27 Hop

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The female inflorescence of hop, *Humulus lupulus* L., is used to flavor fermented malt beverages. This practice dates back to the Middle Ages and probably earlier, when large quantities of dried hops were added to malt beverages mainly for preservative purposes. Today, hops are used primarily for flavoring, and the hop dosage is considerably less than it was in ancient times.

Hop is native to Europe, Asia, and North America (Small, 1978). Wild hop plants are found in many parts of the world, but commercial hop production is generally limited to areas between 30° to 52° latitude. The hop plant is sensitive to day length and generally produces poor yields in latitudes too close to the equator. Due to environmental and economic factors, commercial U.S. hop production is presently confined to certain areas in Washington, Oregon, Idaho, and California. The United States presently ranks first in hop production worldwide, closely followed by West Germany. Over 50% of the United States crop is exported annually to more than 70 different countries.

I. PARENTAL MATERIAL

Taxonomists differ in classifying the genus *Humulus* (Burgess, 1964; Davis, 1957; Small, 1978). Most, however, place hop into the *Cannabaceae* (formerly *Cannabinaceae*) family. This family has two genera, *Humulus* and *Cannabis*.

The genus *Humulus* includes two major species, *H. lupulus* L. (common hop) which has $2n = 20$ ($x = 10$) chromosomes and *H. japonicus* Sieb. et Zucc. (Japanese hop) which has a chromosome complement of $2n = 16$ ($x = 8$) in the female and $2n = 17$ in the male. *Humulus lupulus*, a perennial, is the hop used by the brewing industry. *Humulus japonicus* is an annual that produces only a few resin glands and has no brewing value. Attempts to cross the two species thus far have been unsuccessful.

Common hop is dioecious. Male and female plants have a similar growth habit, but differ markedly in their floral structure (Fig. 1). Occasionally a monoecious plant is found at the diploid and, more frequently, at the polyploid level.

Aneuploids, triploids, and tetraploids are found occasionally in segregating populations, particularly among the seedling progeny of triploids (Haunold, 1970). Polyploids generally resemble diploid hops, except for reduced vigor in some primary trisomics and tetraploids and increased vigor in most triploids.

Research centers that maintain collections of hop germplasm are located at

Dep. of Crop Science, Oregon State Univ., Corvallis, Or.
Dep. of Hop Research, Wye College, Univ. of London, England
German Society for Hop Research, 8069 Hüll, West Germany
Institute for Hop Research, 63310 Žalec, Yugoslavia
Institute for Hop Research, 21470 Bački Petrovac, Yugoslavia
Hop Research Institute, 438-46 Žatec, Czechoslovakia
Institute for Hop Research, Zhitomir, Ukraine, USSR

Other hop research centers are located in Argentina, Australia, East Germany, India, Japan, Mexico, New Zealand, Poland, South Africa, and Spain.

II. PLANT CULTURE

A. Field

The perennial root stock (crown) of *H. lupulus* in early spring produces annual vines from buds below the soil surface. The vines climb a supporting pole or string by twining clockwise to heights of 6 m or more (Fig. 2).

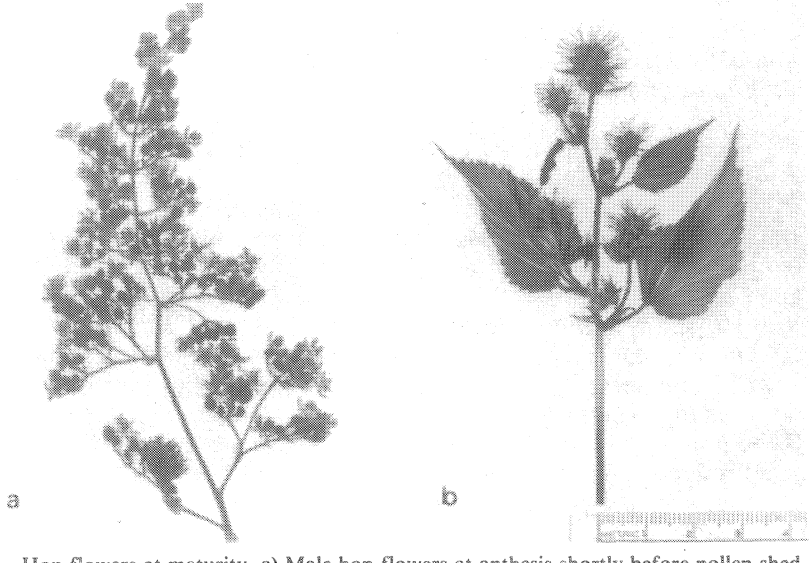

Fig. 1—Hop flowers at maturity. a) Male hop flowers at anthesis shortly before pollen shedding. b) Female hop flowers at the burr stage with receptive stigmas protruding from individual florets. A sidearm of high-yielding cultivars may have over 100 burrs.

Hooked hairs on the leaf petiole and on the main stem aid the climbing process. Depending on the cultivar, flowering occurs in late June to mid-July, at which time male and female plants can be identified.

Hop is adapted to various climates and soil types. Due to the high value of the crop, the choicest agricultural locations are usually selected for hop gardens. They may be well-drained, river bottom soils or alluvial soils of various texture and origin (Brooks et al., 1961; Burgess, 1964).

The hop plant develops an extensive root system. Perennial woody roots frequently penetrate to a depth of 4 m or more. They are supplemented by annual secondary roots near the soil surface, which are formed from perennial roots or from annual vines in late spring or early summer after hilling operations.

The above-ground parts of the plant die during the winter, but crowns that are well covered by soil or snow can tolerate temperatures of −25 C or lower. For optimum spring growth, crown buds require exposure to temperatures below 5 C for at least 4 to 5 weeks.

Soils in most hop growing areas of the United States are neutral or slightly acidic (pH 6 to 7), but occasionally slightly alkaline soils are encountered where hops also grow well (Brooks et al., 1961).

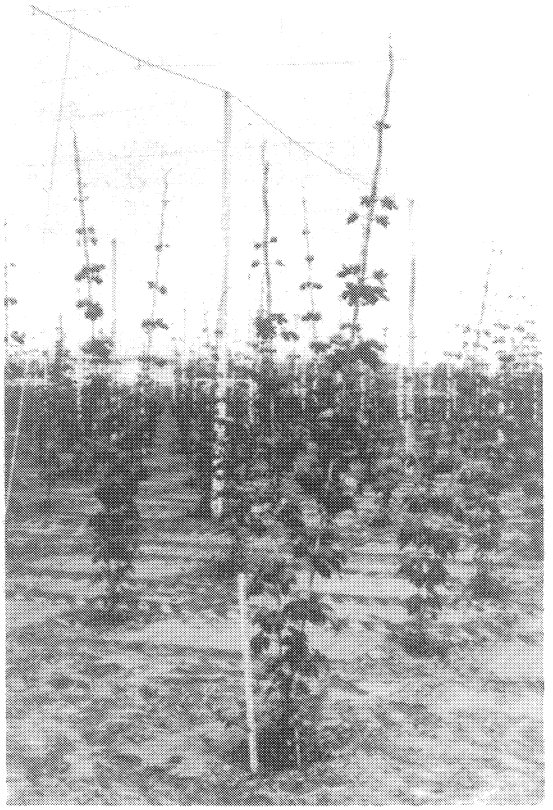

Fig. 2—Hop shoots in early June, about 1 month after training. A yardstick (91 cm) is in the foreground. Sidearms (not yet visible) develop from axillary buds at the stem nodes. Floral initiation takes place at about this stage of growth.

An average American hop crop of about 2,000 kg/ha of dried hop cones, produced on plants that average 5.5 m in height, removes a considerable amount of nutrients from the field. This nutrient loss generally is replaced with commercial fertilizers such as 18:18:18 (NPK) at up to 670 kg/ha before the start of spring operations. Liming with about 6,700 kg/ha of agricultural lime and green manuring with rye, wheat, barley, or ryegrass-vetch mixtures during the off season is used occasionally. Subsequent fertilization may include up to 220 kg/ha of N, applied as either anhydrous ammonia, ammonium sulfate, ammonium nitrate, or urea. Trace elements such as sulfur, boron, zinc, iron, and manganese are applied occasionally.

Growth hormones such as gibberellic acid (GA_3) generally do not stimulate higher hop yields, except for relatively low-yielding cultivars such as 'Fuggle' (Zimmermann et al., 1964; Hartley and Neve, 1966; Thomas, 1970; Thompson and Thomas, 1970). American growers supplement the available soil moisture by artificial irrigation of up to 900 mm during the summer months.

Most commercial hop yards in the United States are planted to permit cross cultivation. Plant spacing may vary from 1.8 × 1.8 m to as wide as 2.4 × 2.4 m, but a 2.1 × 2.1 m or 2.3 × 2.3 m spacing is commonly used, resulting in 2,200 or 1,915 plants/ha, respectively. In early spring, two or three strings are attached to the overhead trellis wires and to the plant below the center of the crown, forming a 'V'-shaped structure for hop shoots to climb (Fig. 2).

Normally two or three shoots are hand-trained on each string in late April or early May. Most remaining basal shoots are removed by hand and later by chemical suckering agents such as dinoseb (2-*sec*-butyl-4,6-dinitrophenol) or paraquat (1,1′-dimethyl-4,4′-bipyridinium ion). In Germany, plant spacing within rows is considerably closer than that used in the United States. Distances between rows may be as close as 1.6 m, and typical plant spacing within rows may vary from 0.9 to 1.4 m, resulting in over 4,000 plants/ha (Kohlmann et al., 1969).

Floral initiation takes place in late May to early June in the northern hemisphere which prompted Thomas and Schwabe (1969) to classify hop as a short-day plant. Flowering of male and female hops, however, occurs during the longest summer days at photoperiods normally exceeding 16 hours per day. Supplemental light for about 5 weeks during the period of floral initiation in the field can dramatically increase cone production (Umeda et al., 1967). The physiological effects of supplemental lighting resemble those caused by gibberellic acid, except that they apparently are not restricted to certain cultivars.

Hop cultivars are usually derived from one seedling plant that was vegetatively propagated; thus, all daughter plants are genetically identical to the mother plant. There is apparently no limit to the number of times a hop plant can be vegetatively propagated. Some commercial hop cultivars still in production today date to the latter part of the 19th century. From a practical standpoint, most hop gardens are removed after 30 to 40 years of production and are replanted after several years of intercropping.

Hops are normally propagated asexually by several methods.

1. Division of the Woody Rootstock

The perennial rootstock (crown) is split into a number of pieces, each with at least one bud. One may get from 5 to 50 propagules from a well-developed crown, depending upon its size.

2. Rhizome Cuttings

Rhizomes develop from shoots that are layered intentionally or are accidentally covered by soil, or from shoots that grow underground and emerge late or fail to break through the soil surface. They may be from 5 to 20 mm in diameter and from 20 to 100 cm long with several buds at each node. Rhizomes are pruned close to the mother crown and are cut into pieces of about 8 to 15 cm in length for field planting. Smaller pieces may be started in greenhouse pots.

3. Soft Wood Cuttings

A vegetative shoot can be cut into small sections composed of at least one pair of leaves and a 5 to 8 cm long stem. The sections may be placed into a mist chamber (Howard, 1965). In 1 to 2 weeks, small roots develop on the stem embedded in the sand and axillary buds start to elongate. Root development can be enhanced considerably by supplementing the carbohydrate resources of the cuttings with additional sugars (Howard and Sykes, 1966) or by treating the basal portion of the cutting with a commercial rooting hormone. Soft wood cuttings may also be placed overnight at 2 to 4 C into a rooting solution composed of 20 ppm indolebutyric acid and 20 ppm boric acid and transferred to the mist bed the next morning, or stems may be dipped briefly in a concentrated solution (about 1,000 ppm) of indolebutyric acid before planting.

B. Growth Chamber and Greenhouse

Except for special purposes such as disease testing, growth chambers are impractical for growing hops. The plants climb to a height of several meters before flowering, which necessitates tall growth chambers.

Hops can be grown successfully from late winter to early fall in greenhouse pots or in a greenhouse soil bed. Extending the day length to about 16 hours by artificial illumination from incandescent or fluorescent lights assures normal development and vigorous growth during early spring. During the winter it is difficult to keep hop plants in an actively growing state even with adequate illumination. Therefore, plants are best moved to cold frames or suitable hardening chambers to experience at least 5 to 6 weeks of near-freezing temperatures. The root stock may also be removed from the pots and be stored at 3 to 5 C.

The temperature requirements for greenhouse-grown hops are not critical. Typical greenhouse temperatures of about 20 to 25 C during the day and 15 to 18 C during the night are ideal, but lower night temperatures or substantially higher day temperatures do not seriously impede plant development.

Due to the dense foliage and luxuriant growth, insect control may be a problem with greenhouse-grown hops. Commercial fumigants or sprays used on other greenhouse plants are generally recommended. The most common pests are two-spotted spider mites (*Tetranychus urticae* Koch), white flies (*Trialeurodes vaporariorum* Westw.), and aphids (*Phorodon humuli* Schrank), listed in order of their difficulty to control. Diseases are rarely a problem in the greenhouse. Powdery mildew (*Sphaerotheca humuli* (DC.) Burr.) is unknown in the western U.S. and propagules infected with downy mildew (*Pseudoperonospora humuli* Miy. et Tak., G. W. Wils.) can be easily recognized and discarded.

III. FLORAL CHARACTERISTICS

Common hop is dioecious. Lateral branches, called sidearms, develop from axillary buds on the main stem of male and female plants in late June. Under field conditions, sidearms may reach a length of 50 to 200 cm each,

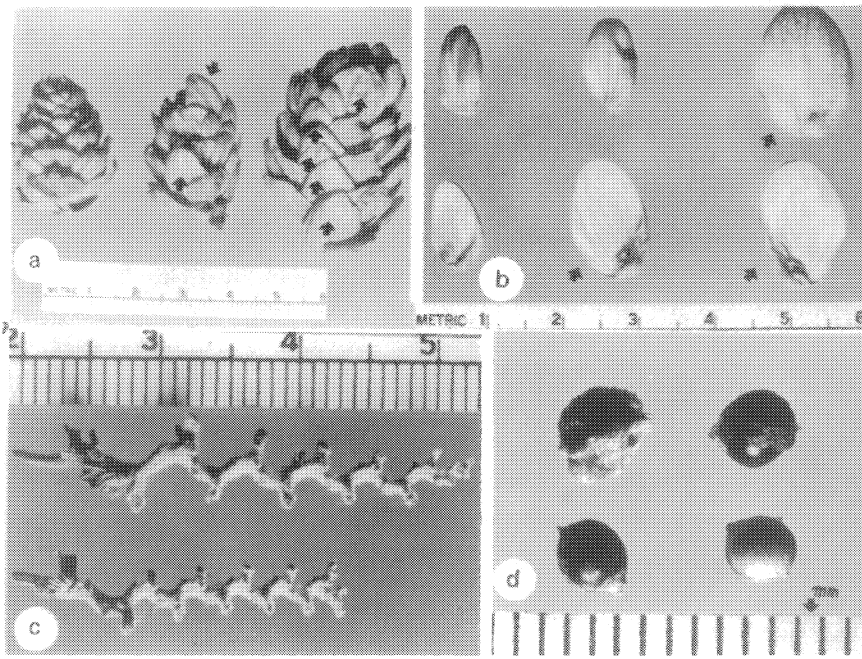

Fig. 3—Seed stage. a) Seeded hop cone (right), seedless cone (left) and partially seeded cone (center) from the same plant (scale in cm). Note larger size of seeded cone and of seed bearing bracteoles (arrows). b) Seed-bearing (arrows) and seedless bracteoles, dorsal view (top) and ventral view (bottom). Note residual stigma attached to the seed, lower right. c) Rachis (strig) of a seeded cone (top) and a seedless cone (bottom) from the same plant. Note differences in size and internode length; both strigs have an identical number of nodes. d) Hop seed with perianth and resin glands (upper left); dark seed coat of well-developed seeds from pollination by different males, with perianth partly removed (upper right and lower left); and tan, non-functional seed, containing an aborted embryo (lower right).

depending on the cultivar. Early development due to loss of apical dominance from mechanical or insect damage to terminal buds is undesirable, because such plants frequently fail to climb properly. On well-developed plants under a 5.5 m trellis, flowering of males or females generally starts on sidearms at nodes about 2.5 to 3 m up the main stem and gradually proceeds toward the top and bottom of the plant.

The mature female inflorescence is a strobile or cone with a zig-zag-shaped rachis known as a strig or core, and two types of small, oval leaf-like structures, the bracts and bracteoles (Fig. 3a,b,c). Two bracts and four bracteoles are found at each strig node (Davis, 1957; Burgess, 1964; Romanko, 1973). They are attached to short pedicels in such a way that in mature cones one bract partly overlaps the base of two bracteoles. The bracteoles produce small, yellow resin glands called lupulin or lupulin glands, primarily at the base where a small pocket is formed and where the seed develop (Fig. 3b,d). Lupulin galnds contain the resins and essential oils values by brewers. The outer seed coat is maternal tissue (perianth), and it, too, is frequently covered with resin glands. Bracts generally carry few, if any, resin glands.

The young receptive inflorescence is 5 to 10 mm in diameter and is composed of 20 or more florets (Fig. 1b). Individual florets consist of a cup-shaped perianth enclosing an ovary and two papillate stigmas that are 3 to 5 mm long. When the stigmas are fully developed, the female inflorescence is called a burr, because of its spiney appearance (Fig. 1b). Female flowers usually develop on secondary and tertiary branches of sidearms and on the upper terminal part of the main shoot, in clusters of 5 to 10 flowers.

Male flowering branches resemble a panicle (Fig. 1a). Male flowers also develop on secondary and tertiary branches of sidearms and on the terminal portion of the main stem. Each flower is 3 to 5 mm in diameter, containing five sepals and five anthers of similar size. All anthers usually are at a similar stage of development and they have comparable pollen-shedding potential. Male flowers produce a small amount of resin glands on the outer side of the sepals and in the furrow of the anthers. Before anthesis, the filament elongates to about 2 to 4 mm. The anther, about 2 mm in length, dehisces in favorable weather by forming a longitudinal slit on each side to release pollen.

Male plants in our germplasm collection frequently start pollen shedding 1 to 2 weeks later than the earliest-blooming females and continue to shed pollen for about 10 to 15 days. Flowering of male or female hop plants occurs from late June through July, depending on the genotype. Pollen, distributed by wind, may travel over distances of several kilometers without loss of viability. If no male plants are present, female flowers remain receptive up to 3 weeks before stigmas begin to drop off. Pollinated flowers develop slightly faster than non-pollinated flowers. However, several days after pollination, freshly pollinated hop flowers appear unchanged from non-pollinated flowers.

Pollen shedding depends on environmental conditions and particularly on air temperature and relative humidity (Brooks and Puri, 1963; Burgess, 1964). Male sidearms frequently have several hundred flowers that may produce from 2 to 5 cm^3 of functional pollen. In Oregon, two stages of pollen shedding are frequently observed, a major one in mid-morning and a second one in late afternoon.

IV. ARTIFICIAL HYBRIDIZATION

A. Equipment

Various types of bags can be used to protect receptive female flowers from open pollination. Bags should be at least 50 cm long and from 15 to 25 cm in diameter to accommodate at least one well-developed sidearm. White, translucent, parchment paper bags or plastic-coated paper bags, similar to those used by bakeries for French-bread wrapping, are ideal. Brown paper bags or special pollinating bags with a clear window are also suitable. Other equipment needed to pollinate females includes a plier-type stapler for securing bags around the sidearm, a 3 to 4 m stepladder, scissors, marking pen with waterproof ink, adhesive tape, an apron to hold paper bags and tools, plastic snap-on marking tags, brightly colored flagging tape, waterproof glue, and cheesecloth for temporary shading.

Pollen can be collected in paper bags directly in the field. When many males have to be visited, the equipment for routine operations includes round clear plastic cylinders, 14 × 45 cm or larger, open on both ends; rimless test tubes, 3 × 20 cm; rubber tubing, about 60 cm long; a bank of fluorescent lights, 4 × 20 W each; a squeeze bottle; a desiccator with saturated calcium chloride ($CaCl_2 \cdot 6\ H_2O$) to maintain 35 to 40% relative humidity at 3 to 5 C; glass shell vials, 15 × 80 mm; cotton; a roll of smooth wax paper; two wooden dowel sticks or metal spatulas, about 45 cm long; 70% alcohol; a refrigerator; adhesive tags; and a syringe, about 1 cm in diameter, with a needle of about 0.5 mm inner diameter.

Fig. 4—Bagging of female sidearm before pollination.

B. Preparation of the Female

Protection of female flowers from outcrossing can be done by planting one or more females in an isolated location. The area should be evaluated for natural seed set and volunteer males must be removed. Bags can also be used to protect females from outcrossing. A vigorous, well-developed female plant of the desired genotype is selected. The plant should have no more than two shoots trained on each string. Before bagging, sidearms should have growth sufficient to distinguish individual flower clusters; however, stigmas should not be visible. One of the opposing sidearms, usually higher than 2.5 m from the ground, is pulled or cut from the main stem. The remaining sidearm is prepared for bagging by removing most leaves. The two large leaves at the main node of the stem are also removed. The sidearm is trimmed to about 50 to 60 cm in length, so that it has two to three nodes and four to six secondary branches. Such a sidearm will provide up to 100 female flowers, each composed of 20 or more florets. The potential seed set per sidearm, therefore, may vary from less than 500 to over 2,000 seeds. In practice, a single pollination produces about 200 to 400 seeds per sidearm. The open end of the bag is folded around the main stem, and is closed with a plier stapler (Fig. 4).

Sidearms should be bagged at least several days before the first florets are receptive. Bagging retards floral development slightly; depending on temperature and weather, it may be up to 1 week or more before flowers become receptive.

Terminal flowers on lateral branches usually are the first to become receptive. They frequently are also the largest burrs. The basal and central florets on each burr are usually receptive first, and late-developing florets near the top of each inflorescence may become receptive up to 1 week later. Additional flowers on lateral branches reach the receptive stage over a 2 to 3-week period and protective bags must remain in place until miniature cones begin to develop and receptive stigmas are no longer visible.

C. Pollination

Paper bags may be placed over pollen-shedding sidearms to collect pollen; however, pollen clings to the inside wall of the bags and is difficult to gather without contamination. A procedure developed at Oregon has been used to collect hop pollen from many genotypes in a relatively short time (Haunold and Zimmermann, 1974). One or two sidearms at anthesis are severed from the selected male plant. The basal stem portion of the sidearm is placed in tap water in a test tube that had been taped inside a plastic cylinder (Fig. 5). A piece of rubber tubing is placed in the test tube extending over the top rim of the cylinder to permit addition of tap water to the tube from a squeeze bottle. The cylinder is placed on a clean piece of wax paper. The top of the cylinder is covered with a paper bag to prevent pollen drift and contamination from adjacent cylinders. A bank of fluorescent lights is placed behind the cylinder for continuous illumination.

Many anthers have dehisced the morning after the sidearm was collected, but lack of wind or vibrations prevents them from shedding most of the pollen. The paper bag on top of the cylinder is carefully removed and the sidearm is gently tapped with a long spatula or a wooden stick. A large amount of pollen is released immediately and rapidly settles on the collection sheet. The portion of the collection sheet outside the cylinder is wiped with a sponge moistened with 70% alcohol. The tapping tool is sterilized in a similar manner. After a few minutes, all pollen has settled and the cylinder is carefully removed. Small insects and plant debris, such as anthers and sepals, are removed with tweezers. Pollen is scraped to one side of the collection sheet with the smooth edge of a piece of plastic or stiff paper and is transferred to a glass vial, which is stoppered with a cotton plug.

One collection from a fresh sidearm usually yields from 1 to 3 cm^3 of pollen. The cylinder is rinsed with hot water and with 70% alcohol. Test tube and rubber tubing are cleaned in a similar manner and set aside to dry. Pollen vials are marked and stored at 2 to 4 C in a desiccator over saturated calcium chloride. Under such conditions, hop pollen remains viable for several months.

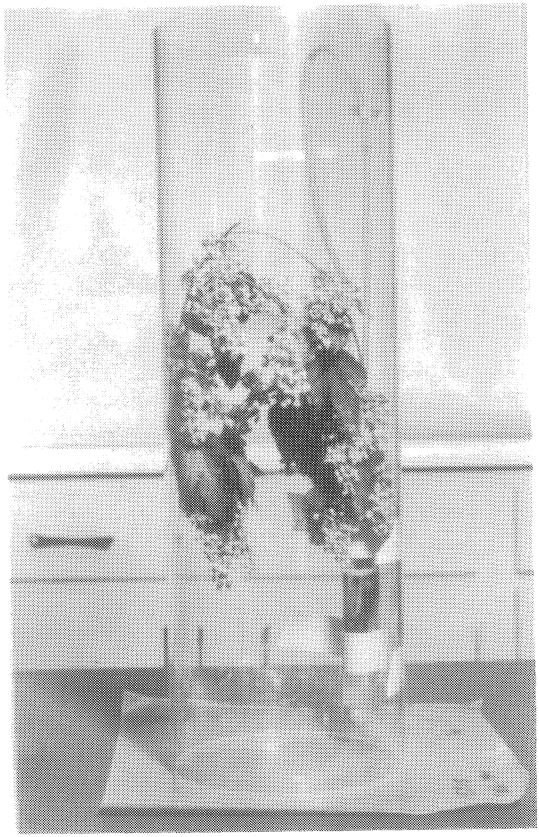

Fig. 5—Male sidearm at anthesis, showing setup for pollen collection in the field laboratory.

For controlled pollination, a small amount of collected pollen or a small sidearm with flowers at anthesis is placed into the bag enclosing receptive female flowers. The bag is closed and the pollen is dispersed by agitation.

Pollination can also be accomplished without opening the bag (Haunold and Zimmermann, 1974). About 0.3 to 0.5 cm^3 of pollen is drawn from the storage vial into a small hypodermic syringe. The needle is inserted directly through the wall of the bag to deposit the pollen (Fig. 6). With the transluscent bags described previously, one can see the pollen dropping into the bag. The needle hole is covered with adhesive tape or a bead of glue and the bag is agitated gently to disperse the pollen.

One pollination generally produces from 8 to 15 seeds per cone and up to several hundred seeds on an average sidearm. For maximum seed production, one or more additional pollinations at 3 to 4-day intervals are recommended to pollinate additional florets that may have become receptive. Crossing date and parentage are recorded on a plastic snap-on tag that is slipped over the base of the sidearm or around the main stem near the pollinated sidearm.

For a few days, pollinated stigmas appear unchanged. After about 1 week they wither, turn brown, and begin to drop off. Small bracts and bracteoles begin to form and a miniature cone takes shape. About 3 weeks after pollination, when all florets in the bag are past the receptive stage and fresh stigmas are no longer visible, the bag may be removed.

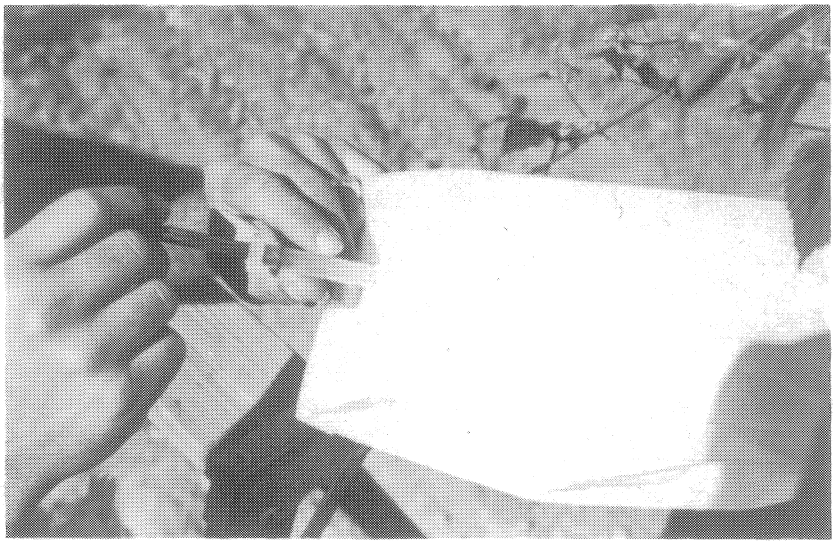

Fig. 6—Pollinating bagged, female flowers with a hypodermic syringe.

V. NATURAL HYBRIDIZATION

Female plants growing near males are usually wind-pollinated, even with considerable differences in flowering dates. In the Willamette Valley of Oregon, five to seven male plants/ha are routinely planted in commercial hop yards. Open pollination usually results in a seed content of 10 to 20% by weight of the cone. Many brewers prefer seedless hops, but growers obtain significantly higher yields from seeded hops. This yield increase is partly due to the extra weight of the seeds, but also to an increase in cone size and weight, caused by stimulation of cone growth from pollination, regardless of seed set (Haunold, 1975).

Collection of open-pollinated seed from desirable female genotypes is easy, but has certain drawbacks for breeding. The male parent of the cross usually is unknown, and the breeder's choice is limited to evaluation and selection of suitable female parents. The use of open-pollinated seed, however, has resulted in several successful hop cultivars (Burgess, 1964; Romanko et al., 1968; Horner et al., 1972).

Controlled crosses by natural hybridization can be made by either planting a selected pollinator in an isolation garden together with female plants, or by bringing pollen or pollen-shedding sidearms to the isolated location and manually dispersing the pollen.

VI. SEED DEVELOPMENT, HARVEST, AND STORAGE

Large cone size and the appearance of individually stimulated bracteoles indicates successful pollination (Fig. 3a,b). One may also bend back individual bracteoles and examine the developing seed at the base. In Oregon, hop seeds are usually mature 45 to 50 days after pollination. Fully developed seeded cones weigh from 125 to 300 mg each. A single hop seed averages from 4 to 7 mg in weight.

Cones are collected in early September and are dried in a forced-air oven at 40 C for 1 to 2 days. Seeds are gently rubbed out by hand. A set of hop sieves used by hop dealers and hop testing laboratories is ideal for seed cleaning. (Sieves are manufactured by Seedburo Equipment Co., 618 W. Jackson Blvd., Chicago, IL 60606.)

Hop seeds are covered with a layer of perianth and resin glands. This layer is partially removed when seeds are rubbed between the hands and a shiny, blue-black seed coat emerges (Fig. 3d). Empty seeds usually are tan (Haunold, 1975). Some genotypes, however, regularly produce brown or tan seeds that are fully viable.

The seed is a fruit (achene) containing a coiled embryo with two cotyledons. The major food reserves of hop seeds are lipids and proteins. Seeds may be stored for a few months at ambient temperatures or for several years in a refrigerator.

VII. TECHNIQUES FOR SPECIAL SITUATIONS

Hop seeds generally do not germinate well, even when seeded into a well-prepared seed bed under favorable conditions of moisture and temperature. Seeds that overwinter in the field and are exposed to cold temperatures readily germinate the following spring. Various types of pretreatment have been attempted (Williams and Weston, 1957), but cold-temperature pretreatment apparently is the most effective method of enhancing hop seed germination.

Hop seeds can either be seeded directly into pots or greenhouse flats which are placed outdoors during the winter months, if minimum temperatures are near freezing (Keller, 1953). Another procedure that assures good hop seed germination consists of surface sterilization, cold-temperature pretreatment, and germination in a germinator under an 8-hour light period, followed by space planting in the greenhouse (Haunold and Zimmermann, 1974).

REFERENCES

Brooks, S. N., C. E. Horner, and S. T. Likens. 1961. Hop production. ARS-USDA Agricultural Information Bull. 240.

———, and Y. P. Puri. 1963. Atmospheric conditions influencing pollen shedding of hops (*Humulus lupulus* L.). Crop Sci. 3:530–531.

Burgess, A. H. 1964. Hops, botany, cultivation, and utilization. World Crops Books. Leonard Hill, London; and Interscience Publishers Inc., N.Y.

Davis, E. L. 1957. Morphological complexes in hops (*Humulus lupulus* L.) with special reference to the American Race. Ann. Mo. Bot. Gard. 44:271–294.

Hartley, R. D., and R. A. Neve. 1966. The effect of gibberellic acid on development and yield of Fuggle hops. J. Hort. Sci. 41:53–56.

Haunold, A. 1970. Fertility studies and cytological analysis of the progeny of a triploid × diploid cross in hop, *Humulus lupulus* L. Can. J. Genet. Cytol. 12: 582–588.

———. 1975. Use of triploid males for increasing hop yields. Crop Sci. 15:833–840.

———, and C. E. Zimmermann. 1974. Pollen collection, crossing, and seed germination of hop. Crop Sci. 14:774–776.

Horner, C. E., S. T. Likens, C. E. Zimmermann, and A. Haunold. 1972. Cascade, a new continental-type hop variety for the U.S. Brewers Dig. 47:56–62.

Howard, B. H. 1965. Regeneration of the hop plant (*Humulus lupulus* L.) from softwood cuttings. I. The cutting and its rooting environment. J. Hort. Sci. 40: 181–191.

———, and J. T. Sykes. 1966. Regeneration of the hop plant (*Humulus lupulus* L.) from softwood cuttings. II. Modification of the carbohydrate resources within the cutting. J. Hort. Sci. 41:155–163.

Keller, K. R. 1953. Seed germination in hops, *Humulus lupulus* L. Agron. J. 45: 146–150.

Kettner, L. 1976. Hallertauer Hopfenbau, Geschichte und Gegenwart. Pinsker Verlag, Mainburg, West Germany.

Kohlmann, H., A. Kastner, and L. Kamm. 1969. Der Hopfen. Hopfen-Verlag Wolnzach.

Romanko, R. R. 1973. Guide to American hops. p. 1–36. *In* Steiner's Guide to American hops. S. S. Steiner Inc., N.Y.

————, S. T. Likens, and J. C. Shephard. 1968. Talisman, a new American Clusters-tye hop variety. Idaho Agric. Exp. Stn. Bull. 496.

Small, E. 1978. A numerical and nomenclatural analysis of morphogeographic taxa of *Humulus*. Syst. Bot. 3:37–76.

Thomas, G. G. 1970. The effect of gibberellic acid on the growth of the hop, var. Northern Brewer. p. 69–71. *In* Annual Report. Wye College, Univ. of London, England.

————, and W. W. Schwabe. 1969. Apical morphology in the hop (*Humulus lupulus*) during flower initiation. Ann. Bot. 34:849–859.

Thompson, F. C., and G. G. Thomas. 1970. Trials on the effect of gibberellic acid on the variety Northern Brewer. p. 65–68. *In* Annual Report. Wye College, Univ. of London, England.

Williams, I. H., and E. W. Weston. 1957. Hop propagation. I. The germination of hop seeds. p. 108–118. *In* Annual Report. Wye College, Univ. of London, England.

Umeda, U., S. Sasaki, S. Kubo, H. Kitami, and T. Sasahara. 1967. Cultivation of hop plants. U.S. Patent 3,309,815. Offic. Gaz. (U.S. Patent Office) 836:819.

Zimmermann, C. E., S. N. Brooks, and S. T. Likens. 1964. Gibberellin A_3-induced growth responses of Fuggle hops (*Humulus lupulus* L.). Crop Sci. 4:310–313.