early in the century (Bray 1910; Cannon 1901; York 1909). The haustoria of Atkinsonia, a root parasite, more closely resemble that of other root parasites (Santalaceae, Olacaceae) than those of loranths parasitic on branches (Menzies and McKee 1959). Other loranths that have been investigated in some detail are Struthanthus spp. (Heil 1926), Dendrophthoe falcata (Singh 1954), and Loranthus micranthus (Menzies 1954).

The term "haustorial system" is used here to denote those secondary structures that unite with the host. These are essentially but not always entirely internal. The primary processes of host penetration are discussed in the section on germination. Morphologists differ in their opinion as to the homology of the haustoria to roots of autophytic plants, although their functional analogy is undisputed.

A haustorial system may involve the following general types of structures: (1) the intracortical strand usually referred to as the "cortical strand" which typically invades the cortical region of the host but which may become exposed in the course of its growth, (2) the sinker which forms a close union with the host xylem, and (3) the extracortical strand or runner which originates from the initial holdfast and which grows appressed to the outside of the host stem to a location where its tip invades the bark to produce a new plant in much the same fashion as the hypocotyl of the seedling. New runners may originate from the base of a new aerial shoot thus formed. They may be long meandering strands (Docters 1954; Singh 1954; Skene 1924) or they may be restricted outgrowths such as those described for *Phoradendron* (Cannon 1901; York 1909).

The typical haustorial system consists of cortical strands and sinkers, though in certain species one or the other may be reduced or absent. Cortical strands originate as lateral outgrowths of the primary haustorium and eventually develop xylem elements but never sieve tubes (Metcalfe and Chalk 1950). They may branch and anastomose. In some mistletoes on certain hosts they may burst through the bark near the base of the aerial shoot to form bands or claws around the host. Sinkers originate in two ways: (1) from the base of the primary haustorium, or (2) as outgrowths from cortical strands. They are usually wedge-shaped structures embedded in a xylary ray of the host. They do not penetrate but rather originate at the cambium layer and grow coincidentally with the host. They increase in thickness as their tips become progressively embedded in woody tissue. A meristem at the cambium enables them to maintain contact with the rest of the mistletoe plant. Like the cortical strands, they develop xylem but no phloem elements. Some of these are in direct contact with vascular elements of the host and others lead to the vascular bundles of the aerial shoot (Melchior 1921; Vodrazka 1928). In certain species a single sinker, originating from the tip of the primary haustorium (or the tip of a runner) constitutes the only union with the host xylem; in other species sinkers may arise also from the cortical strands (Cohen 1954; Tubeuf 1919, 1923).

The union between host and parasite may be characterized by a swelling or knob, or it may be a graft so perfect that the mistletoe appears to emerge as a normal branch (Docters 1954). The swellings may arise from host tissue alone, the parasite alone, or a combination of both (Heinricher 1926b). In the latter case particularly, when the parasite dies and its swollen base deteriorates the host tissue is exposed as a hollow hemisphere with fine ridges of wood radiating in rosette fashion from what was the primary haustorium. Such formations are known as "wood roses" (Tubeuf 1936).

The physiological function of the haustorial system is little understood. Presumably the cortical strands extract some organic substances from the host although histological studies give no suggestion as to how this might be accomplished (Dufrenoy 1936; DeCunha 1941). The cells of the host are separated and disturbed as the strands grow but they are never penetrated nor are there apparent contacts with the plates of sieve tubes that could explain a means of transfer (Tubeuf 1923). The sinkers, on the other hand, develop vascular elements in direct contact with those of the host and thus confirm their presumed function of extracting water and minerals. The dependence of the haustorial system on the aerial parts of the mistletoe presumably decreases as parasitism increases. The ability of the haustoria to live for long periods without benefit of aerial parts is well known in Arceuthobium. There are two reports that Phoradendron libocedri lived without or virtually without aerial shoots for well over 100 years (Meinecke 1912; Wagener 1925).

# Physiology and Parasitism

#### NUTRITION AND TRANSLOCATION

Yarwood (1956) in a recent review of the physiology of obligate parasitism states that the dodders are the only parasitic higher plants that have been grown *in vitro*. Dodder shoots were kept alive for at least 5 months on a medium made up of Hoagland's mineral nutrient solution, minor elements, 4 percent sucrose, and 0.1 gram/liter yeast extract (Loo 1946). Tubeuf (1912, 1923) germinated Viscum album seeds on nutrient agar in sterile flasks; the seedlings grew for periods up to 4 years, but presumably survived on nutrient contained in the seed and not the agar medium. Recently Blakely (1959) reports attempts to grow Arccuthobium douglasii in vitro. Although his efforts to infect Douglas-fir callus cultures with seeds were unsuccessful, the endophytic system of the parasite when present in cultured tissue proceeded to invade the callus.

Attempts to grow the mistletoes *in vitro* should be encouraged. This could provide detailed information on their physiology which in turn should aid in solving practical problems in the chemical control of mistletoes. Perhaps studies on the terrestrial loranths or the more polyphagus mistletoes would give the greatest assurance of initial success. There is also a need for extensive studies on the action of chemical agents on growth such as has been done with fungi and other microorganisms (Cochrane 1958). Work in this field should also have promise in developing control agents.

Before 1900, the relationship between the European mistletoes and their hosts was regarded as a form of symbiosis rather than parasitism, but today a definite host-parasite relationship is generally recognized. However, there is little doubt that there is some translocation of metabolites from the mistletoes to their hosts. This has been demonstrated repeatedly by experiments in which all the host leaves were removed, leaving only the mistletoe foliage to sustain the host (Heinricher 1913a; Molisch in Tubeuf 1923; Winkler 1913). Although defoliated plants with mistletoe usually live longer than those without it, the mistletoes are never able to maintain the host for a normal life span. The maximum period reported is about 6 years in the case of Viscum album on apple (Tubeuf 1923). Where three V. album plants were grafted on a leafless Sorbus aucuparia stock, no leaves developed on the Sorbus but the parasites grew vigorously and the host stem thickened for 2 years before it died (Poeteren 1912).

An experiment with Arcenthobium americanum on lodgepole pine in which all needles from infected and uninfected trees were removed showed that all those with mistletoe were still living after 2 years whereas all uninfected trees had died (Weir 1916b). The fact that there is usually an abundance of stored starch in mistletoe infected limbs could account for this in part.

Translocation from mistletoe to host is also suggested by two field observations of *Phoradendron* on junipers (Phillips 1907; Wagener 1957). In these cases the heavily infected parts of host plants died following a cold snap that killed the mistletoe but not the juniper foliage. Presumably the heavily infected parts of the junipers had lost so much of their foliage as a result of parasitism that they were apparently being sustained by the mistletoe and succumbed when the parasites were killed. Docters (1954) cites several cases where tropical loranths virtually replaced the crowns of their hosts for long periods but does not concede this to be true symbiosis, since the host plant is definitely penalized under such circumstances. He also believes that the long-lived mistletoes represent a higher degree of parasitism than the short-lived ones that are characterized by restricted haustorial systems and relatively few cortical strands that result in the premature death of single branches at the worst.

There is no histological evidence to suggest how exchanges might be made between the parasite and the phloem tissues of the host (Cannon 1901), nor has the phenomenon been satisfactorily demonstrated by experiment. In one case dyes were used to study the relative rates of translocation from the host to *Viscum album* and *vicc versa*. The dyes were said to pass much more readily from the host to the parasite than in the opposite direction, but quantitative information on the rates of movement in each direction were not given (Launay 1950).

#### HOST RESPONSES

The damaging effects of mistletoes on their hosts such as growth reduction, inferior fruit and seed crops, mortality, and hypertrophy are mentioned on page 42.

#### Leaf and Bud Responses

Papaya trees infected by Loranthus retained their leaves in the fall about 1 month longer than uninfected trees (Koernicke 1937). Sugar maple infected with *Phoradendron flavescens* in North Carolina retained its leaves 1 to 2 weeks longer. The chlorophyll content of maple leaves was about 50 percent greater and the maple buds broke dormancy, flowered, and leafed out about 1 week earlier on infected than on uninfected branches of the same tree (O'Kelley 1953). It is reported that Loranthus (Amycma) transfers a substance to its Eucalyptus host that prevents the growth of epicormic shoots on the branch below the mistletoe (Nicholson 1955).

#### Stem and Branch Responses

Infections of *Arceuthobium* may stimulate the growth of a branch presumably well beyond the limits of the endophytic system.

Anderson and Kaufert (1959) describe several distinct types of *Arceuthobium*-caused witches'-brooms in black spruce, and Himmel (1935) observed looped branches in the same tree that were believed to be the result of disturbed tropic responses caused by infections of *A. pusillum*. Hypertrophies on the branches of lime and maple are said to develop only after infection of *Viscum album* declines in vigor (Dallimore 1932).

#### Systemic Effects

Laurent (1901b) observed that varieties of pear immune to *Viscum album* developed necrotic bark where the primary haustorium entered. He considered the toxic principle to be more concentrated in the seeds than in the berry pulp and to be attenuated by heat.

Heinricher (1929) concluded from studies started in 1908 that antitoxins acquired following infection with Viscum album rendered pear trees increasingly resistant or even immune to further attack by the parasite. According to Chester (1933) this is the only case where the question of acquired immunity in plants has been concerned with a phanerogamic parasite, and Gaümann (1950) says that it is the only instance in plant pathology where pre-immunization of the host may occur through local infection such as is common in animal immunology.

However, Paine (1950) questioned the validity of Heinricher's conclusions, primarily because the source of his inoculum was not constant and variation in the ability of different strains of mistletoe to attack pear was recognized. Paine also presented data that suggest increasing susceptibility of the pear to mistletoe infection in each of three successive years of inoculations. He emphasizes that his results apply to new inoculations only and that the effects of previously established mistletoe plants on resistance of the host will require further study.

Further observations on the relationships between Viscum album and pear trees is reported in Scholl's (1957) recent work which indicates that the intensity of the toxic reaction is influenced by several factors including the amount of inoculum, the age of the host tissue, the time of year, the pear variety, and the subspecies of mistletoe.

There are no obvious indications of acquired immunity in North American tree species infested with *Arcenthobium* or *Phoradendron* and Hartigan's (1958a) account of the Australian mistletoes gives no suggestion of such a condition.

There is a report from Hungary (Minev 1951) that no mildew was found on oak trees infected by *Loranthus europaeus* although it occurred on trees without mistletoe. Perhaps there was more succulent, fungus-susceptible growth on the mistletoe-free trees. However, if the phenomenon is a manifestation of antibiotic activity, it is not supported by limited studies *in vitro* which indicate that aqueous extracts of *Viscum album* are ineffective against *Staphylococcus aureus* and *Escherichia coli* (Osborn 1943). Aqueous extracts of the same mistletoe stimulated the growth of a yeast and species of *Aspergillus* in culture tests (Hueber 1938). The insecticidal properties of four mistletoes were tested by several investigators whose work has been reviewed by Jacobson (1958). The results appear to be conflicting and do not suggest practical application.

More detailed studies of the phytotoxins and auxins of mistletoe extracts should help to explain the various host responses that have been observed. These might be approached first by chromatography (Kefford 1955).

#### WATER RELATIONS

Studies of water relations of the mistletoes have been primarily of two types: (1) comparative transpiration rates of the parasite and host, and (2) comparative osmotic concentration studies of the parasite and host. The water relations of parasitic plants (including the Loranthaceae) has recently been reviewed by Härtel (1956).

#### Transpiration

Härtel (1937) showed that during July and August the transpiration rate of *Viscum album* was about six times that of its birch (*Betula*) host. In winter, transpiration by the mistletoe was about one-tenth its summer rate. The transpiration rates for two Venezuelan species of *Phoradendron* were consistently higher than the hosts in both the wet and dry seasons, a condition that was considered to be very detrimental to the host plants, particularly during the dry season (Vareschi and Pannier 1953).

A similar relationship was found between an Australian Loranthus (Amyema) and its host, Acacia. During a 24-hour period the mistletoe transpired  $3\frac{1}{2}$  times as much water per unit leaf area as its host; and in some hourly measurements the rate of water loss for the Loranthus was 8 to 9 times greater (Wood 1924).

The rate of water loss from cut twigs of Viscum album was found to be much less than for cut twigs of two host trees (Populus and Pyrus). However, the rate of water loss for two tropical mistletoes was greater than for cut twigs of their hosts (Kamerling 1914a, 1914b).

#### Osmotic Concentration

Extensive studies of sap concentrations have been made by Harris and his coworkers (Harris 1918a, 1918b, 1934; Harris and Lawrence 1916; Harris et al. 1930a, 1930b). MacDougal and Cannon (1910) seem to be the first to state that in general the cell sap of parasitic plants has a higher osmotic concentration than that of their hosts. This hypothesis was confirmed for *Viscum album* (Arens 1912; Härtel 1956; Senn 1913), where it was found that on the average the osmotic concentration (based on plasmolytic measurements) of the mistletoe was about  $2\frac{1}{2}$  times that of the host.

Harris' osmotic concentration measurements were based on freezing point depressions. In seven Jamaican mistletoes on 19 hosts, the osmotic concentration of the mistletoe leaves was generally, but not invariably, higher than those of the host leaves (Harris and Lawrence 1916). Where one mistletoe was parasitic upon another, it was found that the osmotic concentration was lowest in the primary host, higher in the primary parasite, and the highest in the secondary parasite. Mistletoes (Phoradendron) in the Arizona desert showed the same relationship as in Jamaica: i.e., osmotic concentration was generally higher in the parasite than in the host. The unusually high osmotic concentration of creosote bush (Larrea) was believed to account for the scarcity of *Phoradendron* on it. The only instance where mistletoe has been reported on this host was near a pumping station where soil moisture was unusually high. Here, the mistletoe was able to parasitize the creosote bush even though it had a lower osmotic concentration than its host (Harris 1918a; Harris et al. 1930a).

Harris (1934) gives several thousand osmotic measurements of various plant saps including nearly 300 paired determinations of 20 mistletoes and their hosts. Since this work merely lists the basic data without summaries, his data on three species of *Phora*-*dendron* have been summarized in table 2.

Tissue fluids also generally have a higher specific electrical conductivity and a higher chloride content in the mistletoes than in their hosts (Harris and Valentine 1920; Harris et al. 1930b).

The ratio between sap concentrations of mistletoes and their hosts may be an important factor in the distribution of the parasites and their occurrence (or absence) on certain trees or tree species.

#### ASH ANALYSES

Studies of ash analyses of *Viscum album* and its hosts were made as early as 1844 (Will and Fresenius 1844), and Tubeuf (1890) critically reviewed the previous studies on ash analyses of this species. In most tests, twigs of the host and mistletoe were used for comparison. Although there is some variation in results

	Host		Mistletoe		Diffor
Mistletoe	Determi- nations	Osmotic pressure	Determi- nutions	Osmotic pressure	ence
······································	} Number	A tmos- pheres	Number	Atmos- pheres	Atmos- pheres
P. macrophyllum <sup>*</sup> P. flavescens <sup>*</sup> P. macrotomum <sup>*</sup>	68 21 32	$21.6 \\ 15.8 \\ 17.0$	80 34 57	$\frac{25.2}{21.5}$	-3.6 + 5.7 + 7.5
· · · · · · · · · · · · · · · · · · ·					

 

 TABLE 2.--Comparison of osmotic pressure of three species of Phoradendron and their hosts (Harris 1934)

From Arizonn.

" From southeastern United States.

by the different workers, the proportions of the various elements are fairly uniform. Potassium, phosphorus, sulfur, and magnesium are consistently higher in the parasite than the host, but the converse is true for calcium.

Table 3 shows the average amounts of various elements found by several workers in the ash of *Viscum album* and its hosts. Calcium is most abundant in the host, but potassium is predominant in the mistletoe. There was no consistent relationship between the amount of silicon, sodium, chlorine, manganese, or iron in the mistletoe and the host.

The arsenic content of the leaves of *Viscum album* was surprisingly constant, while that of its host varied markedly (Jadin and Astruc 1912a, 1912b). The ratio of arsenic content between host and mistletoe ranged from  $1_5$  to 2, but the actual amount in the mistletoe remained about the same. Jadin and Astruc (1912c, 1913) report that the amount of manganese in *Viscum album* was usually higher than in the host, but this was not confirmed by other workers (table 3). The uranium content of this mistletoe was much higher than that found in the vegetative parts of the autotropic plants (Hoffman 1943). The principal ash constituents of *Loranthus curopaevs* on oak bore about the same relationship as *Viscum album* and its several hosts (Nicoloff 1923).

A 1931 study of triple parasitism involving three Australian species of mistletoe indicated that there was consistently more potassium and phosphorus and less silicon and calcium in each parasite than its immediate bost (Greenham and Brown 1957, p. 309).

Greenham and Brown (1957) found that when radioactive iron (Fe<sup>30</sup>Cl<sub>2</sub>) was injected into the sapwood of *Eucalyptus* bearing Amycma it moved into the host leaves within 3 days but could not be detected in the mistletoe leaves in 19 days. After 46 days it was found in *Amycma* leaves but in varying amounts. At the end of a year the radioisotope was consistently distributed through the

Element	Approximat	Mistletoe ash/		
	Host plants	Viscum album	host ash	
	Percent	Percent	Ratio	
Calcium	66.7	24.1	0.3	
Potassium	9.1	31.3	3.4	
Phosphorus	5.2	17.1	3.3	
Magnesium	5.2	8.8	1.7	
Manganese	1.0	0.8	0.8	
Sodium	3.1	3.6	1.2	
Silicon	3.6	3.1	0.9	
Others	4.1	7.7		
Total	100.0	100.0	· · · ·	

TABLE 3.—Ash analyses of Viscum album and its host plants<sup>1</sup>

<sup>1</sup> These are approximations based on the combined results of Councler (1889), Erdmann (1855), Grandeau and Bouton (1877), Nicoloff (1923), Reinsch (1860), Will and Fresenius (1944), and Wolf (in Tubeuf 1923). foliage of both plants but the amount per unit of leaf surface in the host was double that in the mistletoe.

Ash analyses show that mistletoes are selective in their mineral uptake; for example, *Viscum album* contains over three times as much phosphorus and potassium as the host, but only about onethird as much calcium. The importance of phosphorus in obligate parasitism of higher plants by fungi has been emphasized by several workers (Yarwood 1956). The fact that the mistletoes are quite selective suggests that possibilities of their chemical control are promising.

#### PHOTOSYNTHESIS AND RESPIRATION

Starch synthesis was demonstrated in Viscum album leaves by Luck (1851), and cholorphyll was isolated from the same species by Reinsch (1860). Freeland (1943) showed that both cholorophylls a and b are present in *Phoradendron flavescens*, and that photosynthesis occurs. Heinricher (1924) noted chloroplastlike bodies in the haustoria of *Arceuthobium oxycedri* and made the questionable assumption that they were green-colored leucoplasts rather than chloroplasts. The photosynthetic activity of the haustoria is presumably limited because of the scarcity of light, yet these parasites may live indefinitely without aerial shoots. More detailed studies of leaf pigments might be the key to a better understanding of synthesis in these parasites. For example, a personal communication from A. G. Greenham indicates that the alcoholic extract of *Amyema pendula* leaves is often blood red.

Maksimov (1908) found that respiration in Viscum album was directly affected by temperature but it did not cease entirely at -20° C., the lowest temperature observed.

#### BIOCHEMISTRY

The qualitative biochemistry of the mistletoes is little known, and there is even less quantitative information. The compounds isolated from various species have been listed by Wehmer (1935). The most comprehensive accounts are those of Viscum album by Wester (1921), Einleger et al. (1923), and a series of papers by Obata (1941-44). Lauterer (1895) noted that the plant saps of Loranthus and its host Eucalyptus resulted in different color reactions to various metalic salts and other reagents. He accepted this as evidence of marked differences in the chemical constituents of the host and the parasite. Certain compounds of economic or pharmaceutical interest are discussed elsewhere in this review.

#### Carbohydrates

Sugars.—In the Javanese Dendrophthoe pentandra (Schoorl 1929) glucose was essentially the only sugar and totaled about 6 percent of the fresh weight of the fruits. Glucose was also found in Viscum album (Einleger et al. 1923). Free fructose has not been reported, but sucrose was detected in Viscum album and Loranthus europaeus (Beguin 1931; Einleger et al. 1923), and 4.5 percent unidentified reducing sugars have been found in *Phoradendron flavescens* (Desantis and Lynn 1937). Sugars that occur in combined forms in various mistletoes include galactose, arabinose, and rhamnose.

The ascorbic acid (vitamin C) content of *Viscum album* fruits was found to be 750 mg. per 100 grams fresh weight (Rikovski and Besaric 1949). This is about 15 times the average vitamin C content of oranges.

Starch.—There are numerous reports of starch in the mistletoes and for the leafy species the amount is greater than in adjacent host tissues. There is disagreement as to how the greater starch concentration in the parasite develops. Brittlebank (1908) suggested that this is due to an accumulation of carbohydrates from the host, but Kerr (1925) believes that an explanation lies in a higher rate of carbohydrate metabolism of the mistletoe. Weir (1918a) reports an accumulation of starch in the witches'-brooms caused by Arcenthobium. In any case, the common occurrence of starch in mistletoes seems to indicate that their carbohydrate supply is plentiful.

Sugar alcohols.—"Inositol" and "racemic inositol" have been isolated from Viscum album berries (Tanret 1907). An intensive study of sugar alcohols in Viscum album and its hosts was reported by Plouvier (1953). He isolated pinitol (d-inositol) from the parasite on 14 species of dicotyledonous trees, but found it in only one of the host trees (black locust), and therefore assumed that pinitol was formed by the mistletoe. He detected quebrachitol (*l-inositol*) in Viscum album on three species of maple and one of Fraxinus. Quebrachitol was abundant in the three maples and therefore may have passed from the host to the parasite, but since none was found in Fraxinus, it was assumed to have been produced by the mistletoe. For quercitol on oak and mannitol on three species of ash, the amount of the compound in the mistletoe and in the host was about the same. He found no sorbitol in Viscum album growing on Cratacgus although this compound was present in the host. Muller (1932) reported d-mannitol in Viscum album.

Glycosides.—Plouvier (1953) also examined the glycosides of Viscum album and seven host species. He found a number of glycosides in the host trees, but in only one was the compound also present in the mistletoe; this was syringoside, which occurred in Fraxinus but also to a limited extent in the stems, but not in the leaves of the mistletoe parasitic upon it. He concluded that the absorption tissues of the parasite are not impermeable to these glycosides, but that their general scarcity in the mistletoe is due to their immediate utilization.

A yellow glycoside, quercitrin, has been isolated from the leaves of two tropical species of *Loranthus* (Wester 1921). No cyanogenetic glycosides have been found in the Loranthaceae or any other parasitic higher plants (McNair 1941).

#### **Plant Acids**

There seems to have been no critical study of the plant acids of the mistletoes, but some mention is made of crystals of calcium oxalate and calcium malate. A single record of calcium malate was found in *Arceuthobium oxycedri* (Livon 1912), but there are many references to calcium oxalate in various mistletoes. Detailed studies on the structure and forms of calcium oxalate crystals found in *Viscum album* have been made (Gerard 1882; Walter-Levy and Strauss 1954). Muller (1932) found acetic and the magnesium salt of d-l-fermentation lactic acid in *V-album*.

#### Nitrogen and Nitrogen Metabolism

Studies of the total nitrogen in the leaves of mistletoe showed that *Viscum album* had about six times as much nitrogen as its host and *Loranthus europaeus* about twice as much (Nicoloff 1923).

Studies in the early part of the century indicate that parasitic plants that contain chlorophyll (in this case Viscum album and Arceuthobium oxycedri) have low nitrate levels, but high total nitrogen, while the reverse was true for the chlorophyll-less parasitic plants (Lutz 1908, 1912). The nitrogenous compounds in a Japanese form of Viscum album include arginine but no free amino acids (Obata 1941-44, I). Seventeen amino acids have been isolated from viscotoxine, a pharmaceutical compound from Viscum album (Winterfeld and Leiner 1956).

Cutter's (1955) anatomical studies of a number of parasitic phanerogams including two mistletoes (*Phoradendron flavescens* and Loranthus globiferus) indicate that mechanical tissue (stone cells, thick-walled parenchyma cells, lignified cell walls) is considerably more common in parasites and saprophytes than in autotrophic plants. She suggests that nitrogen may be a limiting factor in the physiology of these parasites, since Burkholder and McVeigh (1940) found that nitrogen deficiency was associated with xeromorphic characters such as thick cell walls and sclerenchymatous tissue in the corn plant. These authors indicate that when a considerable amount of available nitrogen is present, the carbohydrates are used up in protein synthesis and hence are not available for thick ming and lignification of cell walls. On this basis, Cutter reasons that the prevalence of mechanical tissues in parasitic plants indicates that their carbohydrate supply is adequate and that nitrogen may be limiting. Furthermore, Burkholder and McVeigh found that the apical regions in corn plants developed in direct proportion to the nitrogen supply, and since Cutter observed that both of the mistletoes had unusually small apices, she considered this as further evidence of the importance of nitrogen. Cutter's interpretations are open to question because many factors could be involved in the formation of mechanical tissues and small shoot apices in the mistletoes.

## Phosphorus and Phosphorus Metabolism

The proportionately high phosphorus content of the ash of *Viscum album* (over 3 times that of the host) has already been mentioned.

The phosphorus metabolism of *Viscum album* was studied by Michel-Durand (1934), who measured the amount of the different forms of phosphorus at six dates from May to September. He found that lipid phosphorus remained about the same during the period, phytic and mineral phosphorus decreased markedly as the season progressed, and organic phosphorus increased reciprocally with the decrease in phytic and mineral phosphorus. He concluded that the high phosphorus levels of *Viscum album* make it a choice plant for the study of phosphorus metabolism.

#### Secondary Plant Products

Lipids.—Palmitic is the principal fatty acid in Viscum album and Loranthus europaeus (Einleger et al. 1923). Seven other fatty acids have been found in Viscum album: myristic, stearic, arachidic, cerotic, oleic, linoleic, and linolenic (Braunhauser 1925; Einleger et al. 1923; Obata 1941–44, I). A paraffin  $C_{30}H_{62}$  and a wax alcohol (Loranthylalkohol)  $C_{24}H_{50}$ O were found in Loranthus europaeus (Einleger et al. 1923). The wax alcohol has also been isolated from Viscum album along with ceryl alcohol and cetyl alcohol (Braunhauser 1925; Einleger et al. 1923).

Essential oils.—Oleaic acid is reported to compose 1 to 2 percent of Viscum album leaves (Oba.a 1941-44, III; Winterstein and Hämmerle 1931). Other essential oils found in Viscum album are beta-amyrin and lupeol (Barton and Jones 1944; Bauer and Gerloff 1936; Meyer and Jeger 1948; Obata 1941-44, I).

Betulic acid has been found in Nuytsia floribunda, a terrestrial member of the Loranthaceae from Australia (Anstee et al. 1952).

Tannins.—Tannins seem to be common in the Loranthaceae but little quantitative information on the subject is available. Desantis and Lynn (1937) report 3.9 percent tannin in *Phoradendron flavescens* leaves. There have been several reports of tannin in *Arceuthobium* (Datta 1954; Peirce 1905; Thoday and Johnson 1930, I). Both gallotannins (Reinsch 1860) and phlobotannins (Einleger et al. 1923) are found in the Loranthaceae.

Alkaloids.—Tyramine  $(C_{s}H_{11}N)$  was reported in Viscum album in 1907 (LePrince 1907) and this same alkaloid was found in *Phoradendron flavescens*, *P. villosum*, and *P. californicum*, but not in *P. juniperinum*, *P. bolleanum*, Arceuthobium campylopodum, or A. vaginatum (Crawford and Watanabe 1916; Ostenberg 1915). Other workers report no alkaloids in *Phoradendron flavescens* (Desantis and Lynn 1937). Such discrepancies are discussed by McNair (1941) who suggests that they may be explained by different concentrations of electrolytes, particularly nitrates, in the host trees. He supposes that alkaloids may be formed only under high nitrate concentrations. Hyoscine was found to be the principal alkaloid in Loranthus on Duboisia in Australia (Trautner 1952). There is disagreement as to whether mistletoe on *Strychnos* contains strychnine (Wehmer 1929-31, V.2; Chatin 1891), however, certain loranths are said to be poisonous only when growing on hosts that contain poisonous principles (Blakely 1922-28).

Carotenoids.—There is little information on the carotenoids of the mistletoes. A "considerable amount" of xanthophyll in Viscum album has been reported (Wester 1921). Beta-carotene but no alpha-carotene was found in the leaves of Phoradendron villosum in California (Strain 1935).

#### LIMITING FACTORS

Some of the foregoing information may provide clues to the physiology of the parasitism of the mistletoes, but much of it refers to one or a few compounds and such information cannot be evaluated until the physiology of the mistletoes and their hosts is much better understood.

On the basis of the scanty indirect evidence, one may only speculate as to what may constitute the limiting factors for growth of the mistletoes. Some workers (Launay 1950) have suggested that the water economy of the mistletoes is the limiting factor in their physiology and cite as evidence the common occurrence of xerophytic features in many species. However, the few studies made show that the transpiration rates of the mistletoes are high and in most cases higher than the hosts thus indicating that perhaps water economy is not the limiting factor in their physiology.

Another factor which has been suggested as limiting is the carbohydrate supply. However, the abundant accumulation of starch in the mistletoes, even in those forms such as *Arceuthobium* which are presumably able to manufacture only a small portion of their carbohydrates, would seem to indicate that this is not the case. If one accepts the anatomical interpretations of Cutter (1955), it appears that the carbohydrate supply of these plants is adequate, but that nitrogen may be limiting.

# Factors Affecting Mistletoe Occurrence

#### PHYSICAL FACTORS

The physical factors affecting the occurrence and frequency of mistletoes are poorly understood although one point is evident: most of them seem to thrive best in warm sunny locations.

#### Light

The influence of light on germination has already been discussed. This may explain in part the preference of mistletoes for high treetops, open stands, or the edges of dense forests (Dowding 1929; Fischer 1926; Gorrie 1929; McLuckie 1923). However, species of Arceuthobium frequently occur in the lower crowns of their host trees and Szczerbinski (1956) reports Viscum laxum on the lower trunks of *Pinus sulvestris*. It has been observed that Phoradendron flavescens tends to position its leaves so that the surfaces are parallel to light incidence, thus presumably avoiding direct isolation but providing opportunity for photosynthesis on both surfaces (York 1909). Obaton (1941) studied the reflection of infrared light from leaves and concluded that sun plants had greater reflective powers than shade plants. In searching for an explanation he compared peeled and unpeeled V. album leaves and found so little difference that he concluded the epidermis was not the controlling factor.

#### Geographic Factors

Altitude apparently has a strong influence on the distribution of certain loranths even where suitable hosts exist well beyond the altitudinal limits of the parasite. For example, in the Himalayas, Arceuthobium minutissimum occurs only in the upper (and drier) ranges of its principal host, Pinus griffithii (P. excelsa) (Gorrie 1929). In the same region Viscum articulatum is found from 3,000 to 6,000 feet, and V. japonicum from 5,000 to 7,000 feet (Bamber 1916). A. americanum is absent from the upper ranges of its principal host, Pinus contorta, in the central Rocky Mountains (Hawksworth 1956) and A. vaginatum in the southwestern United States is absent or rare in the lower elevations of Pinus ponderosa, its principal host (Gill 1954; Hawksworth 1959b). Plagnat (1950a) reports that for the fir form of Viscum album in France, the upper limits of the parasite are 200-400 meters below the upper limits of Abies. In Mexico Arcenthobium vaginatum ranges from 9,500 to 10,500 feet, Psittacanthus calyc datus from 5,000 to 7,000 feet, and Struthanthus microphyllus from 1.200 to 7.800 feet (Leavenworth 1946).

Information on the frequency and abundance of species of *Arceuthobium* in relation to aspect and steepness of slopes is given by Hawksworth (1959b), Korstian and Long (1922), and Roth (1954).

Although no quantitative studies seem to have been made on the influence of water and light on mistletoe occurrence, some scattered observations are of interest. Certain local geographic conditions influence the abundance and frequency of mistletoe. Arcenthobium vaginatum and A. americanum, for example, are known to flourish best on ridges (Dowding 1929; Hawksworth 1958a; Korstian and Long 1922; U.S. Forest Service 1954). Arcenthobium pusillum is abundant on its common host, Picea mariana, always in bogs (Stone and Howitt 1920) and in Maine it attacks P. glauca growing close to the seacoast (Fassett 1925). In Australia, the mistletoes of New South Wales are said to be more abundant near water (May 1941), and McLuckie (1923) notes that Phrygilanthus celastroides (Loranthus celastroides) is limited to areas of frequent mists.

A number of broad geographic limitations have been recorded. In the eastern United States, the northern limit of *Phoradendron flavescens* is in southern New Jersey, though some of its common hosts continue far northward (Willis 1873). In the Rocky Mountain region of the United States, the leafless *Phoradendron juniperinum* extends about 300 miles farther north than the leafy species of *Phoradendron*.

Picea mariana, the principal host of Arceuthobium pusillum, extends far beyond the northern and western limits of the parasite but only about 30 miles to the south. The southern limits of the mistletoe are coincident with those of Ledum groenlandicum and Kalmia polifolia (Eaton 1931; Eaton and Dow 1940). A. americanum is common on Pinus banksiana in Saskatchewan and Manitoba but does not follow this host eastward (Riley 1951; Weir 1915a). The same mistletoe species is abundant on the mountain forms of Pinus contorta in the United States and Canada but is absent on the Pacific coast form. A. douglasii is widespread on the interior forms of *Pseudotsuga menziesii* but is absent in the great Douglas-fir forests west of the Cascades (Boyce 1932). A. vaginatum, which is common on the scopulorum form of Pinus ponderosa throughout most of its range, is absent from the Black Hills of South Dakota as well as from the scattered islands of this tree on the Great Plains (Gill 1935; Korstian 1925). Phoradendron densum on Juniperus occidentale and P. pauciflorum on Abies concolor are much more restricted in their range than are their hosts (Wagener 1957). V. album is found throughout Europe and England, but is absent in Scotland and Ireland although it can be cultured in the open in both countries (Monsch 1938; Nicholson 1932). Pollen analyses indicate that it was more abundant in post-glacial Norway than it is today (Hafsten 1957). Dalmon (1929) describes a geographically homogenous area in the Seine and Marne valleys where V. album abounds in one sector and is absent from another although both are frequented by the mistletoe

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thrush (*Turdus viscivorus*). According to Ward (1912) mistletoe is absent from the Yangtse valley of China but increases as one ascends the mountains. He suspected that the distribution was associated with the movements of starlings.

Despite the abundance of mistletoes in Australia and New Zealand, they are absent on Tasmania (Blakely 1922-28). On the other hand, species that are similar to or identical with those of the American continents occur on the Galapagos and Cocos Islands (Stewart 1911; Svenson 1935), and Arceuthobium oxycedri, which occurs from the Western Mediterranean region to India, is found on the Azores (Guppy 1917). Loranthus and Korthalsella occur in the Polynesian islands (Brown 1935). Backer (1929) notes that several mistletoes were common on Krakatao before the volcanic eruption of 1883 but that none were present 40 years afterward presumably because the birds which disseminate them are absent. Eggler (1959) recorded the occurrence of several plants in the vicinity of Jorullo volcano in Mexico where the vegetation was destroyed between 1759 and 1775. After nearly 200 years, only two mistletoes (Phoradendron piperoides and Psittacanthus calyculatus) were found, both on leguminous trees.

#### Soil

Apparently there have been no critical studies of soil in relation to mistletoe populations. Many investigators who were primarily concerned with the pathology and economic significance of the mistletoes have stated that they are most abundant and damaging on poor soils or sites (Dowding 1929; Gorrie 1929; Korstian and Long 1922; May 1941; Pomerleau 1945; Riley 1951). A few have questioned this on the ground that a long-standing infestation in any area gives the impression of poor site simply as a result of parasitism (Gill 1954; Peter-Contesse 1930). Furthermore, Weir (1916a) claimed that Arceuthobium campylopodum f. laricis damage is most severe on sites best suited to the growth of its larch host. Surveys of Arceuthobium damage in the south central Rocky Mountain area show that at least two species (A. americanum and A. vaginatum) are widespread and damaging on average to good sites (Hawksworth 1958a; U.S. Forest Service 1954).

In an early attempt to correlate soil type with mistletoe distribution, Laurent (1900, 1901a) noted that while Viscum album in Belgium is not confined to calcareous soils, it is found most abundant in areas where the soil contains more than one percent calcium. However, Tubeuf (1923) reports that the proportion of calcium in the ash of Viscum album growing on apple was practically the same whether the trees were growing on "lime-rich" or "lime-poor" soils, but made no mention of the calcium content of the trees on the two soil types. He also called attention to the fact that there is no apparent correlation between the distribution of mistletoe and limestone soils in other parts of Europe and that the conifer mistletoes in particular are abundant on very acid soils. It has been suggested without explanation that Arceuthobium campylopodum on Pinus ponderosa in southern Idaho is most common on the basaltic soils of that area (Korstian 1924). Reed and Reed (1951) working with Phoradendron flavescens in Kentucky state that the parasite is best adapted to hosts growing on calcareous formations, viz.: the Ordovician, Silurian, and Mississippian, although in the Pennsylvanian it does occur on sourgum (Nyssa) and some oaks. They further observed that on the Mississippian or Pennsylvanian formations, walnuts (Juglans) are rarely attacked but in the highly calcareous Ordovician (bluegrass) region they are more than 80 percent infected.

#### Climatic Extremes, Cold and Wind

In the western United States low temperatures of brief duration have been observed to kill Phoradendron but not its juniper host (Phillips 1907; Wagener 1957). According to Deam (1940) P. flavescens was once common in the southern part of Indiana but was almost extinct by 1940. Perhaps an early observer (Schneck 1884) holds the explanation of this. Referring to P. flavescens in Illinois he says: "When we have several consecutive mild winters the mistletoe becomes common, but is again almost exterminated by the return of continuous cold weather, in which the thermometer remains at or below zero for a number of consecutive days. The winters of 1878-79 and 1880-81 were remarkable for the great number of continuous cold days, and came near exterminating the species from our flora. The two following winters were comparatively mild, and as a result the mistletoe was quite abundant last fall." Schneck undoubtedly meant that the aerial parts rather than the entire mistletoe plants were destroyed. The quick recovery suggests that resprouting occurred on those endophytic systems that survived the cold. Wagener (1957) suggests that the northern limits of Phoradendron densum and P. pauciflorum in California are determined by occasional very low temperature.

Strong winds are believed to assist in the spread and intensification of mistletoe. Weir (1916b) observed Arccuthobium seeds  $\frac{1}{4}$  mile from the nearest infected tree and concluded that they had been carried at least that distance by strong winds. Viscum album is said to have increased as a result of being widely distributed in a cyclonic storm (Bellegarde 1919, 1920). On the other hand, Tubeuf (1920) reasoned that storms may damage both the mistletoe bushes and the crowns of host trees to the extent that spread of the parasite is markedly reduced for several years. He also suggests that the migrations of the mistletoe thrush are reduced during cold winters.

#### **BIOTIC FACTORS**

#### Hosts

It would almost appear that no tree or shrub is immune to mistletoe attack under the right conditions. In one locality, a
species of mistletoe will show distinct preference for certain hosts, whereas in another, the preference may change to an entirely new group. In most instances preference is not associated with close phylogenetic relationships between hosts; *Viscum, Phoradendron*, and *Loranthus*, for example, are found on a variety of both angiosperms and gymnosperms. *Arceuthobium*, on the other hand, is restricted to conifers and the individual species normally occur on one or a few selected hosts (Kuijt 1955). However, it is not uncommon fcr a species of *Arceuthobium* to develop on unusual hosts especially where the latter occur in heavily infected stands of a normal host (Hawksworth 1952, Hawksworth and Peterson 1959; House 1935; Kuijt 1956).

The host relationships of *Viscum album* are complicated and have been studied extensively. Tubeuf (1923), after considering various proposals by others for subdividing the species, and after conducting extensive cross infection experiments of his own (1913, 1917), recognized three distinct races as follows:

1. Form species pini occurs in nature mostly on two-needled pines, notably Pinus mugho (P. montana) and P. nigra (P. larico). In southern Europe it is common on P. sylvestris. Two American species, P. resinosa and P. banksiana, were artificially infected, but trials with three- and five-needled pines were unsuccessful, except for a few takes on P. cembra. It occurs rarely in nature on spruce (Picca excelsa) and has been cultured artificially on larch and willow (Fliche 1889; Tubeuf 1923). It does not grow on fir (Beer 1925).

2. Form species abietis is never found on pine. It attacks Abies alba (A. pectinata) throughout its range and has been reported on various species of fir in parts of Europe. It has been cultured on larch and on a number of American species, namely Abies balsamea, A. fraseri, A. lasiocarpa vars. lasiocarpa and arizonica, A. grandis, A. concolor, A. amabilis, and silver maple, Acer saccharinum (Delacoste 1922; Tubeuf 1923).

3. Form species mali occurs naturally on a great many angiosperms embracing some 16 families (Boerner 1955-56; Boodle 1924: Genty 1932; Heinricher 1921; Hess 1920; Hodson 1931; Kreh 1958; Makowiecki 1931; Nicholson 1932; J. Roth 1926; Schenk 1951; Somerville 1914; Spaulding 1956; Tubeuf 1923, 1928, 1930; Wende 1925). In contrast with the preceding races, which sometimes grow on hardwoods, this one does not occur on conifers (Beer 1925) and is the only form reaching as far north as Norway (Hanssen 1933). Like the fir mistletoe, it will grow on Accr saccharinum. It is noteworthy that two of each form species have common hosts but there is no host common to all three. The separation of these three forms on morphological and chemical grounds has recently been proposed (Singer 1958).

Contrary to popular opinion, the native European oaks are rare hosts to Viscum album. Most reports of this mistletoe on oak were based on (1) cases where V. album parasitizes Loranthus curopeaus which in turn parasitized Quercus, or (2) instances where L. europeaus was mistaken for V. album (Boros 1926; Nicholson 1932; G. Roth 1926; Singer 1959; Tubeuf 1907, 1914, 1923, 1931). According to Boodle (1924) Q. palustris and Q. rubra, two North American species, planted in Europe have been attacked by V. album. Mothes (1930) cites a rare case of V. cruciatum on oak in Sicily. Chemin (1941) cites a case of Viscum album on oak where the latter was growing amid heavily infected poplars. The mistletoe was vigorous, suggesting that oak is a suitable host but that perhaps the parasite has difficulty penetrating the bark.

Tubeuf (1923) gives a detailed list of the Viscum album hosts in Europe, Gross (1931) listed them for northern Poland; and Kreh (1958) for the Neckar River region of Württemburg, Germany. The host lists prior to 1923 contained numerous errors due to the fact that (1) mistletoe was mistaken for witches'-brooms, *Hedera*, broken branches, etc., (2) the host was not properly identified, and (3) some authors considered a mistletoe plant to be successfully established even though the newly germinated seeds had developed no leaves. Yew is said to be free from mistletoe in England though plants have been observed to be frequented by thrushes loaded with mistletoe seeds from nearby apple trees (Trevor-Battye 1917).

In Phoradendron the species or varieties on angiosperms are usually morphologically distinct from those on gymnosperms although there are a few striking exceptions. Fosberg (1941) reports P. bolleanum (Seem.) Eichl. var. bolleanum on Arbutus, whereas its usual host is Juniperus. If one accepts Fosberg's (1941) conception of Phoradendron flavescens (Pursh) Nutt., its five varieties occur on various hardwood trees from southern New Jersey southward to Texas and Mexico, thence northward along the Pacific Coast to northern Oregon. The following quotation from Schneck (1884) is indicative of the manner in which its host preferences change from one area to another. On the route between Mount Carmel, Ill., and Washington, D.C., via Louisville, Ky., it was:

"Abundant but only on American elm until we came to Winslow, Ind. Here for the first time I observed it on black gum. From this point on I found it on this species as often as on the elm. In the bluegrass region of Kentucky, I found it common on the black walnut and wild cherry. In West Virginia, it was common on the red maple but had disappeared from the walnut and cherry. East of the Blue Ridge, I observed it on a beech." He found it on 13 species in Vandenburg County, Ind., alone.

Reed and Reed (1951) found Phoradendron flavescens in 76 of the 120 counties in Kentucky. It occurred on 24 species in 19 genera. James (1958) lists it on trees of 11 genera in one locality in eastern Tennessee. Carya was the most common host. Bray (1910), working in Oklahoma and Texas, lists P. flavescens on 30 species (several exotic) in 20 genera scattered through 14 families. He also observed changes in host preference from one area to another throughout the two States. Bray does not list Populus as a host, but it is the primary one attacked in the Rio Grande Valley of New Mexico (Goodding 1938). Spaulding (1958) reports P. californicum and P. flavescens on several introduced trees in the United States.

Many Loranthoideae have broad host affinities. Singh (1954, 1956) lists *Dendrophthoe falcata* as serious on 14 hosts of economic importance, and present on a total of 246 including both angiosperms and gymnosperms. Fischer (1926) recorded *Loranthus* on 274 hosts in India. L. falcatus (L. longiftorus) alone attacked 153 species or varieties. Millingtonia was the only tree genus that appeared to be immune, but trees with resinous sap appeared to be less acceptable than trees with milky juice, and those with compact evergreen foliage or thick scaly bark seemed to be parasitized less frequently. Although he detected no evidence of racial specialization as described for Viscum album, he observed that the host affinities for certain species varied from one locality to another.

### Birds

The Dicaeidae (flower-peckers or mistletoe birds) play an important part in the pollination and dissemination of mistletoes. The Javanese forms have been described in detail by Docters (1954) who also includes an extensive review of the ornithological literature pertinent to the life history of the Loranthaceae. Sunbirds (Nectariniidae) are also important pollinators in the tropics (Ali 1931, 1932). Dicaeum hirundinaceum is one of the more important vectors in Australia (Ashworth 1896; Blakely 1922-28; Keast 1958).

In Europe, the mistletoe thrush (*Turdus viscivorus*) is the principal vector of *Viscum album*. These birds migrate from Africa to Europe in late winter (January to March) and during this period feed almost exclusively on mistletoe berries. They utilize only a portion of the pulp and eliminate the seeds in a viable condition. Their migration paths are believed to influence the abundance of mistletoe in central Europe. The titmice (Paridae) follow close upon the thrushes and where their paths coincide they feed extensively on the extruded mistletoe seeds which they actually destroy. Next to the mistletoe thrush, the waxwing (*Bombycilla garrulus*) is the most important vector of V. album. Other birds that contribute to the spread are martins, doves, starlings, and additional species of thrush (Mayaud 1948; Peter-Contesse 1930; Tubeuf 1923).

Apparently the North American species of *Phoradendron* are distributed by a number of different birds, the more important of which are cedar waxwings (*Bombycilla cedrorum*), euphonias (*Tanagra* spp.), and *Phainopepla*. Others that have been observed to feed on the berries include mockingbirds, bluebirds, linnets, sparrows, quail, woodpeckers, thrushes, grosbeaks, finches, robins, grouse, crows, and flycatchers (Bailey 1928; Bleitz 1955; Bray 1910; Condit 1940; Cowles 1936; Grinnell 1914; Martin et al. 1951; Sutton 1951). Which of the latter simply eat the berry pulp and evacuate the viable mistletoe seeds is not clear.

Sutton (1951) concludes that the stomach of Tanagra is adapted

to the passage of great numbers of mistletoe fruits and in this passage the outer skin is digested but the viscous covering of the seed remains essentially intact.

## Mammals

The use of mistletoes as fodder by big game animals is mentioned in the section on mistletoes and man. The extent to which animals affect the distribution of the parasites either by spreading it or destroying it is little known.

The shoots of Arceuthobium are eaten by porcupines which often girdle the infected conifer stems and thus destroy the parasites to some extent (Taylor 1935). Ring-tailed cats are known to eat *Phoradendron* shoots (Martin et al. 1951) and are suspected of spreading the parasite in Texas (Bowman 1947). In Australia there are conflicting reports as to whether opposums and koala bears restrict or spread mistletoes (May 1941).

## Insects

Some insects favor the propagation of mistletoes by acting as pollinators, others are limiting agents that destroy the aerial shoots. An exhaustive monograph on the entomology of the Loranthaceae was prepared by Schumacher (1918), and Tubeuf (1923) gave a complete account of the insects associated with Viscum album. Contributions in this field have been meager since that time and reveal no serious enemies of the European mistletoe (Durham 1932; Pfeffer 1929; Massee 1947).

The insects taken from Phoradendron flavescens were catalogued by Tucker (1922). His work includes original observations on two weevils and their parasites together with a review of the entomological literature. Of more than 50 insects noted, a few, particularly some coleopterous and lepidopterous borers, were destructive to individual plants but none could be regarded as influencing the abundance or distribution of mistletoe. In addition to the insects on *P. flavescens* cited by Tucker, the homopterous insects *Aphalaroida spinifera* (Psyllidae) and *Diaspis parasiti* (Coccoidea) have been described (Crawford 1914; McKenzie 1947).

Although relatively few insects are reported on Arceuthobium, our own observations indicate that several are associated with those mistletoes in the southwestern United States. A spittle insect, Clastoptera obtusa (Korstian and Long 1922), and an undetermined lepidopterous larva are common and destroy large numbers of shoots in some years.

We have observed an undetermined species of thrips (Frankliniella sp.) in abundance during the flowering period and suspect these insects of being important pollinators. Mitoura spinetorum and M. johnsoni (Lepidoptera) have been reported to feed on shoots of Arceuthobium campylopodum, A. zmericanum, and A. vaginatum f. cryptopodum (Comstock and Dammers 1938; Remington 1958; Skinner 1904) and a plant bug Neoborella tumida (Hemiptera) has been observed on A. vaginatum (Knight 1927). Insects noted on the European A. oxycedri include the Coccoidea, Chionaspis striata and Diaspis visci (Schumacher 1918).

Several species of butterflies, including Delias and Ogyris (Lepidoptera) are destructive to the shoots of Loranthus in India and Australia (Bingham 1907; Froggatt 1907; Ghosh 1914; Maxwell-Lefroy 1909; Rainbow 1907). The fruits of this mistletoe are also destroyed by fly larvae (Diptera, Tephritidae Trypstidae), *Cryptodacus silvai* in Brazil (Costa Lima 1947) and *Ceratitis loranthi* (Froggatt 1911) in Australia. Scale insects (Coccoidea) are known to inhabit Loranthus (Fuller 1899) and other tropical mistletoes. They have been suspected of causing heavy mortality in certain areas in Australia, whereas in others they are abundant but not damaging (May 1941). A number of gall-forming insects have been described on Loranthus in Java (Docters and Docters 1909).

### Fungi

There are no comprehensive accounts of the fungi growing on the Loranthaceae. Tubeuf (1923) discussed those found on Viscum album. Pathogenic species, mostly on Phoradendron flavescens, have been listed (U.S. Bur. Plant Indus. 1952) and Kuijt (1955) mentions the fungus-caused diseases on North American species of Arceuthobium.

A summary of the nearly 100 fungi reported on mistletoes is given in table 4. The fungi are classified according to the scheme of Ainsworth and Bisby (1945). In general, the names originally proposed by the authors were considered valid unless synonymy is indicated by Saccardo (1882–1931). Both saprophytes and parasites are listed because no mention was made of the condition of the mistletoe plants in many reports.

A leafspot caused by Sphaeropsis visci is somewhat damaging to Viscum album and Phoradendron flavescens (U.S. Bur. Plant Indus. 1952; Tubeuf 1923; Wolf 1910). There seems to be some confusion in the literature as to whether or not Sphaeropsis visci (Westend.) Archer on Phoradendron (Rhoads 1943) is synonymous with S. visci (Solum.) Sacc. on V. album.

There are two well-known destructive diseases of North American species of Arceuthobium. One is caused by Wallrothiclla arceuthobii and has been studied in detail by Dowding (1931b). Observations subsequent to her publication have been recorded by Bourchier (1955a, 1955b) and Kuijt (1955). The disease prevents fruits from maturing. It has been found on A. americanum, A. douglasii, A. campylopodum f. abietinum and f. microcarpum throughout the West and or. A. pusillum in the East. It tends to persist in local areas but not necessarily moist ones as was first thought to be the case (Kuijt 1955). Our own observations indicate that dwarfmistletoe damage to Douglas-fir in the Sacramento-White Mountain area of New Mexico would be much more severe if it were not for Wallrothiella. Here the disease is by no means restricted to moist habitats.

#### THE MISTLETOES; A LITERATURE REVIEW

Class and order	Genera	Species	References
	Number	Number	
Phycomucetes			
Saprolegniales	2	2	Tubuef 1923; Saccardo 1882-1931, 24:24.
Peronesporales	1	1	Narasimhan 1930.
Myriangiales	2	2	Saccardo 1882-1931, 22:769; Jen- kins and Limber 1952.
Dothideales	1	1	Jenkins and Limber 1952.
Hemisphaeriales.	6	12	Saccardo 1882-1931, 9:1060, 9:1062, 22:541, 24:409, 24:457-58, 24:482; Stevenson 1946; Ryan 1924; Orejuela 1944; Docters 1954.
Erysiphales	1	4	Saccardo 1882-1931, 1:63, 24:311; Yates 1917.
Hypocreales	4	4	Saccardo 1882-1981, 25:375, Sey- mour 1929: Tubeuf 1923.
Sphaeriales	9	10	Linder 1938; Saccardo 1882–1931, 1:455, 2:132, 3:295, 9:757, 16:489, 24:744, 24:877; Sey-
Helotiales	2	3	Rhoads 1944; Saccardo 1882–1931,
Pezizales	1	I	Saccardo 1882-1981, 18:173.
Tremeliales	, i 1	1 1	Rhoads 1944.
Uredinales Fungi Imperiesti	5	24	(See table 5, p. 36.)
Sphaeropsidales .	14	21	Bonar 1942; Ciccarone 1951; Doidge 1942; Moesz 1922; Rhoads 1944; Saccardo 1882– 1931, 2:260, 3:113, 3:532, 10:282, 16:389, 22:909–10, 22:959–60, 22:997, 22:1112, 22:1157, 25:248, 25:284, 25:513; Seymour 1929
Melanconiales	5	5	Darling 1940; Ellis 1946; Parmeter et al. 1959; Saccardo 1882–1931, 25 al. 959; Saccardo 1882–1931,
Moniliales	6	9	25:549; 100eul 1923. Burnett 1958; Petrak 1954; Sac- cardo 1882-1931, 4:155, 18:609, 25:945, 25:994; Seymour 1929; Tubeuf 1923.

TABLE 4.—Summary of fungi reported on Loranthaceae

The other notable disease is caused by Septogloeum gillii. This is an anthracnose which destroys large numbers of dwarfmistletoe shoots in localized areas during certain years. In his detailed study of the disease in the U.S.A., Ellis (1946) reported it as occurring naturally on Arceuthobium douglasii and seven forms of A. campylopodum in six of the western States. The range has since been extended to include A. americanum and the western Canadian provinces (Bourchier 1954b, 1955a, 1955b; Gill 1952). The fungus may hold some promise as a biological control agent, although it apparently is not destructive to the endophytic system of the mistletoes and has never been observed to eradicate its host even where it was abundant for several successive years. It has been successfully introduced into an infestation of *A. americanum* on lodgepole pine by means of a water spore suspension spray. Heavy infection followed the spraying but the disease failed to maintain itself in the area (Mielke 1959).

Linder (1938) described a new species, Metasphaeria wheeleri, on Arceuthobium campylopodum f. campylopodum near Monterey, California. The fungus girdled the dwarfmistletoe stems and resulted in mortality of the distal parts of the shoots. The disease appears to be local and of no great consequence in influencing the abundance and frequency of this dwarfmistletoe species. A disease of A. campylopodum f. abietinum in California caused by Colletotrichum gloeosporioides has recently been described by Parmeter et al. (1959). In areas where the disease was intensive, fewer than 20 percent of the mistletoe plants bore healthy shoots. Cytospora abietis has been observed to kill branches and stems of red fir (Abies magnifica) infected with Arceuthobium campylopodum f. abietinum (Gill 1935; Wright 1942).

At least 24 rusts (Uredinales) have been reported on various Loranthaceae (table 5). A key to eight species of *Uromyces* on mistletoes is given by Cummins (1939).

Rust	Mistletoe	1	Location	Reference
Aecidium bulbifaciens.	Phrygilanthus hetero- phyllus (Loranthus heterophyllus)	;	Chile	Dietel and Neger 1896.
A. cookcanum <sup>4</sup> .	Viscum, Loranthus	i	S. Africa,	Cribb 1955; Cooke 1885
A. goyazense	Phthirusa (Dendrope-	1	Brazil,	Hennings 1895;
A. loranthi Thum.	Loranthus <sup>2</sup>		So. and Central America	Kern 1938. Kern 1911; Lorentz 1878.
A. phrygilanthi .	Phrygilanthus eugenioides		Bolivia	Jackson 1927.
A. schimperi	Loranthus schimperi		Ethiopia	Baccarini 1917.
A. struthanthi	Struthanthus marainatus	2	Brazil	Jackson 1927.
Chacenia texcusis	Phoradendron macrophylium		U.S.	Seymour 1929.
Purcinia heroica	Loranthus		New Guinea	Cummins 1941
P. lorunthi	Psittacanthus cordatus (Loranthus cor- datus)		Argentina	Spegazzini 1902.
P. loranthicola	Phrygilanthus celas- troides (Loranthus celustroides)	· !	Australia :	McAlpine 1906.
P. luculenta	Loranthus folcatus (L. longiflorus)	:	India	Ramakrishnan and Ramakrish- nan 1948.
P. macrocarya	Loranthus		New Guinea	Cummins 1941.
P. visci	Loranthus, Viscum		S. Africa	Cribb 1955.

TABLE 5.—Uredinales reported on Loranthaceae

Rust	Mistletoe	Location	Reference	
Uredo phoradendri.	Phoradendron	U.S.	Arthur 1934; Hawksworth	
Uromyces circumspectus. U. euphlebius	Oryctanthus, Loranthus <sup>2</sup> Phoradendron	Chile, Trinidad Mexico	Dietel and Neger 1896. Sydow and Sydow 1920	
U, evastigatus	Phthirusa pyrifolia	El Salvador	Cummins 1939.	
U, loranthi U, nilagricus	Loranthus <sup>*</sup> Loranthus	Brazil India	Jackson 1927. Ramakrishnan and Ramakrish- nan 1950.	
U. ornatipes U. phtirusae	Phrygilanthus Phthirusa p <b>yrifolia</b>	Mexico South Amorica	Arthur 1915. Jackson 1927.	
U. socius	Loranthus <sup>2</sup> , Struthan-	Guatemala	Arthur 1918.	
L', urbanianus	Oryctanthus spicatus	Trinidad	Hennings 1897.	

TABLE 5.--- Uredinales reported on Loranthaceae--- Continued

Synonymous with Accidium loranthi Cooke, not A. loranthi Thum.
 The American mistletoes originally classed as Loranthus are now assigned to other genera.

# Mistletoes and Man

## AS USEFUL PLANTS

#### In Legend and Folklore

Mistletoes have long been credited with mystic powers. They have found their way into religious rites, mythology, healing arts, and superstitions throughout the world (Dengler and Dengler 1946; Feucht 1953; Fleming 1952; Frazer 1951; Muller 1939: Piper 1884; Randolph 1947). The aura of legend. symbolism, and magic that surrounds Viscum album of Europe has been the inspiration for countless writings most of which have been summarized and evaluated in a few comprehensive treatments (Bishop 1951; Kanner 1939; Tubeuf 1923). A paper by Gaultier (1938) is noteworthy for its reproductions of old illustrations of mistletoe in art and story. Some of the folklore attached to V. album has been transported across the Atlantic and vested in the North American Phoradendron flavescens and related species (French 1923; Pennsylvania Dept. Forests and Waters 1951), as well as in several South American genera (Santos Biloni 1946). The dwarfmistletoes (Arceuthobium spp.) have acquired little or no symbolism although Fernald (1900) says that long before A. pusillum was known to science, the women of the St. John and St. Lawrence River valleys wore sprigs of this tiny mistletoe in their hair while attending dances.

The Navajos used Arceuthobium vaginatum and A. campylopodum f. divaricatum in medicine (Vestal 1952). The Indian women of the southwestern United States drank a tea made of juniper twigs preferably bearing *Phoradendron juniperinum* to promote muscular relaxation prior to childbirth and also to hasten catamenia (Curtin 1947; Stevenson 1915). Extracts of the same mistletoe were also used for the treatment of warts (Wyman and Harris 1941).

The Aino people of Japan hold Viscum album (Yadorigi or Hoya) in veneration, especially when it grows on the sacred willow. It is regarded as a medicine for nearly all diseases. The leaves are often eaten by barren women to promote conception and chopped leaves are sown with crop seeds to promote fertility (Batchelor and Miyabe 1893).

In Malay village medicine, certain mistletoes are used as follows (Burkill and Haniff 1930):

1. Loranthus ferrugineus Roxb.—childbirth, snake bite, wounds, fever, and beri-beri.

2. L. pentandrus L.—childbirth.

3. L. grandifrons King-ringworm.

4. Elytranthe globosa (Roxb.) G. Don and Macrosolen cochinchiensis (Lour.) van Tiegh.—headache and childbirth.

Mistletoes are used as medicine by tribesmen in Australia (Blakely 1922-28) and other parts of the world (Baillon 1892).

## As Pharmaceutical Plants

In the early 18th Century, Sir John Colbatch (1719-20) stated that mistletoe was a "most wonderful specific remedy for the cure of convulsive distempers." He referred to Viscum album which has since left the realm of witchcraft, herbalism, and quackery to become an accepted pharmaceutical plant. An excellent well-documented account of this transition is given by Kanner (1939) who states that until the middle of the 19th century, the plant enjoyed a prominent place in the medicine and pharmacology of the day. It then fell into disrepute and was not used except as an external treatment for dermatitis (Riehl 1900a). Gaultier (1906) discovered a depressor action in its extract which restored its medical prestige in France and subsequently other European countries. Today, there are over 200 papers dealing with the pharmacology of V. album. Many of these papers do not mention the host although Bardier and Martin (1920) found great differences in the toxicity of aqueous extracts of V. album from spruce, apple, and poplar. When these were injected intravenously into rabbits and dogs the extract from mistletoe on poplar was much more toxic than those from the other two hosts.

Following is an abridged chronology of *Viscum album* in 20th century medicine and pharmacology:

1900-1910.—Depressor action of the extract was observed in human patients and demonstrated by injection into animals (Gaultier 1906; Gaultier and Chevalier 1907), and man (Gaultier 1910). Choline compounds were isolated from the extract (LePrince 1907). Therapeutic directions were formulated based on the demonstrated ability of the extract to (1) cause hypotension, (2) have diuretic action, (3) tone the cardiac muscle, (4) check hemorrhages, and (5) act as an antispasmodic with slight toxic qualities (Lesieur 1910).

1911-1928.—The therapeutic use of Viscum album increased in popularity (Barbieri 1912; Bonnamour and Niquet 1918; Cusmano 1919; Esser 1928; Gaultier 1912; Grossmann 1928; Holste 1928; Itallie et al. 1928; Kroeber 1922; Lestrat 1911; Selig 1912). However, clinical studies of 100 patients suffering from hypertension indicated that oral doses were ineffective (O'Hare and Hoyt 1928). Studies on the physiological effects on animals were continued into the next decade (Bijlsma 1926; Dossin 1911; Henze and Ludwig 1937; Jarisch and Henze 1937; Richter and Schröcksnadel 1938).

1929-1938.—Testimonies on the use of the extract for treatment of hypertension continued (Gaultier 1937). The extract was extended to the treatment of arteriosclerosis in persons exhibiting psychiatric symptoms as a result of hypertension (Baldauf 1936). Active principles were isolated and identified (Dressler et al. 1933; Ebster and Jarisch 1929). Dilute concentrations of sapogenin  $(C_{31}H_{60}O_3)$  were found in the blood stream following intravenous injections of the extract (Winterstein and Hammerle 1931). The element affecting blood pressure was thought to be a mixture of choline derivatives; propionyl—but not acetyl—choline was identified (Winterstein and Hammerle 1931). It was found that the mechanism causing reduced blood pressure in the hepatic vessel of cats was a reflex coming from both the vagus and sympathetic nervous systems following injection (Jarisch and Henze 1939). Reviews of the pharmaceutical literature were made (Janssen 1938; Jarisch 1939).

1939–1948.—Pharmacological studies on the chemistry and physiological effects of the extracts continued (Feuchtinger 1940; Jarisch 1941; Jarisch and Richter 1940; Richter 1940; Richter and Amann 1940; Winterfeld and Dörle 1942). Enders et al. (1940) demonstrated the presence of two pharmaceutical substances which affect (1) heart action and (2) blood pressure. The material affecting heart action is insoluble in common organic acids but is soluble in water, ether, and glacial acetic acid. Both are stable in acids and sensitive in alkali. Plenosol was recognized as a component of the extract (Drüen 1943; Giesbert 1942) and was considered to be useful in the treatment of rheumatic arthritis (Legel 1942) and cancer (Kraft 1940). It was demonstrated that oral doses were ineffective for reducing blood pressure in cats and rabbits (Enders et al. 1941).

1949–1958.—Efforts were made to extend therapeutic values to the treatment of inoperable cancer (Brück 1950, 1954). Chemical and physiological studies were continued (Hebrant and Goffart 1952; Winterfeld and Rink 1949; Zipf 1950). Sroka (1950) summarized the established medical facts but cited only the names of investigators without reference to their specific papers. Sajner and Veris (1957) isolated histamine and showed that it accounts for a large part of the hypotension action of this mistletoe.

The mistletoes other than Viscum album are of minor importance in medicine or pharmacology. Phoradendron is unimportant in the materia medica of the United States (Desantis and Lynn 1937). Some workers (Crawford 1911; Crawford and Watanabe 1914, 1916) claim that its extract caused a pressor action when injected into anesthetized dogs; others (Hanzlik and French 1924) claim a depressor action that should be useful in the treatment of uterine inertia and for obstetrical cases. One author (Thun 1943) claimed that *P. flavescens* contained no therapeutic principles, and others (Cary et al. 1924; Hyams 1898; Muenscher 1951; Pammel 1911) report that some persons, particularly children, have been poisoned from eating the berries.

On the basis of experiments with animals and clinical data, it has been said that the extract of *Phrygilanthus flagellaris* raised blood pressure and facilitated coagulation (Rojo 1929) and that it had useful veterinary proprietaries (Santos Biloni 1946, 1956).

Extracts of North American species of Arcenthobium were said to have a pressor action (Crawford and Watanabe 1916), whereas those of A. *axycedri* were claimed to have the same properties as Viscum album (Livon 1912).

## As Food and Fodder

Primitive peoples apparently used mistletoes as food to some extent. Blakely (1922-28) mentions this usage among the Australian tribes. *Phoradendron* berries were eaten by the Indians of the southwestern United States (Castetter 1935; Elmore 1944; Krochmal et al. 1954; Russell 1908).

The forage value of Viscum album is well recognized in Europe. It is relished by game animals (Tubeuf 1908, 1923) and has proved to be a nutritious food for livestock (Cerecelet 1948; Giniesis and Ray 1905; Letacq 1923). In the United States various species of *Phoradendron* have been successfully fed to hogs and cattle (Cary et al. 1924; Muenscher 1951). It has, however, been suspected of causing abortion in goats if eaten during the kid season (Baker 1903). *P. flavescens* on mesquite (*Prosopis*) is said to be a prized food for Texas cattle especially during the drouths and severe winters (Bowman 1947; Heald and Wolf 1912). The mistletoe is cut from the host trees and left on the ground for the cattle to eat. Bowman warns against the excessive eradication of mesquite for range improvement because of the insurance value of the mistletoe it supports.

Cattlemen of the Shasta Valley in California are said to have cut *Phoradendron* from juniper and fed it to their stock during severe years when other food was not available. This practice involved some danger as it was likely to cause abortion in pregnant cows.<sup>2</sup>

Various species of *Loranthus* in Australia and New Zealand are eaten by cattle, sheep, and camels (Blakely 1922-28; Hartigan 1958a; May 1941; Pescott 1946). In Turkey, a forest conservation problem has been created by stockmen who cut and waste trees in order to make mistletoe available to their herds. The trees suffering from this practice are oaks bearing *Viscum* and *Loranthus* and junipers bearing *Arcenthobium* (Acatay 1954).

Deer apparently relish mistletoe shoots. Their fondness for *Arccuthobium* in the southwestern United States is well known, although this seems never to have been mentioned in the literature. California Indians placed sprays of *Phoradendron* in strategic places to lure deer into favorable position for shooting (Barrett 1933).

*Phoradendron* is regarded as a fairly important honey plant in California and parts of Texas and Arizona (Coleman 1921; Oertel 1940; Richter 1911) especially as a winter source of nectar and pollen (Pellett 1926, 1947). The honey is said to be very sweet but gluey and hard to extract.

#### Miscellaneous Uses

In the north temperate zone, Viscum and Phoradendron are highly prized for winter holiday decorations (Harper 1928; Sher-

<sup>\*</sup> Personal communication from W. W. Wagener.

man 1910). This has often resulted in profitable local industry where mistletoes are abundant (Griffis 1956; Tubeuf 1923).

There is considerable interest in the culture of mistletoe as a garden curiosity, particularly *Viscum* in Europe and *Phoradendron* in North America. Propagation by seed is not difficult and various techniques have been suggested for the benefit of the home gardener (Gay 1856; Marriner 1951; Paxton 1901; Tubeuf 1923; Wyman 1949). In addition, there are a number of more technical contributions on the culture and propagation of mistletoes and other parasitic seed plants primarily for use in botanical gardens and scientific studies. Success has been obtained with both seeds and infected scion wood (Beer, 1951; Hedgcock and Hunt 1917; Heinricher 1907, 1910, 1913b, 1920b; Plateau 1908; Weir 1918b). Mistletoe culture on a commercial basis appears to be virtually nonexistent.

Viscum album has long been used for the manufacture of bird lime (Howard 1904) although there is very little call for the product today. Mistletoes are known to contain small amounts of caoutchouc (Fernandez 1947; Iltis 1911; Riehl 1900b) and some Venezuelan species have had limited use as commercial sources of rubber (Warburg 1905). Other mistletoes have been considered as sources of mucilage (Balavoine 1946; Weir 1921).

"Holzrosen" or wood roses (Tubeuf 1936) formed at the points of attachment of certain tropical loranths are sometimes sold as curios.

## AS DESTRUCTIVE PARASITES

The mistletoes are widely recognized as damaging agents to trees. Their victims include park and shade trees, horticultural plants, and forest crops. The degree of damage varies with the species of mistletoe, its longevity, and intensity of parasitism. Some of the short-lived tropical loranths invade only a local area of host tissue and at their worst cause premature death of relatively small branches distal to the point of infection. Intense multiple infections of this type may be quite damaging or even fatal to the host. The longer lived ones may virtually supplant the crown of the host and cause its untimely death (Docters 1954). The more parasitic forms typified by Arceuthobium and some of the Phoradendrons are characterized by a long-lived ramifying absorbing system that, once established, continues to sap its host as long as the tree can live. The production of aerial shoots is not necessary for the growth and development of these highly parasitic forms (Meinecke 1912; Wagener 1925).

The effects of mistletoes on their hosts may include any combination of the following: reduced vigor and growth rates, poor fruit or seed crops, malformation of the woody tissues, sparse foliage, top dying, predisposition to insect and other disease attack, and premature death.

Munns (1919) found that Jeffrey pines infected with dwarfmistletoe had smaller seeds than thrifty trees, also germination was 20 percent lower and the seedlings were not as vigorous. The reproductive value (yield per tree in pounds of clean seed  $\times$  number of clean seeds per pound  $\times$  final germination percent) of ponderosa pine heavily infected by *Arceuthobium* was only one-fourth that of uninfected trees (Korstian and Long 1922).

Excessive mortality in heavily infested forest stands may result in destructive soil erosion (Greenham and Brown 1957).

## In Europe

*Viscum album* causes damage to parks, boulevard plantings, orchards, natural forests, and plantations from the Mediterranean northward to Germany (Huberty 1900; Konig 1952; Letacq 1923; Tubeuf 1923). Apple is severely attacked but almonds and cherries also warrant protection from the parasite; losses are manifested in smaller fruit and lighter crops long before the trees reach an advanced state of decadence. In some areas the damage to ornamental and forest trees has been so severe that replacement with more resistant species has been necessary (Plagnat 1950b; Tubuef 1923). Pine forests in northeastern Germany have been damaged (Tubeuf 1923) and in France, Switzerland, and Yugoslavia fir forests and poplar plantations are injured (Klepac 1955; Lanternier 1944; Matagrin 1948; Peter-Contesse 1930, 1931a; Wraber 1948). Studies on the evaluation of loss in fir forests leave no doubt as to the ability of this parasite to materially reduce wood increment and quality (Peter-Contesse 1931b, 1937; Plagnat 1950a). In far northern Europe, V. album is not significant as a pest (Hoeg 1957).

The damage from Loranthus and Arceuthobium is unimportant. Viscum cruciatum attacks olive in the Mediterranean countries but apparently presents no serious horticultural problems (Tubeuf 1923).

## In Africa

Here the destructive mistletoes are mostly in the Loranthoideae. They are damaging to tea plantations in Nyasaland (Harler 1950), to citrus groves in the Belgian Congo (Staner 1929), and to park trees in Natal (Van der Bijl 1920).

## In Asia

Many broad-leaved trees in India are plagued by an imposing number of mistletoes (Brandis 1906; Kumar 1944; Rao 1920, 1923). Tea (Delacroix 1902; Kumar 1939; Narasimhan 1920; Singh 1954; Troup 1921), citrus (Sarma 1952), and mango are among the more important horticultural crops that require protection. Sal (De 1941, 1945) and teak (Koppikar 1948; Madras Presidency Dept. of Agr. 1942) plantations are attacked and heavy damage to mom oak has been reported (Rodger 1926). One commercial timber species in the Himalayas, *Pinus griffithii (P. excelsa*), is subject to severe losses due to *Arcenthobium minutissimum* (Bagchee 1952; Gorrie 1929; Parnell 1930). In Indonesia a large number of cultivated trees are attacked by species of *Loranthus* and related genera (Sands 1924). Among the more important crops affected are rubber (Brooks 1914a, 1914b; Petch 1921; South 1924; Steinmann 1925) and kapok (Grist 1923; Haan 1928) plantations.

In China and the Philippines, various species of Loranthoideae cause serious damage to citrus (Anon. 1911; Lin 1947; Philippine Island Dept. of Agr. and Natural Resources 1926; Reinking 1919, 1921; Teng 1938), Castanea, Camphora, Diospyros, Liquidambar, Psidium, and Pyrus (Chiu 1941). Both Loranthus and Viscum are damaging to plantations of lansome (Lansium domesticum) and lanutan (Bombycidendron vidalianum) in the Philippines (Sulit 1931).

### In Australia

Australia appears to have experienced increasing mistletoe damage in recent years (Coleman 1949, 1950; Hartigan 1960; May 1941). The genera include Loranthus (Amyema), Phrygilanthus, Korthalsella, Notothixos, and Viscum. Although fruit, forage, and ornamental trees are often severely damaged, the heaviest losses occur in commercial timber including the important native Eucalyptus spp. (Bidie 1875; Blakely 1922–28; Greenham and Brown 1957; Victoria Forests Comm. 1951; Wyborn 1947–48). Timber increment is reduced to 55 percent of normal when mistletoe supplants 38 percent of the crown (Nicholson 1955). Loranthus (Amyema) has been found on Pinus muricata and P. radiata (P. insignis) (Pescott 1946; Rawlings 1950) but does not presently pose a threat to these introduced timber species (Hartigan 1958a).

### In South America

In Brazil, the rubber tree (*Hevea brasiliensis*) is attacked by a number of mistletoes, of which *Dendrophthora porppigii* and *Phthirusa brasiliensis* are the most important (Bateson 1911; Weir 1926). Other Brazilian crop plants that are subject to mistletoe damage are cacao, citrus, mango, cashew, and avocado (Weir 1926). Although mistletoes attack a number of forest and horticultural trees in Argentina, they are not regarded as serious pathogens (Hauman and Parodi 1921; Hauman-Merk 1915). However, citrus crops in British Guiana are damaged by *Loranthus* (Bancroft 1915, 1918; Harrison et al. 1916), and *Phoradendron* sp. is a serious pest of coffee in Bolivia (Hauman-Merk 1915).

### In Central America, The West Indies, and Mexico

Severe damage to nurse trees of coffee plantations in El Salvador is caused by species of *Phoradendron*, *Phthirusa*, and *Struthanthus* (Alvarenga 1944). Avocado in Costa Rica is sometimes damaged by *Phoradendron* (Zentmyer 1952). Teak plantations and other economic trees in Trinidad are attacked (Nowell and Ulrich 1922; Trinidad and Tobago Forest Dept. 1954). Arcenthobium damages pine forests on Hispania. In Puerto Rico citrus and other economic species are attacked by Dendropemon (Phthirusa) (Stevenson 1917).

In Mexico, Arcenthobium sp. causes heavy losses in pine forests and Phoradendron attacks a number of hardwood trees (Roldan 1918, 1924; Sosa 1939) including avocado (Zentmyer 1952). Psittacanthus calyculatus (Loranthus calyculatus) is regarded as a damaging parasite of citrus (Gandara 1910).

## In the United States and Canada

The losses caused by Arceuthobium are of serious consequence to forestry in the western parts of this region where conifers constitute the main commercial species (Bier 1949; British Columbia Dept. of Lands and Forests 1951; Gill 1935, 1953a, 1953b; Gill and Bedwell 1949; Hedgcock 1913, 1915; Jack 1900; Kimmey 1957; Kuijt 1955; Leiberg 1900; Weir 1918a; Weir and Hubert 1918).

Pinus ponderosa is plagued with two species, Arceuthobium vaginatum and A. campylopodum f. campylopodum, both of which are among the more serious diseases of that tree. A. vaginatum occurs in the southern and eastern parts of the ponderosa pine range, coinciding generally with P. ponderosa var. scopulorum except that it does not extend north or east of Colorado (Andrews 1957; Gill and Hawksworth 1954; Korstian 1925; Korstian and Long 1922; Krauch 1926, 1930; Pearson 1912, 1923, 1939, 1940, 1950; Pearson and Marsh 1935; Pearson and Wadsworth 1941; Perry 1922; Sperry 1934; Woolsey 1911). A. campylopodum f. campylopodum is found in the western and northern range of the host but is of no consequence east of the Bitterroot Mountains (Cooper 1906; Kimmey and Mielke 1959; Munger 1917; Weidman 1936).

Western hemlock, Tsuga heterophylla (Raf.) Sarg. is damaged by Arceuthobium campylopodum f. tsugensis throughout its commercial range (Allen 1902; Buckland and Marples 1952; Kimmey and Stevenson 1957; Wellwood 1956). In addition to the direct effects of parasitism this dwarfmistletoe creates courts of entry for heartrotting fungi (Englerth 1942; Foster et al. 1953, 1954). A. campylopodum f. laricis causes heavy losses in western larch, Larix occidentalis (Weir 1916a). A. campylopodum f. abietum is widespread on Abies concolor and Abies magnifica in California but is relatively harmless to fir elsewhere (Kimmey 1957; Oosting and Billings 1943). Douglas-fir, Pseudotsuga menziesii is attacked by A. douglasii which is practically specific to that host. Lodgepole pine, Pinus contorta, and jack pine, P. banksiana, are damaged by A. americanum (Gill 1957, Hawksworth 1958a, 1958b; LeBarron 1948; Mason 1915; Nordin 1954; Riley 1948, 1951; Weir 1915a).

In the northeastern United States and southeastern Canada, black spruce, *Picea mariana*, in bog sites is attacked by *Arceuthobium pusillum* (Anderson 1952; Anderson and Kaufert 1953, 1959; Bernard 1957; Faull 1908; Freeman 1905; Gifford 1901; Lorenz 1937; Pomerleau 1942, 1945). Phoradendron does not occur in Canada but in the United States there are several species that damage both hardwoods and conifers. *P. flavescens*, the distribution of which is given on page 31, is damaging to native trees only in the western parts of its range (Bray 1910; Crozier 1877; Perry 1923; Schrenk 1914) but is reported as a disease of pecans in Florida (Matz 1918; Weber 1938) and of citrus in Texas (Edson and Wood 1936). In California it is troublesome in walnut groves (Graser 1952, 1954) and persimmon orchards (Condit 1940). Other species of *Phoradendron* sometimes reach damaging intensities on fir, juniper, incense cedar, and a number of desert shrubs (Gill 1953a; Rose and Standley 1912).

#### MISTLETOE CONTROL

Control of mistletoe has been advocated and frequently practiced throughout the world where the parasites were damaging trees and shrubs of economic or esthetic value. The principles on which direct control measures have been developed include (1) physical removal of infected trees or their parts by pruning, poisoning, or burning, and (2) chemical treatments designed to kill the endophytic system. Control of either vectors or pollinators has been suggested but presumably has never been practiced (Ali 1931; Davidson 1945; Haan 1928). Natural resistance has been considered but thus far has not been used for control (Bates 1927; Gäumann and Peter-Contesse 1951; Paine 1950; Pearson 1944). Biological control by fungi and insects has been suggested (Mielke 1959; Wyborn 1947-48) but is without practical application as yet; its potentials are discussed in more detail in the section "Factors Affecting Mistletoe Occurrence." Finally, quarantines should be effective in preventing the inadvertent introduction of a dangerous mistletoe into new territory.

In an unpublished release, Dr. J. S. Boyce<sup>\*</sup> has pointed out the danger of introducing Viscum album into the United States because of its demonstrated ability to attack American trees and because it is so similar in appearance to Phoradendron flavescens that it could easily escape unnoticed, until it is well established. Kreh (1958) reports Viscum album on seven tree species foreign to Germany. Spaulding (1956) lists V. album on 23 American tree species planted in Europe and reports (1953) P. flavescens on five exotics planted in the United States.

### Physical Removal

Control of mistletoe by forest management and silvicultural practices that will result in physical removal of the parasite has been advocated since the early part of the century (Bagchee 1952; Freeman 1905; Korstian and Long 1922; Meinecke 1914, 1916,

<sup>&</sup>lt;sup>3</sup> Boyce, J. S. Notes on tree diseases in western Europe. Unpublished report. Yale Univ. and U.S.D.A. Bur. Plant Indus., Div. Forest Pathology. 59 pp. 1950.

1925, 1931; Parker 1942; Perry 1922; Troup 1921; Weir 1915a, 1915b, 1916a, 1916b, 1916c, 1918a, 1923; Weir and Hubert 1918, 1919). In western North America efforts against *Arceuthobium* were at first limited to the removal of the worst infected overstory trees in the course of logging operations. Under partial cutting systems with long cutting cycles, the practice had little beneficial effect except perhaps to establish a consciousness of the parasites among foresters.

Since the 1930's, action against dwarfmistletoe has become more aggressive partly because more intensive management and silvicultural practices are being followed, partly because research has provided more specific guides for practicing control (Anderson and Kaufert 1953; Andrews 1957; Buckland and Marples 1952; Dowding 1929; Gill 1954, 1957; Gill and Hawksworth 1954; Hawkworth 1958a; Kimmey 1957; LeBarron 1948, 1952; Parker 1924; Pearson 1950; Roth 1953, 1954), and partly because the economic importance of the pests has been crystallized in special surveys and general papers dealing with the subject (Gill 1953a, 1953b; Gill and Bedwell 1949; Hawksworth 1958a; Hawksworth and Lusher 1956; Kimmey and Stevenson 1957; Riley 1951). At this writing the control of dwarfmistletoe is an important activity on many forests in the western United States.

Spread and intensification of *Arceuthobium* is accomplished primarily by explosive fruits rather than by animal vectors. Therefore, once the parasite is eradicated or materially reduced in an area, there is no practical problem of reinfection from the outside.

Removal of *Loranthus* and related species by pruning has long been practiced in tropical horticulture and forestry (Ali 1931; Altona 1929; Ayliffe 1949; Davidson 1945; De 1941; Haan 1928; Koppikar 1948; Madras Presidency Dept. of Agr. 1942; Mathur 1949; Rao 1920; Sarma 1952; Stevenson 1917; Troup 1921; Tunstall and Sarmah 1947; Wyborn 1947-48). Since birds constantly carry seed into the orchards, plantations, or forests to be protected, control involves a continuous process of removal and must often extend far beyond the boundaries of the area to be protected. Flames have been used to destroy the parasites in lieu of pruning them (Anon. 1949; Coleman 1949).

There has been no great effort to reduce *Phoradendron* in the northern hemisphere, though pruning techniques have been described (Bray 1910; York 1909). Removal from some orchards is practiced (Weber 1938) and is recommended for rubber plantations in South America (Weir 1926). In recent years there has been a growing interest in reducing *Phoradendron* in the arid southwestern parts of the United States where certain desert shrubs and trees of high esthetic value are severely damaged (Gill 1953a). Because of its unique habit and its value for holiday decorations, the public is usually more concerned with the preservation than the reduction of *Phoradendron*.

A similar attitude toward *Viscum album* exists in Europe. The plant is highly regarded by most people and no large scale efforts

have been made to control it. Tubeuf (1923) did not consider it as a particularly damaging agent in the German forests but Peter-Contesse and others have pointed out the need for silvicultural control in Switzerland and France (Anon. 1934, 1948; Cercelet 1948; Gäumann and Peter-Contesse 1951; Matagrin 1948; Peter-Contesse 1930, 1931a, 1931b, 1937; Piagnat 1950a, 1950b).

## Chemical Control

The greatest progress in chemical control of mistletoe has been made in Australia where sprays and injections of various chemicals. particularly formulations of 2,4-D have been successful in killing Loranthus (Amyema) and related genera, mainly on Eucalyptus (Anon. 1954; Australia Council for Scientific and Industrial Research 1946-47; Australia Forestry and Timber Bureau 1949, 1953, 1954, 1957; Greenham et al. 1951; Hartigan 1949, 1953, 1958a; Nicholson 1955; Wyborn 1947-48).

In recent summary of this work, Greenham and Brown (1957) came to the following conclusions:

1. Injections with triethanolamine salt of 2,4-D killed 70 to 100 percent of the mistletoes (particularly  $Amyema \ pendula$ ) growing on several species of *Eucalyptus*. The treatment may cause partial defoliation and about 5 percent of the hosts may die.

2. About one-half the parasites 2 years after treatment may be killed by a second treatment. A single treatment causes no marked changes in resistance to 2,4-D in either the host or parasite.

3. Treatment of individual trees or groups is not satisfactory because reinfestation rapidly occurs, thus 80 percent kill would be as effective as 99 percent.

4. The treatment of large areas is a practical possibility with a small capital investment.

In their published work, Greenham and Brown (1957) used diameter alone for calculating dosages. Recent experiments ' indicate that a more effective mistletoe kill can be obtained where crown size is also taken in account, i.e. trees with small crowns receive a substandard dose for their diameter and vice versa. Promising results ' have also been obtained with MCPB (4-chloro-2-methyl phenoxybutyric acid) which may facilitate mistletoe control in hosts subject to injury from 2,4-D.

Hartigan (1949, 1953, 1958a) reports successful killing of *Amyema* with sprays of 2,4-D but recommends its use only on *Eucalyptus* and related genera, since other hosts appear to be damaged by the hormone. His experience with injections was less successful than in the work reviewed above (Hartigan 1958b), but he did not follow the recommended techniques exactly (Greenham and Brown 1959).

In India. Loranthus pulrerulentus was successfully controlled by injections of CuSO<sub>1</sub> and Feroxone into the host (Kadambi 1954), but tests with NH<sub>1</sub>-sulfamate,  $K_2Cr_2O_7$ , CuSO<sub>4</sub>, 2,4-D (Na salt) and 2, 4, 5-T (K salt) when used as sprays did not provide

<sup>&#</sup>x27; Privately communicated; released with permission of Mr. C. G. Greenham.

a basis for recommending them as control agents (Seth 1958). They were either ineffective or caused damage to the host except that concentrations of 0.5 percent 2,4-D in two applications one month apart or a single 1 percent solution killed *Dendrophthoe* falcata in 5 months. D. falcata was killed by spraying with 30 percent diesel oil emulsion during periods of high temperature. Higher concentrations were needed to kill the parasite at low temperatures (Singh 1959).

In North America, sprays applied during the dormant period of the host have been successful in controlling *Phoradendron* in California walnut groves (Graser 1952, 1954). A number of chemicals have been tested for the control of *Arceuthobium* but none have proved to be satisfactory (Bourchier 1954a). Research is active in this field today and several workers are engaged in basic studies of host-parasite physiology in an effort to develop a differential chemical.

The application of chemicals, particularly carbolineum, to mistletoe-infected stems and branches has met with some success (Bryce 1920; Molz 1909). Milder preparations such as asphalt paint followed by wrapping of the infected area with burlap have killed the endophytic system of *Phoradendron flavescens*, although neither the paint nor the wrapping alone were successful (Bray 1910). These treatments have proved to be too costly and cumbersome for wide use. Observations in Arizona indicate that the aerial parts of *Phoradendron* on juniper may be killed over large areas exposed to smelter smoke (Long 1922) and fluoride fumes are known to be highly toxic to *Viscum album* (Holland 1910). There appear to have been no attempts to control mistletoe by fumes.

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