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Ecological Studies on Dodder (*Cuscuta japonica* Choisy) in Hokkaido : Seed Germination and Host-Dodder Relationship

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abstract

The present studies deal with the seed germination of the Japanese dodder (*Cuscuta japonica* Choisy) and the host-parasite (the dodder) relationship.

The seed germination of the dodder is promoted by the pretreatments which are effective on the removal or destruction of the seed coat by submerging in conz. sulfic acid and by scarification. The germination of the acid pretreatment is 58% at 5°C in 15 days and 98% at 30°C in 2 days. The burial depth of seeds seems to be effective on the seed germination, paricularly in shallower depth. In the burning experiment the percentages of the seed germination at a 0.5 cm depth are from 2.6% to 5.7% for dormant seeds and 76% for non-dormant seeds. The process of the germination due to burning can be attributed to (1) the burning temperatures and heat pretreatment which break the dromancy of seeds and accelerate the germination at shallower depths and (2) the presence of non-dormant seeds which escape from the damage of fire at deeper depths and can germinate successfully in the post-fire recovery period.

There are two host groups : major host groups and minor host groups. These 2 host groupes are ientified by the author's idea based on 5 criteria and a scoring method. On major hosts, the dodder produces relatively long filaments and show high values of the survival potential ; On minor hosts, the dodder produces short filaments and fails to set fruits.

Key words : Acid pretreatment, Burning, Dodder, Host-parasite relationship, Scarification, Seed germination, Survival potential

1. Introduction

Cuscuta species (dodders) are parasitic seed plants unlike normal weeds which suppress crop plants by competing with them on a more or less equal basis for environmental resources needed for growth and production. Dodder does not really compete with crop plants for resources, but it rather connects itself to the vascular system of the host plant and then absorb the resources which the hosts have been collecting for growth and production. A dodder plant may cover several square feet and produce thousands of hard seeds in the presence of a favourable host. Some seeds germinate in the season following to their production and some will remain dormant in the soil for many years (Ashton and Santana 1976). Therefore, once a field has been infested by dodder seeds, a troublesome problem may remain for several years even though no additional seeds are added.

In the laboratory, dodder seed requires special pretreatments to break its dormancy to germinate. These pretreatments include submersion of seeds in concentrated sulfuric acid for a time, and grinding the seeds with sand paper (Gaertner 1950 ; Allred and Tingey 1964 ; Hutchison and Ashton 1980). Factors responsible for breaking dormancy in field conditions are not precisely known. However, it was reported earlier that dodder seeds ingested by domestic animals were found to germinate. Recently, it has been noticed dodder built up and established in farmland where farmyard manure is used (Furuya *et al.* 1980 ; Bloomfield and Ruxton 1977). These facts indicate that animals play a significant role of break down of dormancy of dodder seed. The dormancy of *Cuscuta campestris* Yunck. buried at various soil depths is expected to be broken by overwintering (Hutchison and Ashton 1980). However, the seeds of *Cuscuta japonica* Choisy which overwintered in natural conditioins for one season at least were still 97% dormant and required special pretreatments to accelerate germination. In this species the dormancy seems to be broken by grassland fires. An exciting flush of dodder on *Rosa rugosa* community was observed when fire burned over of the community in the spring of 1980 (Ito *personal communication*).

In the field, the seeds can germinate in the soil and after then, they are dependent upon the food stored within the seed, although the period is very short. Dodder plants will die if they are not able to attach and establish on a suitable host plant within several days after germination (about 25 to 30 days in *C. japonica*) because they are not autotrophic but parasitic. Once dodder plants established themselves on the sustaining host they are dependent on the host for nutrients, water, etc. Consequently, the host has less food for its own growth, and its yield and quality will be reduced.

The fact that many species of the genus will parasitize a large number of plants led to the destructive nature and the widespread of dodders. Some species that attack important crop plants have been studied comprehensively with respect to their distribution, biology and control methods.

Dodders growing on natural habitat are not by any means of less importance than those growing on crops. These, if unchecked, will deteriorate the value of local landscape. Moreover, the ability of these species to produce a large number of hard seeds which can remain dormant in the soil for many years enable them to distribute in time. The possible invasion of these species into farming land may cause drastic losses in crop plants. It is, therefore, necessary to study the ecology of these dodder species to determine factors responsible for their germination and their host range.

In Japan species of *Cuscuta* are familiar to botanists and are found throughout the country (Ohwi 1983). *C. japonica* Choisy is widely distributed along the coastaline of the Okhotsk Sea in northeastern Hokkaido. *C. japonica* is often of importance, because it is parasitic on the important members of the grassland meadow community checks their growth and development, and depreciates their scenic value.

The aim of this work firstly, is to clarify the life history of *C. japonica* in relation to the attempts which complete the so-called Biological Flora. The studies of the Biological Flora has been designed by the British scientists and the work has been continued and published in the Journal of Ecology, British Ecological Society.

Secondly, the work aims at investigating precisely factors responsible for breaking dormancy, and the process of germination. This is because dodders are parasites which primarily reproduce by seeds, and because the initiation of their life history is by germination.

Thirdly, is to study the host-dodder relationship.

2. Geographical Distribution and Taxonomy of the Genus *Cuscuta* (Dodders)

2.1. Geographical Distribution of Dodders

Cuscuta spp. (dodders) are parasitic plants of Mediterranean origin. They are world wide in distribution. There are about 170 species with the largest number of species recorded from the Northern Hemisphere. There is no country from Southern Canada in the north to Chile and Argentina in the south is without dodder (Yuncker 1932).

In the old world they extend from about 60 th parallel north in Europe and Asia to the Cape region of South Africa. According to Giemisi (1965) after 1870's dodders could be found everywhere in western and southern European countries. In Sweden it reaches 64 th parallel and it has even found its way to Greenland. Outside Europe dodders could be found in Africa, Asia and, to less abundance in Australia, New Zealand and the Indo-Malayan region.

Parker (1980) reported that dodders occur sporadically through the humid tropics but are perhaps most widespread and troublesome in the semi-arid subtropics where they attack cultivated crops.

Many dodder species have been introduced to many countries where they did not occur at first, because of the similarity of the size of their seeds to that of the seeds of certain hosts such as alfalfa and flax. For example the North American species *C. gronovii* Willd. becomes a weed in several European countries (Yuncker 1932) ; and *C. campestris* Yunck. from the same homeland has reached Afirca, Europe, South America, China, Australia, India and Japan. The European dodders *C. epithymum* Murray and *C. epilinum* Weihe., are now found nearly throughout the world. The Asian species *C. approximata* Bab. was reported from England. According to Kuijt (1969) many *Cuscuta* species are now naturalized in their new homeland and must be counted with the natural vegetation there.

In Japan, five *Cuscuta* species : *C. japonica* Choisy (Nenashikazura), *C. australis* R. Br. (Mamedaoshi), *C. europea* L. (Kushironenashikazura), *C. chinensis* Lam. (Hamanenashikazura), and *C. epilinum* Weihe. are found throughout the country (Ohwi 1983). Recently *C. campestris* Yunck. and *C. pentagona* Engel. have been reported to parasitize several cultivated crops in Kyushu, Honshu and Hokkaido (Takabayshi *et al.* 1980). They attributed its introduction to the importation of seeds from North America.

2.2. Taxonomy of the Genus Cuscuta (Dodders)

The genus Cuscuta (dodders) first described by Tournefort in 1700 (Gaertner 1950). It was included in the tetramerous group class *Tetrandira digyna* (Linnnaeus, 1750 "Species Plantarum"), and then followed by Roxburg (1820) in "Flora Indica I" (Bhattacharya and Mukerjee 1978). The genus was later included in the Convolvulaceae Juss. by Choisy (1845) in De Candolle's "Prodromus". The same opnion was followed by Engelmann (1859) in "Systematic Arrangement of the Genus Cuscuta", Bentham and Hooker (1873) in " Genera Plantarum", and Yuncker (1921) in "Revision of the North American and West

Indian Species of *Cuscuta*" and other publications by Yncker.

Dumortier (1829) separated the genus from Convolvulaceae and established the monotypic family Cuscutaceae. He was followed by Des Moulins (1853) who treated the group as a separate family because of its parasitic nature. Hutchinson (1926 & 1973) revived the family Cuscutaceae in "Families of Flowering Plants" and since then it has been recognized by many authors ; Wettstein (1935), Frnald (1950) in "Gray's Manual of Botany", Cronquist (1968 & 1981) "The Evolution of Classification of Flowering Plants" & "An Integrated System of Classification of Flowering Plants", Britton and Millsaugh (1962) in "The Bahama Flora" and Bhattacharya and Mukerjee (1978) "Indian Cuscutaceae". Ashton and Santana (1976) stated that although there is some controversy on whether the genus Cuscuta belongs to the Convolvulaceae or to the Cuscutaceae, most taxonomists place it in the family Cuscutaceae.

2.3. Taxonomic Classification of Dodders

The place of dodders (*Cuscuta* spp.) in taxonomic hierarchy of classification could be as follows :

- Kingdom Plantae
  - Division Spermatophyta
    - Class Dicotyledonae
      - Order Solanales
        - Family Cuscutaceae
          - Genus Cuscuta

Dodders are twining, usually annuals, but certain species such as *C. nitida* Mey. believed to perennate within the host tissues (Cornquist 1981, Vicer 1981). Stems thread-like, usually orange or yellow in color. The leaves reduced, scale-like but often with stomata. Flowers small in size, clustered in dense cymose inflorescence with or without bracts. The number of floral parts, mainly of the sepals and petals are mostly 5 oftenly 4 and rarely 3. Calyx tube entire, corolla sympetalous, with imbricate lobes. The corolla tube usually with infrastaminal scales believed to be arised from the base of the filaments late in the flower development (Musselman 1987). Stamens are epipetalous and inserted at or near the sinus of the corolla tube. Anthers are short, tetrasporanigate and dithecal, opening by longitudinal slits, pollen-grains (2) 3-nucleate, smooth, 3-6-colpate. Gynoecium of 2 or 3 carpels united to form a compound, superior ovary with locules as many as the carpels, styles distinct, partially or completely united. Stigmas are variosly discoid, capitate, conic or cylinderic ; ovules 2 in each locule, erect on basal-axile placentas.

Fruit is a capsule circumscissile or irregularly dehiscent or indehiscent. Seeds are small about 1.3 to 3 mm in diameter. The embryo slender, filiform-cylindric, acotyledonous, the size of the embryo fall within the range of (1.5−6 ×0.5−0.4 mm) to (20−28× 0.2−0.85 mm) (Nemli and Ikiz 1984).

3. Review of Literature

3.1. Seed Germination

3.1.1. Why are dodder seeds dormant ?

The maintenance of the dormant state in dodders (*Cuscuta* spp.) has been attributed to inhibition of water absorption by the hard seed coat (Gaertner 1950 ; Sitkin 1976). According to Barton (1965) hard seeds are found in certain members of the Leguminosae, the Convolvulaceae, the Solanaceae, and others. Coats or certain layers of hard seeds are impermeable to water or gases. The immature seed coat of dodder consists of the following layers (Hutchison and Ashton 1979) : (i) epidermis with external cuticle, (ii) hypodermis consisted of elongated thin walled cells, (iii) pallisade layer which is rich in organelles and small vacuoles, and (iv) many rows of parenchyma cells containing starch. After drying the epidermis cells plasmolyze and the outer tangential walls collapse causing reticulation of the mature seeds coat. Drying causes the cytoplasm of the hypodermis to coagulate and the secondary wall-thickening of the pallisade layer develops into macro-sclerieds. After this process seeds are hard coated and lead to dormant condition. In the case of dodders, the location of impermeable layer is in a region above the light line and at the junction of the hypodermis and the pallisade cell layer (Hutchison and Ashton 1979). It was believed to be deposited during desiccation of the hypodermis. Yuncker (1942) observed that immature seeds of *Cuscuta nevadensis* Johns. could germinate in the capsule. Gaertner (1950) confirmed this report and concluded that desiccation was, in part, responsible for the dormancy.

3.1.2. How to break dormancy in dodder ?

As mentioned already, the dormancy in dodders is imposed by the hard seed coat which is impermeable to water. Removing or dissolving parts of this hard seed coat will allow water to enter into the seed and initiate to germinate. In the laboratory, hard seed coats were removed mechanically or chemically as follows :

a. *Mechanical scarification of the seed coat*

This method has proved to be useful in break-down of dormancy of several species of dodder. Walzel (1952) found that abrassion of seeds of *C. gronovii* with glass-dust in almost total darkness resulted in quick and equal germination. Ashton and Santana (1976) found that rubbing seeds between fine sand paper gave almost 100% germination of *C. campestris*.

b. *Chemical scarification by using conc. sulfuric acid solution (98%)*

This method was first described by Kinzel (1901). Most of dodders were found to germinate by the acid pretreatment for a predetermined time.

(1) *Cuscuta campestris* Yunck. : Dormancy of dry stored seeds could be broken by treating them with conc. sulfuric acid. Two year-old seeds gave 57% germination within 4 days after a 65-min. of soaking in the acid solution (Gaertner 1950). Increasing the time of the pretreatment to 80 min. increased the germination up to 65% in 20-year-old seeds. According to Allred and Tingey (1964) an acid pretreatment for 30 min. accelerated germination of *C. campestris.*

(2) *Cuscuta cephalanthi* Engelm. : Gaertner (1950) showed good germination in seeds

which had been stored in dry conditions for three to four months, or 13 months, if the seeds were treated with conc. acid solution prior to the test. Submersion of seeds into the acid from 15 to 75 min. was more effective.

(3) *Cuscuta gronvii* Willd. : Gaertner (1950) showed good germination in seeds stored in dry conditions at room temperature for from two to four years, if the seeds were pretreated with conc. sulfuric acid solution for 30 min.

(4) *Cuscuta indecora* Choisy : Allred and Tingey (1964) found that seeds of *C. indecora* submerged conc. sulfuric acid for 30 min. germinated by 20-30% at temperatures ranging from 2 to 7°C. Fortyfive-year-old seeds taken from herbarium germinated only after acid pretreatment (Gaertner 1950).

(5) *Cuscuta suaveolens* Ser. : Seeds of unknown age may be older than 30 years, were germinated after sulfuric acid pretreatment for from 60 to 100 min. (Gaertner 1950).

(6) *Cuscuta occidentalis* Millsp. : Fortynine-year-old seeds taken from herbarium specimens germinated only after acid pretreatment. They gave 60% and 10% germination after being pretreated for 10 and 20 min., respectively.

(7) *Cuscuta petagona* Engelm. : According to Gaertner (1950), 51-year-old seeds gave 20% germination after the pretreatment with conc. sulfuric acid for 50 min. Untreated seeds failed to germinate. Seeds of this species germinated after 30 min. pretreatment of conc. sulfuric acid solution (Furuya *et al.* 1980).

(8) *Cuscuta chinensis* Lam. : Hassawy (1973) reported that the pretreatment of conc. sulfuric acid solution for from 25 to 30 min accelerated germination of both one-year-old and freshly collected seeds.

(9) *Cuscuta approximata* Bab. var. *ureolate* (kune) Yunck. : Tingey and Allred (1960) found that acid treatment alone was not effective in the break-down dormancy in this species. However, the dormancy was readily broken by wet chilling of seeds which pretreated for 2 to 3 weeks at 2 to 7°C. Submersion in the conc. sulfuric acid was most effective for 5 to 15 min., but for 30 min. or longer resulted in abnormal sprouts in some instances.

(10) In the case of *C. europaea* L. pretreatment of conc. sulfuric acid did not accelerate germination. Seeds readily germinated at 27°C in condition that the harvested seeds stored at least three month in moist peat at 0°C (Gaertner 1954).

3.1.3. Factors responsible for breaking dormancy of dodder in field conditions

The mechanism by which dormancy of dodder seed is broken in the field conditions has not precisely known. However, the following factors may play a significant role of break-down of dormancy. According to Gaertner (1950) seeds can germinate by passing through the digestive tracts of various animals including sheep, rabbit, pigeon and skylark. Other reports indicated that the use of farmyard manure leads to a significant build up of dodder (Furuya *et al.* 1979 ; Bloomfield and Ruxton 1977). Barton (1965) suggested that impermeability of hard seeds can be lost by soil microorganism attack of seeds, by the ingestion of domestic animals, weather conditions, and brush fire. In case of *C. japonica*, Ito (*personal communication*) noticed the establishment of dodder was made by the grassland fires in eastern Hokkaido.

Environmental factors such as overwintering might be effective on the break-down of dormancy. Hutchison and Ashton (1980) reported that dormancy of *C. campestris* seeds buried at different soil depths was broken by overwintering, and that older seeds and those close to the soil surface germinated best.

Temperature and heat-pretreatment as factors which induce the germination has been thoroughly investigated in many leguminous species. However, a search in literature failed to furnish enough information on the effect of the temperature in inducing germination in dodder seeds. Seeds of many plant species are tolerant to heat, and seeds of grassy species can tolerate temperatures of 82 to 116°C for 5 min (Wright and Bailey 1983). Most species could tolerate temperatures of 115 to 117°C for five min and these temperature exposures usually increased the percentage of germination (Went 1952). Heat pretreatment was found to accelerate germination of *Rhus javanica* L. (Iwata 1964, Washitani 1986). Iwata (1966) attributed the appearance of many *Lespedeza* spp. after burning in the field to the rise of soil temperature, which induces seed germination. Mallik and Gimingham (1985) reported that heat pretreatment at 100°C for short period of 30 seconds to two min was found to stimulate the germination of *Genista anglica* L. and *Hypericum pulchrum.* L. Takahashi and Kikuchi (1986) found that heat pretreatment induced seed germination of *Rhus javanica* L., *Purearia lobata* (Willd.) Ohwi and *Lespedeza homoloba* Nakai. In early investigations, aiming at the destruction of the viability of dodder seeds, high temperatures were reported to cease the viability of dodder seeds. Stewart (1926) found that heat treatment destroyed the viability of seeds. It was enough to destroy the viability to dip the seeds of *Cuscuta gronovii* Willd. in boiling water for one second. Seeds of *C. pentagona* were killed by steaming them at 100°C (Furuya *et al.* 1980). It was also stated by Gayed (1986) that proper sterilization of tobacco seed bed with steam eradicated *C. gronovii.* But there is no evidence that temperature can induce the seed germination in dodders.

3.1.4 Temperatures required for seed germination

After the dormancy is broken, favourable moisture, and soil temperature can influence on the germination. Several investigators, so far, determined temperatures required for the germination of several species of dodder. Allred and Tingey (1964) found that seeds of *C. indecora* Choisy., *C. campestris* Yunck. and *C. approximata* Bab. germinated best at 15.5°C or higher temperatures in green house experiment. They found from field experiment that seeds of *C. approximata* germinated first at a soil temperature of 4°C, and that *C. indecora* germinated at 10°C 7 to 10 days later, and *C. campestris* began to germinate at 15.6°C further two to four days. Very few seeds of C. approximata germinated in mid-May, but seeds of *C. indecora* and *C. campestris* continued to germinate throughout the summer season. In Yugoslavia the seeds of *C. epithymum, C. prodani* and *C. tinei* germinated best at 20°C, while seeds of *C. campestris, C. pentagona, C. lupuliformis* and *C. monogyna* Vahl. germinated best at temperatures between 30 and 33°C (Stojanoric and Mijatovic 1973). In Japan Furuya *et al.* (1980) found that scarified seeds of *C. pentagona* Engelm. germinated in constant temperatures between 25 and 30°C and in alternate temperatures of 30 and 20°C temperatures under light and dark conditios. They also showed that the seeds did not germinate at 10°C but germinate at 15°C. Hutchison and Ashton (1980) found that the scarified seeds of *C. campestris* germinated best from 30 to 33°C. But at temperatures below 18°C and above 39°C seeds remained fully imbibed with water and did not germinate.

Dawson and Ashton (1984) showed that *C. planiflora* Teu. germinated at lower temperatures than *C. indecora* and *C. campestris* and emerged earlier in the spring. Musselman (1987) stated that *C. pentagona* and *C. campestris* will germinate best at about 20°C, while *C. compacta* Juss. and *C. gronovii* willd. germinate best at between 22 and 23°C.

3.2. Host—Dodder Relationship

3.2.1. Damage of dodders on crops

Dodders beside their destructive effect on forage legumes such as lucerne, where it reduces the yield and deteriorates the value of the hay it is suspected of poisonous effects. In Australia, *Cuscuta australis* R. Br. was believed to have poisonous effects on livestock fed on dodder-contaminated hay. Movsesian and Azarian (1971) reported poisoning of cattles fed on hay containing 50% *Cuscuta campestris* Yunck.

In Japan there are so far five species of dodders (*Cuscuta* spp.) distributed throughout the country (Ohwi 1983 ; Takabayashi *et al.* 1981). Takabayashi *et al.* (1981) reviewed the distribution of dodder and their parasitic damage on various field crops, and ornamentals throughout the country. This review can be summarized as follows :

(i) Most of the damage on crops was found to be caused by *C. campestris* and *C. pentagona*. Seeds of these two species were believed to be introduced by seed importation from North America (Asai 1975).

(ii) In Hokkaido, dodder was reported on 20 crop plants. The most common crops damaged by dodders include potato, sugar beet, onion, clover and carrot. However, the market value and yield of these crops were not significantly degraded due to the dodder infection.

(iii) In Kanto area dodders were found more frequently in greenhouses and PVC houses. The most common host crops include members of the Compositae and the Solanaceae. The dodder infection suppressed the growth of many vegetables, preventing fruit setting, and deteriorated their market value.

(iv) In Kyushu, particularly in Kumamoto prefecture, the host crops include members of the Cucurbitaceae, the Compositae, and the Solanaceae.

(v) The remaining species of dodder include *C. japonica* Choisy, *C. europaea* L., *C. chinensis* Lam. and *C. australis* R. Br. and they were frequently found in road sides and in natural landscape.

According to King (1966) dodders are considered noxious weeds in 47 states of the contagious United States. There are many species in the United States. Some parasitize only certain non-crop plants, and are of little economic importance. Others have wide host range and attack many crop plants. According to Dawson *et al.* (1984) three species which cause most of the damage are *C. indecora* on forage legumes in the West and the East and occasionally in the South, *C. campestris* on many crops all over the country, and *C. planiflora* on alfalfa in the West. Dodder suppresses the growth and development of alfalfa, reduces the seed yield significantly, and deteriorates the quality of seeds because of shriveled seeds and of the presence of dodder seeds (Dawson *et al.* 1984). Other crops damaged by dodders are carrot, tomato, sugar beet, onion and potato. Dodder has also been found to harm several ornamental plants, particularly those at home gardens. Some of the ornamental species which are most susceptible to dodders are *Chrysanthemum, Dichondra, Pachysandra,* several *Hedra* species, various *Querucus, Ixora,* and *Citrus* (Dawson *et al.* 1984 ; Ashton and Santana 1976).

In USSR, parasitic weeds were found to cause more destruction to host (crops) than heavy infestation of the worst non-parasitic weeds (Fisyunor 1977). According to Alpatev (1969), there are about 36 species of dodder ; at least 10 species of them (Rogachev 1969) were found to be noxious in Kirgizia SSR on many field crops. Among them *C. campestris* and *C. approximata* are most troublesome in field crops, while *C. lupuliformis* Krock. and *C. lehmanniana* Bunge infest woody plants. The amount of losses caused by dodder was indicated by the fact that at least 30000 ha of lucerne and non-crop land were treated by chemicals and found to reduce the dodder infestation by 20000 ha in 5 to 6 years. *C. epilinum* was also reported to infest 25000 ha of crop land (Shamaev 1970). *C. campestris* was found to parasitize up to 40% of sugar beet crops in Kirgizia SSR (Belyaeva 1978). It was estimated that the reduction was to be 1.5 to 1.9% in sugar content and 3.5 to 4 t/ha in sugar yield.

According to Gimesi (1965) dodder could be found everywhere in western and southern European countries, but be responsible for serious damage only in central and southern regions. Sarpe *et al.* (1970) described 18 species of dodder as the most dangerous for cultivated plants in Romania. The greatest damage done by *C. campestris, C. europea, C. epilinum, C. epithymum*, *C. suaveolens*, *C. lupuliformis* and *C. monogyna.* In Yugoslvia, Dorovic (1970) stated that about 50 to 70% of lucerne in Stiga region was infested by dodders and about 30% of the infested area had to be plowed in. Many crops such as forage crops, sugar beet, tobacco and some vegetables were infested. Wolswinkel (1974) reported *C. lupuliformis* growing on blackberry and *Vicia faba* in the Netherlands. He noticed that dodder inhibited fruit setting when *Vicia faba* L. parasitized at the time of flowering.

In India, there are 17 species of dodder (Bhattacharya 1978). The most noticeable is *C. reflexa* Roxb., a frequent pest of ornamental trees and shrubs as well as herbaceous plants. Muthappa (1973) reported that coffee was seriously affected by this species. *C. chinensis* was reported to cause serious grain losses on *Guisotia abyssinica* Cass. (Rath 1974). The loss was estimated to be 60 to 65% in grain yield (Misra 1981). *C. campestris* was reported on several crops and ornamentals.

In the Middle Eastern countries, dodder is frequently considered to be an important pest on sugar beet and other vegetable crops. Villarias (1978) found that dodder was the most important pest of sugar beet in Italy, Turkey but relatively of minor importance in Greece. In a field study in Turkey, Syria, Lebanon, Iraq and Iran Mamluk and Weltzien (1978) found that 12.5% of the fields examined were infected by *C. planiflora.* The most common crops infested include sugar beet, lucerne, tomato, cucumber, pepper and egg plant. Hassawy (1973) reported that *C. chinensis* seemed to be the most common species in central Iraq. It parasitized 30 different host species including 15 field crops, fruits and ornamentals.

In Australia, three species of dodder were reported from New South Wales. They parasitized on many native and introduced plants. Among the crops attacked lucrene, red clover, carrot and beet root are there.

C. campestris which is the most wide spread and aggressive, is the species most often involved as an economic weed problem in Africa (Parker 1980). It seems to be established by importation of seeds from North America. This species was also found in South Africa on several host species (Nel 1955 ; Vicer 1982). Hocking (1966) reported the occurrence of *C. cassytoides* Nees V. Esenb. in a nursery near Arush, Tanzania, and this dodder caused high mortality of seedlings in center of infestations.

As described above dodders, as crop pest can be found all over the world on various crops. However, certain species are responsible for much of damage on crops.

3.2.2. Host specificity of dodders

Musselman (1987) demonstrated that some species may be characterized by what they did not attack ; such as *C. indecora* which found to parasitize *Lezpedeza striata* vigourously, as did *C. pentagona* and *C. campestris*. But the only dodder found on *Iva frutescens* was *C. indecora*. He also noted that *C. compacta* Juss. can be found on many different host, but no other dodder species was found on *Alnus serrulata*, a favorite host for *C. compacta* Juss. These facts clearly suggest that dodders are a host generalist ; but prefer certain host species to others.

Extensive lists of host species for nine species and one variety of dodder was compiled by Gaertner (1950). The first include 609 species in 320 genra in 79 families parasitized by dodder. According to this list *C. europaea* was on 237 species ; *C. gronovii* on 175 ; *C. epithymum* on 147 ; *C. campestris* on 69 ; *C. pentagona* on 47 and *C. epilinum* on 8 host species. A list of 108 species not parasitized by dodder was also provided. Erdos (1971) found that *C. epithymum* parasitized 89 and *C. campestris* 85 species in Hungary. *C. chinensis* was reported on 47 species in India (Rath 1975) ; and on other 30 species in Hongkong (Yung 1979). However, Rath (1975) noted that *Gozitia abssynica* Cass. was the main host of *C. chinesis*. In Hokkaido, *C. pentagona* was reported on 20 cultivated plants which were mainly vegetables and ornamentals ; high incidence of parasitisim was on crops belonging to the Solanaceae and the Leguminosae (Takabayashi *et al.* 1981).

However, lack of discrimination between sustaining or major hosts and minor hosts depreciates the value of the many extensive host lists. *C. europaea* was reported on at least 25 Gramineae species in the lists provided by Gaertner, which were generally accepted as resistant species to dodder infection. In addition, *C. europaea* was reported to parasitize *Rhinasthus crista-galli*, but elsewhere it was said to be unable to support the same dodder (Kuijt 1969). *Beta vulgaris* and *Satureja vulgaris* were sometimes susceptible to and sometimes resistant to *C. gronovii*. Tomato (*Lycopersicon esculentus* L.) was found to be infected by *C. pentagona* (Fujimoto 1980) but was not infected by the same species (Furuya *et al.* 1979). In all records of dodder hosts the exact circumstances of the observation needs to be examined carefully.

Atsatt (1983) stated that a distinction must be made between major hosts and minor hosts in the local lists of hosts. He noted that the ability to grow and reproduce on another plant is not sufficient for the determination of hosts. Roth (1978) demonstrated that *Arcethobium laricis* may develop and reproduce on *Abies concolor, Tsuga mertensiana, Pinus contorta* and *Pinus ponderosa, Picea engelmanni* and *P. monticola*, but damage can be seen only in the presence of the principal host, *Larix occidentalis*. A similar pattern can occur in dodders where it is often difficult to identify either major or minor hosts.

In this respect there are a few reports in which a clear distinction was made between major hosts and minor hosts. Khron (1934) was the first botanist who classified the potential host species of dodder into three groups : i) Good food providers for dodder ; ii) Hosts on which dodder can survive ; and iii) hosts serving only to support dodder. In studies in *C. hyalina* Roth. Narayana (1956) observed that this species especially parasitized weeds, and several annual and perennial herbs ; it was found to parasitize a total of 42 species which were classified into primary, secondary and tertiary hosts. A group of the primary host belonged to such a geneus as *Tribulus* (Zygophyllaceae), while members of the Gramineae and Cyperaceae merely served to support *C. hyalina*.

There are some reports in which no definite distinction was made between host species. For example, Olifirenco (1961) listed 68 hosts of *C. arvensis* Beyrich. and noted that some plants such as timothy and black poplar were weakly affected by dodder (Ashton & Santana 1976). It was reported that the damage caused by *C. pentagona* was strong on egg plant and potato and intermediate on tomato and clover (Fujimoto 1981). Furuya *et al.* (1979) reported that tomato was not infested by the same species.

3.2.3. Susceptibility and resistance of host plants to dodder

In considering what hosts might be attacked by a parasite, one must take into account for the susceptibility of the host species, degree of virulence of the parasite, the resistance of certain plants to attack and related topics (Kuijt 1969). The survival of a parasite on a host species is a product of genetic variation of both the parasite and the host. In addition, the genetic complexity may determine the success of a parasite on a host. At a glance of the extensive host lists of dodder, or in observation of a dodder vine attacking several hosts, it is extremely difficult to interpret the genuine parasitism of dodder. For example, a plant which is not attacked by a dodder, even though neighbouring plants are attacked, does not necessarily indicate a resistant plant to dodder.

In the earlier records of the *Cuscuta* host range was thought to be limited (Yuncker 1932). Gaertner (1950) reviewed the host-dodder relationship. She concluded that : i) Dodder is host generalist and no species was found limited to one host ; ii) Succulent plants were frequently parasitized by dodder ; iii) The age of host might provide mechanical obstruction of infection to dodder ; and, iv) the survival and reproductive capacities of dodder were dependent on the physiological conditions of the host. Sitkin (1976) confirmed that the susceptibility of a particular host to dodder can vary according to age. He found that *C. campestris* can attack young tomato but hardly attack tomato plants older than 21 days. Dawson *et al.* (1984) reported that *C. campestris* will parasitize tomato at any stage of growth, but it is particularly serious on the young seedlings of tomato which will no longer survive after infection, although older ones suffer severe yield losses.

It has been frequently reported that causes of apparent resistance of host to dodder may be the biochemical incompatibility between both, and the presence of mechanical barriers. Kuijt (1969) reported that the high acidity of the tissues of *Oxalis* and *Begonia* was believed to be responsible for their immunity to dodder and that alkaloids and other toxic substances in *Euphorbia, Papver* and *Datura were* responsible for their resistance to dodder. But some plants containing smoe toxic substances has been reported as host of dodder (Gaertner 1950). Walzel (1952) demonstrated that all materials present in the host were not transferable to the parasite.

Mechanical barriers seem to be very important in halting the advancement of haustoria into the vascular system of the host. It is true for some plants which possess an effective sclerenchyma barrier as seen in the branches of *Quercus* and *Digitalis* and in the leaves of *Pinus, Picea* and many Gramineae species (Kuijt 1967 ; Tsivion 1979). In some cases sclerenchyma differentiates into a mechanism of defense. Capderon and Ozenda (1985) reported an active resistance system in *Gossibium hirsutum* L. when it was parasitized by *C. lupuliformis* Krock. They found a structure which formed on the surface of the infected host. It consists of a layer of suberized cells surrounding the haustoria which leads to the trophic isolation. Then secondary parenchyma developes, invading the space previously filled by the haustoria, and ultimately expelled the dead parasite. The reaction was suggested to be phytohormonal.

In some instances, mechanisms which are not really based on mechanical barriers or biochemical incombatibility allow a host to escape from infection. The phenomenon of hypersensitivity as known in fungus phytopathology is not commonly known in parasitic higher plants. However, Tsivion (1979) attributed resistance of tomato plant to *C. campestris* to the hypersensitive reaction to the parasite. He described that when *C. campestris* comes into contact with the stem of tomato, the latter set off a reaction that kills the adjacent bark and makes it impossible for the *C. campestris* to become established. He also found that infection of tomato was partially successful despite the hypersensitive reaction. While infection of Gramineae was prevented by mechanical barriers.

In some instances, where some species of dodder were supposed to be restricted to a particular host plant, it might be due to other environmental factors. For example, *C. exaltata* is found ordinarily on trees, while *C. salina* Englm. prefers saline shrubs (Yuncker 1932). Musselman (1987) reported that *C. indecora* which parasitizes many hosts was the only dodder on *Iva frutescens* ; likewise no doodders except for *C. compacta* was found on *Alnus serrulata*.

4. Study Area

Study area is divided into two subareas : the so-called Koshimizu Gensei Kaen subarea and the Hamakoshimizu or Yanbetsu subarea. Koshimizu Gensei Kaen subarea is an area from Tofutsu Bridge which stands at the far West edge of this subarea to Hamkoshimizu JR station which stands the far East edge of this subarea. It stretches about 7.5 Km in length and about 100 m in width on average. The width, however, range from 100 m in narrowest part to 250 m in widest part (Fig. 1).

The middle of this subarea is appointed to be a special area of Shiretoko National Park and the most valuable area from the view of point of scientific interesting and sightseeing.

The dune formation has ceased, and dunes have fixed at present. Thus, the vegetational arrangement from the beach to the inland is typically observed, particularly at near

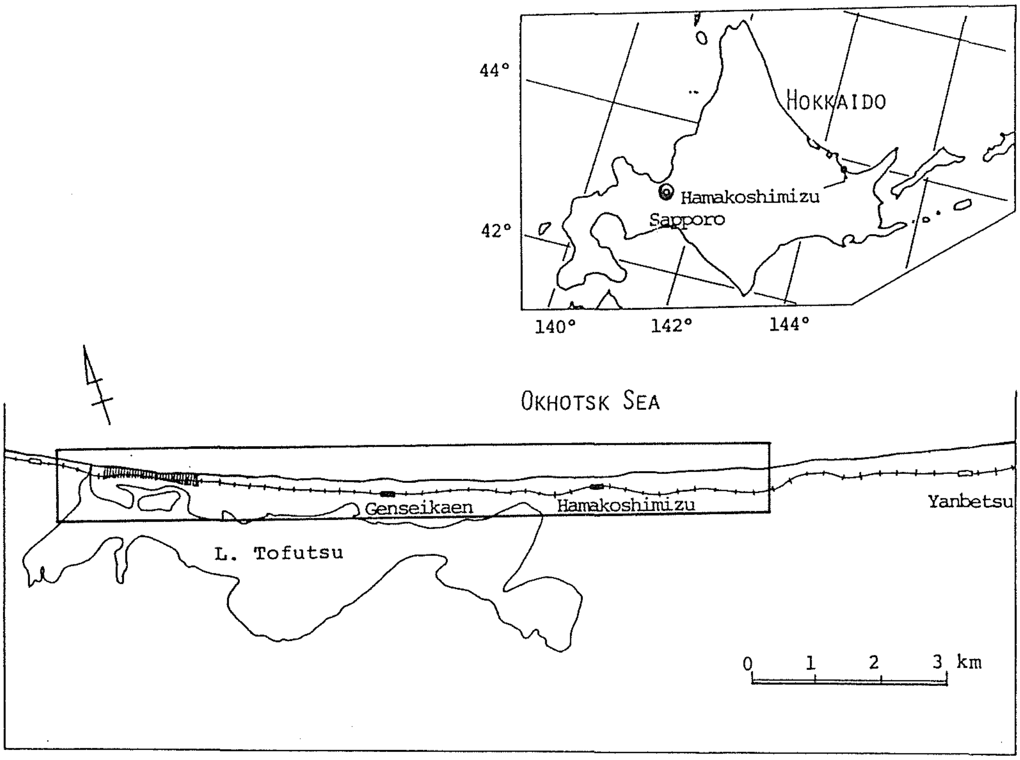

Fig 1. Study area : shaded area in the detailed map shows the area burned in spring 1987.

Hamakoshimizu JR station. The height of dunes is different, and generally falls in the range of 5 m to 20 m in height.

The vegetation in that area is seminatural in origin. The area had been used as pasture in the past. At present the human interference to the vegetation has ceased. The establishment of the so-called Genseikaen, that means the premeval vegetation which are rich in flowers and herbs, has been believed that human activities on the sand dune vegetation in the past had induced the appearance of this kind of vegetation. In this case, the most strong pressure was grazing by horses and cattles, and the maintaning agent of this Kaen was burning which introduced by the locomotives. At present, grazing has been stopped and the locomotives substituted for the Diesels. Therefore, the vegetation has been degrading, and the people has been trying to recover the vegetation by introducing horses and cattles to it and by burning it in early spring. The vegetation is sometimes recovering, but as seen in this study, a part of the vegetation has locally been suffered from the damage of *Cuscuta japonica* Choisy, although it gives a good chance of study.

The vegetation belongs to the General Coastal Meadow Formation, which is characteristics of sand dune vegetation in Hokkaido, and forms the *Rosa rugosa*-Herbs sociation, as a sense of plant ecologists of Hokkaido University. This kind of vegetation is characterized by the dominance of *Rosa rugosa* and by scattering occurrence of *Malus baccata* var.

mandshurica in the first layer which ranges from 1 m to 3 m in height. It is clearly distinguished from the sand beach vegetation by the more complexity of species richness, diversity and development of humus layer on the surface of old sand dunes.

In the study area, which includes two subareas, the main components of the community or the vegetation are as follows : *Achillea alpina* var. *angustifolia* (Hara) Kitam., *Arabis stelleri* var. *japonica,* (A. Gray) Fr. Schm., *Carex caryophyllea* var. *microtricha* (Fr.) Kukenth, *Celastrus orbiculatus* Thunb., *Dianthus superbus* L., *Elymus mollis* L., *Festuca rubara* L., *Geranium yezoense* Fr. et Sav., *Hemerocallis middendorffii* Trautv. et Mey., *H. yezoensis* Hara., *Lathyrus japonicus* Willd., *Lilium davuricum* Ker-Gawl., *Moehringia laterifolia* (L.) Frenzl., *Picris hierachioides* var. *glabrescence* (Regel) Ohwi, *Polygonatum humile* Fisch., *Scutellaria strigilosa* Hemsley., *Vicia japonica* A. Gray, etc.

5. Seed Germinatin

5.1. Objectives

As most of the seeds of dodder are hard coated, thy are impermeable to water and oxygen. A pretreatment is frequently required to accelerate the germination. For example, the submersion of seeds in conc. sulfuric acid solution or grinding them with sand paper and sometimes followed by cold storage accelerates the germination (Gaertner 1950, Allred and Tingey 1964, Ashton and Santana 1976, Hutchison and Ashton 1980).

There is a few information on factors responsible for the break of dormancy of dodder seed in natural conditions. Ingestion of seeds by domestic animals (Khun 1877, according to Gaertner 1950), and overwintering of the seeds at different soil depths break dormancy (Hutchison and Ashton 1980).

In *Cuscuta japonica* dormancy of seeds seems to be broken by the effect of fire (Ito *personal communication*). Ito observed an exciting flush of dodder on *Rosa rugosa* Thunb. community at Yambetsu in early spring of 1980, when fire burned some areas of the community. The phenomenon is very comparable to the prosperity of *Lespedeza bicolor* Turcz. in eastern Hokkaido, or of *Epilobium angustifolium* L. after frequent fires in Alaska. Heat pretreatment had been found to break the dormancy in *Lespedeza homolobe* Nakai (Iwata 1964), *Rhus javanica* L. (Iwata 1964 ; Washitani 1986) and other plant species. A particular interest in the effect of heat pretreatment on the germination in dodder as shown already that for example the flush of dodder following grassland fire at Koshimizu, NE Hokkaido.

Recently, it is proved that solarization (heating the soil by using plastic-mulch) proved to be effective in controlling several weeds including parasaitic plants. Horowitz *et al.* (1983) reported that temperature of soils covered with plastic mulch reached 60 °C and caused thermal death of hydrated organisms. Burning crop residues and weeds will also help to kill or to stimulate buried seed populations depending on temperatures and the position of seeds in the soil. Therefore, it is important to investigate effect of burial and related factors on the germination, because germination studies can yield basic ecological information on requirements by the seeds and the subsequent development. Knowledge of temperatures and the pretreatment of seeds for germination assesses the potential of seeds.

This information provides insight of the establishment potential.

This study aims at the following objectives :

1. To determine an expedient method to accelerate the germination.
2. To investigate temperature required for germination.
3. To investigate factors responsible for the break of dormancy and their subsequent effects on viability of seed.

5.2. Materials and Methods

5.2.1. Seed collection

Seeds of *C. japonica* were collected from dodder plants on *Rosa rugosa* Thunb. and *Artemisia montana* (Nakai) Pampan. of the General Coastal Meadow community dominated by *Rosa rugosa* in Koshimizu, Gensei-Kaen, northeastern Hokkaido, in the spring of 1985. These seeds had overwintered under natural conditions before the collection. The seeds were stored in glass jars at room temperature (20°C) in the laboratory and used in all of the following experiments throughout this work.

5.2.2. Pretreatment of seeds for the removal of the seed coat

a. *Mechanical scarification by using a sharp blade*

This method is simple but requires intensive labor and time. It is useful only in determination of viability of seeds in conditions such as high temperatures. Seeds were picked one by one and pricked with a sharp blade.

b. *Submerging the seeds in conc. sulfuric acid solution (98%)*

This method was first described by Kinzel (1901) and was found to accelerate the germination of many species of *Cuscuta*. In this experiment the effect of acid pretreatment on viability and germinability of *C. japonica* was investigated and compared with the method described above. Seeds of *C. japonica* were submerged in conc. (98%) sulfuric acid solution 1 : 2 v/v (one part seeds and two part acid) for 5, 10, 15, 20, 25, and 30 min.

5.2.3. Determination of temperatures required for dodder seed germination

The seeds pretreated in conc. sulfuric acid and non-treated seeds were placed in moistened filter paper in petri-dishes. These were replicated four times each containing 25 seeds and then placed in an incubator at six temperature regimes, namely 5, 10, 15, 20, 25 and 30°C. Germination was recorded over the first two weeks every two days. Then, the non-treated seeds were kept for 16 weeks at 25°C until no germination was recorded. These were then tested for viability.

5.2.4. Effect of burial depth on dormancy and viability of dodder seeds

The effect of burial depth and duration on the dormancy and viability of dodder seeds was investigated in the following : Seeds were 97% to 100% dormant viable seeds obtained from the field. On 17 June 1985 approxamately 300 seeds (1.6 g) were placed in polyester cloth bags, which are permeable to water, and attached to a plastic coated wires to facilitate recovery. The wires were anchored to the soil surface. The seeds were then buried at 1, 5, 10 and 15 cm indepths. It was replicated four times in a randamized block design. Air temperatures and soil temperatures measured at one and five cm soil depth were obtained from the Nursery of the Experimental Forest, Department of Forestry, Faculty of Agriculture, Hokkaido University.

Since the first recovery in September of the same year did not show any change in the germination. The recovery were then made immediately after snow melted on 17 April, 17 May, and 17 June of the year 1986. The total buried seeds were analyzed immediately after recovery in order to determine the percent of the germination *in situ* and the remaining seeds were incubated at 25°C for a four weeks. The seeds germinated during this period were recorded and calculated as percent of the total buried seeds. The remaining seeds were submerged in conc. sulfuric acid solution for 20 min. to test their viability.

5.2.5. Depth of seedling emergence

To see the depth of emergence of dodder seedlings 50 acid-pretreated-seeds in four replicates were put in 1, 2, 3, 4, 5, 6, 7 and 8 cm in depth in wooden flats. Soils were sandy and clay soil. Emergence of dodder was recorded during the period from mid-June to the third week of July when there was no emergence. The wooden flats were kept outdoors and water was supplied when necessary.

5.2.6. Effect of burning on dormancy and viability of dodder seeds

The effect of burning on the germination could not be conducted easily in the field, because experimental conditions hardly adequately controlled. Fire temperatures, however, were measured at two sites of the General Coastal Meadows, Koshimizu Gensei-Kaen, when burning (Noyaki) was practiced for the purpose of recovery of *Rosa rugosa*, by Koshimizu Town office in the spring of 1986.

a. *Measurements of temperatures in field conditions*

Temperatures during and after burning in Koshimizu Gensei-Kaen was measured using a computerized temperature recording system called Data collecter (AM 7001, Kairyogata, Anritsukeiki CO. Ltd.) which can measure up to 1200°C. Sensors connected to this instrument were placed at the following depths : 0.0, 1.0, and 2 cm. Moreover, two sensors were placed at 5.0 and 15 cm above the soil surface. Then the instrument was adjusted to record the temperatures at 10 seconds interval.

b. *Burning in experimental conditions*

The effect of burning on the germination and on the viability was studied in the laboratory. In two kinds of experiments temperatures at different soil depths were measured during burning as well as their effect on buried seed germination and viability was examined. For this purpose wooden flats were used. The size of the wooden flats was $120 \times 30 \times 10$ cm, and the flats were divided into small compartments of which size were $30 \times 30 \times 10$ cm. Each of them assigned the following depths : 0.0, 0.5, 1.0, and 1.5 cm. The wooden flats were then filled with soil. The sensors were fixed at each depth and connected to the computerized temperature recording system. Temperatures at 5 and 15 cm above the soil surface were also measured at the same time. The flats were then covered with a layer of dry grass, which was ignited and burned.

i. In the first experiment 150 non-treated seeds were put at each depth and recovered for germination tests which were replicated three times.

ii. In the second experiment 150 seeds from the non-treated and 150 seeds from acid-pretreated seeds were put at each soil depth in the wooden flats. In order to facilitate

recovery, the seeds were first placed in 9 cm petri dishes filled with soil which was meshed to remove the gravels. The seeds were put into the wooden flats as follows :
Petri dishes were marked by a line at 0.5 and 1.0 cm in depth. Then, soil was put up to the marker and the seeds placed into the different depths of soil.

After burning, the seeds were washed through a series of meshes to remove soil particles and then subjected to germination and viability tests. These were replicated three times.

c. *Heat-pretreatment by exposure to contolled oven temperature*

This experiment was conducted to determine the burning effect on the germination when fire passed on the ground which contain dodder seeds at different depths. The effect of heat-pretreatment on germination of two-year-old dodder seeds were studied in the following :

Seeds were washed in tap water to remove destroyed seeds ; dried ; and then divided into two groups. One of them was submerged in conc. sulfuric acid solution for 30 min to remove the hard seed coat. Seeds from the dormant (non-treated) and seeds from the acid-pretreated were incubated at 25°C in four replicate for four weeks to determine germinability. Then twenty five seeds taken from each group were placed in three discs of 9 cm filter paper moistened by 5 ml of water put in petri-dishes. The treatments replicated four times seeds were then exposed to controlled oven in which temperatures were 40, 55, 70, and 85°C for 10, 20, 30, and 40 min, respectively. They were placed in an incubator at 25°C for four weeks. Non-germinated seeds were tested for viability by the mechanical scarification. The germination was recorded every two days and those attained 0.5 cm or more in length were considered. Deformed and injured seedlings, unless recovered, were considered not to be viable. Some of seeds exposed to high temperatures were examined under the microscope for the observation of physical changes on the testa.

5.3. Results

5.3.1. Pretreatment of seeds and temperatures required for germination

Table 1 shows the germination percentage of the non-treated, mechanically scarified and acid pretreated seeds on the 15 th day of incubation at six regimes of temperatures from 5 to 30°C.

Table 1. Germination percentages of non-treated, and acid-pretreated seeds on the 15th day after incubation at different temperatures

Temperatures (℃)	Nontreated	Scarified by a blade	Submerged 5	10	in con. 15	sulfuric 20	acid 25	solution for 30 min
5	0	70	14	30	77	53	56	58
10	0	99	33	75	98	99	99	83
15	0	98	40	64	99	99	97	98
20	2	98	48	68	98	99	99	98
25	3	98	60	70	98	97	98	86
30	1	94	62	70	98	99	98	98

* The test was carried out by placing 25 seeds per petridish and replicated four times

a. *Effect of mechanical scarification and acid-pretreatment*

Non-treated seeds germinated poorly at at higher temperatures from 20 to 30°C and gave only from 1 to 3% in germination within 15 days. When the incubation at 25°C continued for 16 weeks no seeds germinated. The mechanical scarification and the acid-pretreatment broke the dormancy and increased the germination significantly. In the former pretreatment at least 70% of the seeds imbibed water and embryos emerged at low temperatures of 5°C within 15 days in the incubator. But the method was inconvenient because it was time consuming and with intensive labor. Moreover, it was difficult to cut the seeds evenly. Therefore the whole embryo protrudes through the cut opening when it was too large. Relatively high percentage of germination was due to the facts mentioned above.

Acid-pretreatment, in which seeds were submerged in conc. sulfuric acid for 15 min was adequate in the break of dormancy and resulted in high percentage of germination up to 98%. Fig. 2 shows that increasing the time of the acid-pretreatment improved the percentage of germination ; even at relatively low temperatures it was effectve in the increasing of the germination. Seeds submerged in the acid solution for 5, 10, and 15 min and incubated at 5°C germinated by 14%, 30%, and 77%, respectively. Increasing of the time of the acid pretreatment for more than 15 min did not increase the germination.

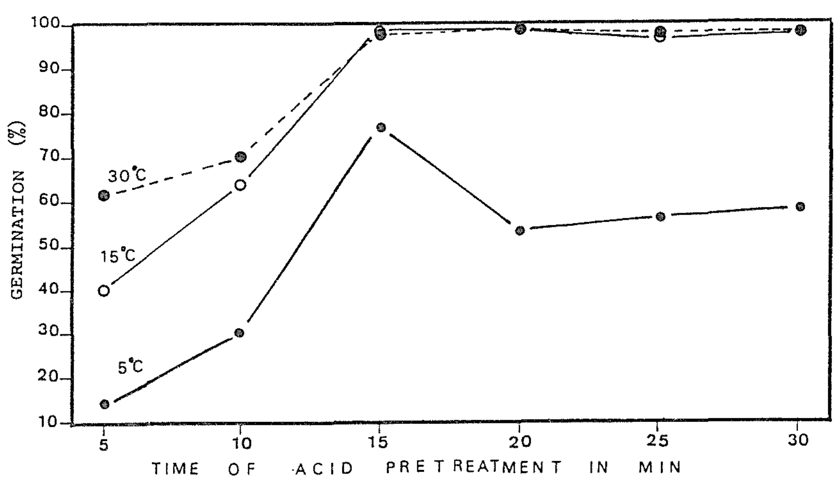

Fig 2. Effect of acid-peretreatment and temperature on germination of dodder (*C. japonica* choisy)

b. *Temeratures required for germination of pretreated seeds*

The mechanical scarification and the acid-pretreatment had apparently removed some part of the seed coat layers allowing water to enter and germination to occur. The results presented in Table 1 shows that most of the seeds which were subjected to these treatments germinated at temperatures from 10 to 30°C within 15 days. There were no apparent differences in percentage of germination obtained at the 15 th day after incubation.

Fig. 3 shows that the increase of temperatures was related to decreasing days which required for germination in acid pretreated seeds. In this case seeds submerged in conc. sulfuric acid for 30 min germinated by 58% in 15 days at 5°C while the same seeds germinated by 98% in 48 hours when incubated at 30°C.

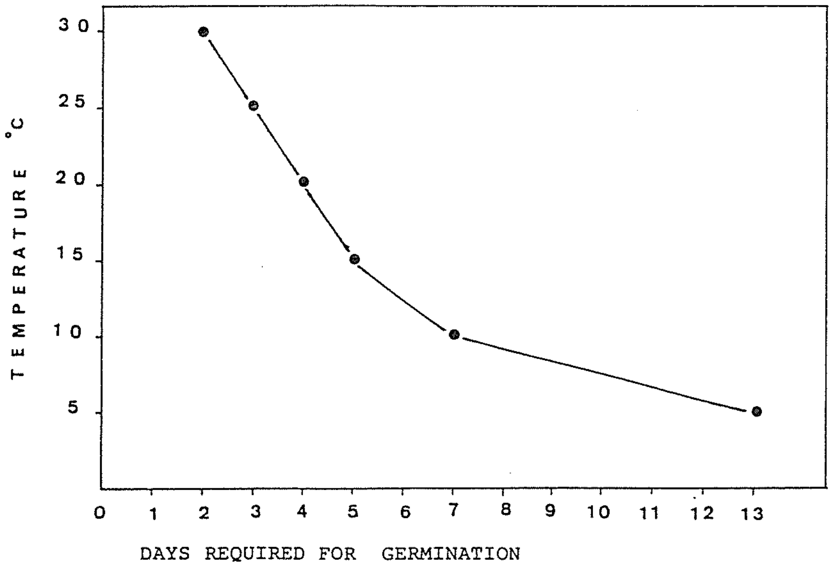

Fig 3. Relationship between temperatures and time required for germination

5.3.2. Depth of seedling emergence

Table 2 shows the emergence pattern of *C. japonica* seedlings at various depths in clay and sandy soils. Seeds which placed at 1 to 8 cm in depth in mid-June started to emerge within 4 to 5 days from 1 to 2 cm depths, and the emergence continued by the third week of July, depending on the depth of placement. The delayed emergence of seedlings in the presence of favourable moisture and temperature conditions was apparently due to the

Table 2. Emergence of dodder seedlings at various depths in clay and sandy soil

Depth of Placing seeds	Percentage of Clay soil	Emergence from Sandy soil
1 (cm)	56.0 ± 4*	0.0
2	53.0 ± 5.9	30.0 ± 8.6
3	58.5 ± 7.7	34.0 ± 5.9
4	59.0 ± 8.3	34.0 ± 7.1
5	56.5 ± 7.7	20.0 ± 4.3
6	50.0 ± 5.9	20.0 ± 6.2
7	43.5 ± 5.9	14.0 ± 3.7
8	34.5 ± 6.6	10.0 ± 3.7

* The mean ± SD

different depths of placement. The drying of the upper soil layers during the period was partially responsible for the low percentage emergence which was prominent in sandy soil.

5.3.3. Effect of burial depth on dormancy and viability of seeds

Table 3 shows the monthly average air and soil temperatures at 1 and 5 cm depths during the time of burial near the experimental site.

Seeds recovered at different times in various burial depths were analyzed as follows : (a) Seeds germinated *in situ* ; (b) Seeds germinated in four weeks of incubation at 25°C after recovery in dark condition during 4 weeks ; and (c) Seeds germinated only after acid pretreatment codition for 20 min. Fig. 4 and 5 show the effect of burial depth on the dormancy and viability of seeds after 10 and 12 months of burial at the different soil depths. These show that viability of dodder seeds was not affected by the burial after 10 and 12 months at all depths investigated. Seeds which were broken dormancy were highest in the 1 cm depths in percentages of germination *in situ* and reduced gradually to deeper parts of soil.

Table 3. Monthly average of air and soil temperature at 1 and 5cm depth during the period from June 1985 to June 1986 near the burial experiment site, Hokkaido University, Faculty of Agriculture, Forest Nursery.

Month	Air Temperatures		Soil Temperatures at		
	Maximum	Minimum	1.0 cm	5.0 cm	depth
	(℃)		(℃)		
June 1985	26.6	10.9	14.4	13.6	
July 〃	24.5	16.5	18.9	18.5	
August 〃	30.8	20.8	22.5	21.9	
September	22.2	12.8	16.3	16.7	
October	16.9	6.5	10.6	10.8	
November	8.8	0.5	4.6	5.0	
December	2.0	− 8.2	− 0.7	0.1	
January 1986	− 0.1	−10.5	− 0.7	− 0.1	
Feberary	2.3	−11.8	− 1.0	− 0.6	
March	5.5	− 3.9	− 0.1	− 0.1	
April	13.2	1.7	5.6	5.1	
May	17.4	5.0	11.2	10.3	
June	21.8	11.3	14.9	14.2	

Table 4 shows percentage of germination *in situ* of seeds which recovered three times in one monthly interval after being buried in the soil at 1, 5, 10 and 15 cm depth for 10, 11, and 12 months. The first recovery was carried out on 17 April 1986 after snow melted and soil temperature was about 3.3°C (the average of the first half of April) at one and 5 cm depth. During that time 18% of the seeds (Table 4) imbibed water (initiation of germination) and they germinated at 25°C in the incubator after two days. In the seeds recovered one month later the germination *in situ* increased slightly by 2% at 1 cm depth. Seeds recovered in June after one year germinated by 23.9% *in situ*, and produced longer seedlings and increased in size significantly more than those recovered earlier. In the laboratory, however, it has been consistently observed that dodder seeds germinated at 5°

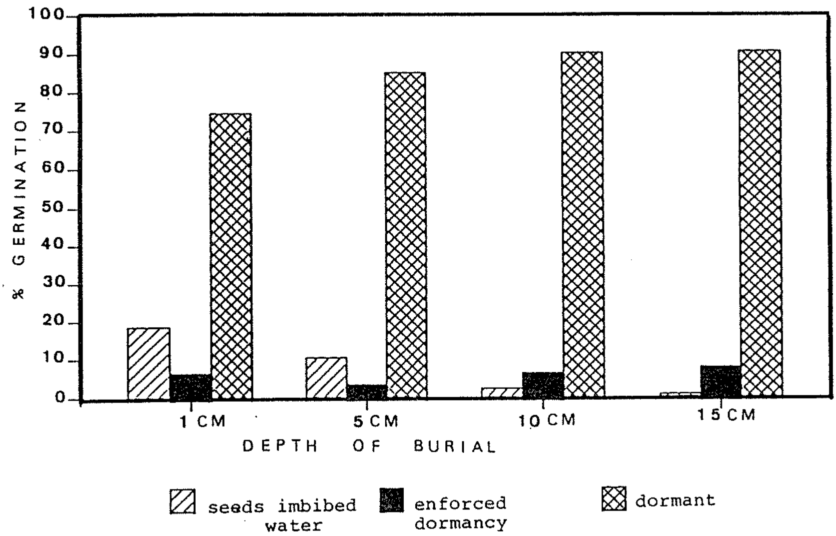

Fig 4. Effect of burial depth on dormancy and viability of dodder seeds recovered after 10 months of burial at different soil depths (recovered in April 1986)

Fig 5. Effect of burial depth on dodder seed dormancy and viability after one year of burial at different depths (recovered in June 1986)

C remained unchanged in size for the first four to five weeks after emergence, and that resumed normal growth when exposed to higher temperature. Generally, percentage germination *in situ* was decreasing significantly by an increasing depth of burial in the soil from 1 to 10 cm. At the 10 and 15 cm depth germination *in situ* remained unchanged during the three times of recovery. The germination *in situ* of seeds recovered in June 1986 was significantly larger than that in April 1986 at 5% level of probability. These

Table 4. Percentage of germination *in situ* of seeds buried at different soil depths and recovered after 10, 11, and 12 months, in April, May and June

Soil depth	Percentage of germination *in situ* after			
in cm	10 (April)	11 (May)	12 (June)	Months
1	18.3*	20.2	23.9	(4.09) **
5	10.4	13.3	14.1	(2.11)
10	2.3	3.1	3.6	
15	0.7	2.2	2.1	
	(3.98)	(6.62)	(4.73)	Lsd.

* These seeds were found imbibe water at time of recovery and germinated at 25 °C in the laboratory within two days.

** Figures in parenthesis indicate Lsd. (least significat difference at 5% level of probability).

facts suggest that the dormancy is broken in response to the sudden changes of environmental factors near the soil surface, and that the germination increases gradually in accordance with the increase of soil temperature during the season.

Table 5 shows the percentage of seeds under enforced dormancy, which buried and recovered after 10, 11, and 12 months at different depths. As seen in Table 5 there were no significat changes at different soil depths and also at the first and second recovery. In seeds recovered in June, after one year, seeds under enforced dormancy at 1 cm depth was signifcantly larger than those at 10 and 15 cm soil depths at 5% level of probability. It suggests that the germination and consequently the emergence of seedlings in *C. japonica* differs from other species which are known for their continuous germination and prolonged emergence (Dawson 1964).

Table 5. Percentage of enforced dormant seeds buried at different soil depths and recovered after 10, 11, and 12 mounths

Soil depth	Percentage enforced dormant seeds after		
in cm	10	11	12 Mounths
1	6.2	6.4	8.7
5	3.4	4.9	6.6
10	6.4	3.1	4.5
15	7.6	2.5	4.4
	N.S	N.S	(2.66)Lsd.5%

5.3.4. Effect of burning on dormancy and viability of seeds

a. *Burning temperatures*

Table 6 shows soil temperatures at the soil surface and 1 cm in depth, and air temperature at 5 and 15 cm above the soil surface at Koshimizu Gensei Ka-en. The highest temperature measured at the soil surface was 256°C and temperatures in the range between 40-256°C continued for 4 min 40 seconds. But the temperatures above 100°C continued for only 2 min. Temperatures at 1 cm depth rose slightly from 15°C before burning to 39°C during burning, and the temperatures between 25-39°C continued for 5 min 30 secnds after burning.

Table 7 shows soil temperatures at the surface, 0.5 cm and at 1.0 cm depths measured

Table 6. Temperatures rise during burning in field conditions at Koshimizu Gensei Ka-en in the spring of 1987

Position of Sensors	Maximum Temp (%)	Range of Temp (%)	Duration min	sec.
5 cm above SS *	430	51－430	8	40
At the SS	256	40－256	4	40
At the SS	184	40－184	8	30
1 cm depth	39	25－ 39	5	30

* SS indicate the soil surface

Table 7. Temperatures rise during in experimental conditions

Position of Sensor	Maximum temp (℃)	Range of temp (℃)	Duration min	sec.
5 cm above SS*	451	45－451	6	40
At the SS	187	45－187	8	50
0.5 cm depth	77	45－ 77	11	
1.0 cm depth	45	40－ 45	9	

* indicate the soil surface

in the laboratory conditions. The temperatures measured in the experiment were nearly similar to those measured in the field conditions. In the experiment condition soil temperature at 0.5 cm depth was 77℃ and as seen in Table 7 the range of temperatures between 45-77℃ cotinued for 11 min.

b. *Effect of burning on dormancy and viability of seeds*

Table 8 shows effect of burning on dormancy and viability of seeds at different soil depths. The dormancy was broken by 5.7% at 0.5 cm depth where soil temperature rose

Table 8. Effect of burning on dormancy and viability of dodder seeds buried at different soil depths in experment 1

Soil depth (cm)	Germination* (%)	Viability (%)
0.0	0.0	42.6
0.5	5.7	87.3
1.0	3.3	94.0
1.5	0.0	95.0

* 50 seeds in three replicates at each soil depth

Table 9. Effect of burning on dormancy and viability of dormant and non-dormant seeds buried at different soil depths in experiment 2*

Soil depth	Dormant	Seeds	non-dormant seeds
	Germination	Viability	Germination**
(cm)	(%)	(%)	(%)
0.0	0.6	74.0	13.3
0.5	2.6	94.6	76.0
1.0	1.3	95.3	81.3

* 50 seeds in three replicates at each depth.
** Acid-pretreated seeds.

to 77°C during burning. As seen in Table 8, 57.4% of the seeds lost viability at the soil surface. Table 9 shows effect of burning on both dormant and non-dormant seeds. The dormancy broken by 2.6% on seeds put at 0.5 cm depth and dormant seeds lost viability by 26%. Non-dormant seeds put at the soil surface lost viability by 86.7%, but those buried at 0.5 and 1.0 cm depths were safe from high temperature caused by burning.

c. *Effect of heat-pretreatment*

Fig. 6 shows effect of heat-pretreatment on the dormancy and viability. Germination percentages of dormant seeds heat-pretreated at temperatures of 70°C for 10-40 min were 7-17%. Similar germination percentages were obtained in seeds heat-pretreated at temperatures of 85°C for 10 and 20 min. As seen in Fig. 6 the heat-pretreatment at temperatures of 85°C for 30-40 min destroyed the viability of seeds.

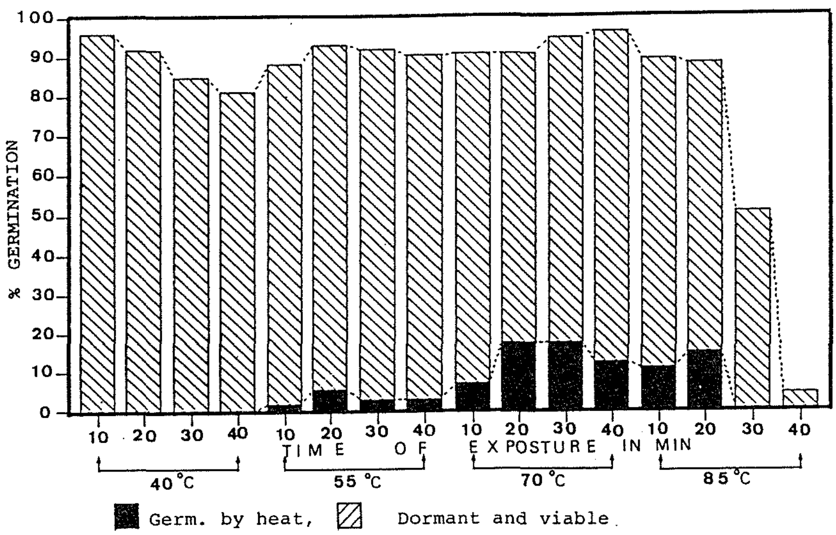

Fig 6. Effect of heat-pretreatment on dodder seed dormancy and viability.

Table 10 shows the effect of heat-pretreatment on viability of acid-pretreated seeds. The results showed that heat-pretreatment at 40-55°C for 10-40 min, and at 70-85°C for 10 min did not destroy viability of acid-pretreated seeds. However, the heat-pretreatment at 70-85°C for 20-40 min destroyed viability.

The results indicated that dormant seeds could germinate after heat-pretreatment at temperatures up to 70-85°C for 10-20 min. But 96% of the seeds lost their viability after heat-pretreatment at 85°C for 30-40 min (Fig.6). On the other hand the acid-pretreated seeds were safer than heat-pretreatment at 70-85°C (Table 10).

5.4. Discussion

5.4.1. Pretreatment of seeds and temperatures required for germination

a. *Pretretment of seeds*

Dormancy of seeds of *C. japonica* was broken by mechanical scarification and by

Table 10. Effect of heat-pretreatment on viability of acid-pretreated seeds*

Oven temp (°C)	Duration (MIN.)	Germination (%)
40	10	100
40	20	98.7 ± 2.3
40	30	97.3 ± 2.3
40	40	98.7 ± 2.3
55	10	100
55	20	100
55	30	98.7 ± 2.3
55	40	94.7 ± 2.3
70	10	100
70	20	93.3 ± 8.3
70	30	64.0 ± 10.6
70	40	21.3 ± 12.2
85	10	93.3 ± 6.1
85	20	52.0 ± 3.6
85	30	0.0
85	40	0.0

* 50 seeds replicated three times in each treatment.

submerging the seeds in conc. sulfuric acid for 5 to 30 min. Mechanical scarification of the seed coat increased germination of dormant seeds of dodder from 70% at 5°C to 94-99% at 10 to 30°C. Barton (1965) reported that mechanical scarification promoted the germination of dormant seeds of the Leguminosae. He stated that the reason for the effects of mechanical scarification on the promotion of germination was ; the opening allows the movement of water through normally impermeable hard seed coats ; it might also make seed coats permeable to gas diffusion ; and it lessened mechanical restriction of radicle protrusion. Hutchison and Ashton (1979) found that mechanical scarification of seeds of *C. campestris* by sand paper increased germination to 98%. They demonstrated that the removal of the epidermal layer and portion of the hypodermal layer increased germination from 1 to 48% and that the removal of both layers increased germination up to 92%.

In case of *C. japonica* the removal of part of the epidermal layer seemed not to promote the germination of dormant seeds. In seeds which buried for 3 months the germination was not improved despite the removal of part of part of the epidermal layer. It indicates that the removal of the epidermis, hypodermis and parts of the macrosclerieds allows water to enter and causes germination to initiate.

By the submersion of the seeds in conc. sulfuric acid solution for 5 min germination increased to 14% at 5°C, 40% at 10°C, and 62% at 30°C. By elongation of the time of acid submersion from 5 to 15 min germination increased from 14 to 77% at 5°C, 40 to 99% at 15°C, and 62 to 98% at 30°C (Table 4, and Fig. 2). It suggests that the epidermal layer and part of the macrosclerieds layers are dissolved by the acid in the acid-pretreatment for 5 min. Elongation of the time of acid pretreatment up to 15 min removed the impermeable layers completely and improved the absorption capacity of the seeds. As a result the germination improved and reached 98%, that means, most of the seeds were able to germinate.

Hutchison and Ashton (1979) found that acid-pretreatment broke the dormancy of seeds of *C. campestris* but was not as effective as mechanical scarification by sand paper. Their results showed that the acid-pretreated seeds for 60 min germinated by 61%. Moreover, they demonstrated that by submerging the seeds in the acid for 5 min, the epidermis swollen and by extending the time of the pretreatment to 15 min, the epidermal and the exodermal layers were hydrolized. In the present study the acid-pretreatment for 5 min did not cause swelling of the epidermal layer but apparently caused the dissolution of it. Moreover, as a result of the extension of the acid-pretreatment, most of the layers were dissolved gradually and the germination rose (Fig. 3). It suggests that the impermeable layer is not restricted to specific region such as above the light line and at the junction of the hypodermis and the palisade layers as suggested by Hutchison and Ashton (1979). The acid-pretreatment was as effective as mechanical scarification in the break of dormancy of seeds of *C. japonica.* The most effective was submersion of the seeds in conc. sulfuric acid for 15 min.

b. *Temperatures required for germination*

The mechanical scarification and the acid-pretreatment removed or dissolved parts of the impermeable layers of hard seed coat and consequently accelerated germination. Seeds submerged in the acid for 30 min started to germinate at 5°C, giving 58% germination ; by increasing temperature to 10–30°C 83% to 98% of the pretreated seeds germinated within 15 days (Table 4). The days required for the seeds to germinate, increased gradually by increasing temperature from 5 to 30°C. The acid-pretreated seeds for 30 min began to germinate after 13 days in 5°C incubation, but after 48 hours in 30°C incubation (Fig. 4). These facts showed that seeds of *C. japonica* required longer time at lower temperatures of 5°C in germination than at higher temperatures. The ability of seeds of *C. japonica* to germinate at a wide range of temperatures is characteristic of this species and services the chances of survival. Germination of acid-pretreated seeds of some other species behaved differently in response to temperature. For example, Allred and Tingey (1964) found that germination in *C. approximata* Bab. was 25–30% at 1.5–7.2°C, and maximum of 51% at 15.5°C ; in *C. indecora* Choisy was 4% at 4.5–7.2°C, 75% at 10°C and maximum of 88% at 21.1°C ; and in *C. campestris* Yunck. 7% at 10°C and maximum of 31% at 15.5–35°C. They demonstrated that *C. approximata* germinated rapidly at 1.4°C ; *C. indecora* at 10°C ; and *C. campestris* at 15.5°C. In Yugoslavia the seeds of *C. prodani* and *C. tinei* germinated best at 20°C, while seeds of *C. campestris, C. pentagona* and *C. monogyna* germinated at 30 to 33°C (Stojanoric and Mijatavic 1973). In Japan, Furuya *et al.* (1980) demonstrated that acid-pretreated seeds of *C. pentagona* germinated at both constant (25 to 30°C) and alternate (30 and 20°C) temperatures in light and dark conditions. They showed that seeds did not germinate at 10°C but did at 15°C.

5.4.2. Effect of burial depth on dormancy and viability of dodder seed

The percentage of total viable seeds of *C. japonica* at various soil depths was not afected after one year of burial in the soil. By partitioning the recovered seeds into ; (1) seeds germinated *in situ*, (2) seeds under enforced dormancy which germinated after being incubated for a period of four weeks, and (3) dormant seeds (hard coated seeds). The results revealed several interesting facts.

Firstly, the seeds at shallower depths germinated *in situ* higher than at deeper ones, when seeds were recovered three times in one month interval from 17 April to 17 June. In seeds recovered on 17 April *in situ* germination initiated because they imbibed water at that time and could germinate easily within 48 hours at 25°C of incubation. The results showed that the seeds could begin to germinate at low temperature of 5°C. However, these seeds sometimes issued the radicle few mm during period from 3 to 4 weeks and resumed normal growth when exposed to more favourable temperatures. These suggested that germination of non-dormant seeds began early in the spring when soil temperature was lower about 5°C. One month later when soil temperatures rose the recovered seedlings showed pronounced emergence of radicle, but the germination *in situ* was not significantly different between the first and the second recovery observed. In the third recovery, germination in situ at 1 cm soil depth increased significantly than first recovery. The results indicated that the dormancy in *C. japonica* was broken in response to soil-burial conditions. These changes showed pronounced effect at the upper 1 to 5 cm soil depth.

Barton (1965) suggested that dormancy of hard seeds can be broken by attack by soil microorganisms and by weathering. He also reported that in natural seeding in the field or in dry storage for overwinter, 80 to 100% of their hard seeds of sweet clover softened by the middle of the following April. He concluded that exposing the seeds to fluctuating temperatures near the freezing point for two or more months required for effective softening of the seed coat. Hutchison and Ashton (1979) reported that cold storage at 4°C will break dormancy of *C. campestris*. They examined samples of seeds which showed 80% germination after storage under Stereoscan Electron Microscope but did not observe any morphological changes, such as cracks or pores which might explain loss of impermeability. Hutchison and Ashton (1980) reported that the dormancy of seeds buried at various soil depths was broken by overwintering ; by 2-27% in new seeds and 18-42% in old seeds.

In this study seeds which were buried on 17 June were dormant when recovered three months later. Samples from these seeds examined under Scanning Electron Microscope showed morphological changes in seed coat, which shows removal of parts of the epidermal layer. It indicates that soil conditions such as temperature, moisture and soil microorganisms help to remove parts of the hard coat. However, the mechanism is not known in details.

The germination percentage of the seeds recovered after overwinter was 2-24% (Table 4). It suggested that removal of parts of the hard seed coat was effective in softening the seed coats. The changes were significant at 1 and 5 cm depths, and it indicated that the fluctuation of temperatures during winter was effective in softening the hard seed coats and breaking dormancy.

Moreover, the rise of soil temperatures during days in summer season, provided that the experimental plots were kept bare throughout the period of burial, seemed to supply sufficient heat to the seeds buried near the soil surface. This in turn will provide the cumulative temperature required for the germination. Dawson (1965) showed that seeds of *C. campestris* planted at various soil depths in bare plots germinated more than those in shade plots, because the soil was warmer in the former than in the latter. He found that soil temperatures in bare plots rose twice as high as in shaded plots during days in summer. The facts mentioned above indicate that the heating of the soil during summer season can also facilitate breaking of dormancy of seeds.

Secondly, during every time of recovery there was small part of the buried seeds which were non-dormant but non-germinated i. e. under enforced dormancy (Table 5). one of the factors commonly thought to be responsible for inducing the state of enforced dormancy in buried seeds is carbon dioxide narcosis (Harper 1972).

5.4.3. Effect of burning and heat-pretreatment on dodder seeds

Seeds of many plant species, if slightly covered by soil can survive a relatively intense fires (Wright and Baily 1982). These authors also reported that the grassland fires wound probably have only slight effect on the mortality of dormant seeds, even if they were lying on the soil surface. However, according to the present burning experiment 26% to 57% of the dormant seeds which were placed artifically on the soil surface lost viability during the burning (Tables 8 and 9). Whereas the non-dormant acid-pretreated seeds lost viability by 87% (Table 9). Despite of such an unusal treatment for removing the seed coat at least 13% of the non-dormant seeds were safe from high temperature of 187°C on the soil surface (Table 9). The seeds buried at 0.5 cm depth were not affected by high temperature in burning experiment (Table 9). Dormant seeds which exposed to heat-pretreatment at 85°C for more than 30 min lost viability by 96%. The non-dormant seeds exposed to 85°C for more than 30 min lost viability 100% (Table 10). These facts suggest that the hard seed coat can to some extend protect the embryo from burning and high temperatures.

Percentages of germination in seeds at 0.5 cm depth in burning experiments were 2.6-5.7% for dormant seeds, and 76% for non-dormant seeds (Tables 8 and 9). Percentages of germination of dormant seeds in heat-pretreatment were 17 and 14% at 70°C for 20 min and 85°C for 10 min, respectively (Fig. 6). Samples from heat-pretreated seeds observed by naked eyes and examined under light microscope showed rupture of the seed coat. Moreover, all the non-viable seeds which heated for more than 30 min at 85°C imbibed water. It indicates that heat-pretreatment ruptures the seed coat and improves permeability to water and lead to break the dormancy. But extension of the time of heat-pretreatment the seed lost viability.

The effect of heat-pretreatment on inducing germination of hard seeds has been reported for several species. For example, Mallik and Gimingham (1985) found that the heat-pretreatment of seeds of *Hypericum pulchrum* resulted in high germination percentage at 100°C for 2 min. Takahashi and Kikuchi (1986) found that heat-pretreatment induced seed germination of *Rhus javanica, Purearia lobata* and *Lespedeza homoloba*. According to Takahashi and Kikuchi (1986) these species were among the important species of the initial post-fire vegetation at Nankita Hill, Miyagi prefecture, Honsyu. Examples about fire-induced germination of *Cuscuta* seeds are scarce. However, as already mentioned, a flush of *C. japonica* was observed after grassland fire (Ito *personal communication*). According to him, the phenomenon is very comparable to the prosperity of *Lespedeza bicolor* in eastern Hokkaido or *Epilobium angustifolium* after frequent fires in Alaska. Furthermore, *C. japonica* made an appearance again in 1987 following the burn in early spring at Koshimizu Gensei Kaen. Based on the results obtained in this investigation the flush of *C.*

japonica after grassland fires could be attributed to the following : (1) Germination of dodder seeds could be induced by fire or burning ; (2) A small part of non-dormant seeds buried in the soil escape high temperatures caused by fires. These can germinate successfully in the post-fire recovery period ; (3) During the period of recovery after burning, a rise of soil temperatures near the soil surface may accelerate dodder seed germination. The rise in soil temperatures during post-burning was reported by Philips (1919, 1930). He noted that large differences in soil temperatures between burned and unburned grasslands during the period of recovery following the burn, and that the soil surface temperature on burned veld may rise twice as high as on unburned one, but that the temperatures may drop several degrees lower on burned one during cold nights than unburned one.

In brief, dormancy of dodder (*C. japonica*) cound be broken by mechanical scarification as well as by submersion in conc. sulfuric acid in the laboratory conditions. In the field, dormancy could be broken by the combined effect of soil factors and overwintering. In the soil, the seed coat could be removed gradually preparing the seeds for effect of winter which soften the seed coat and accelerate germination. Burning and high temperatures caused by burning could also break dodder seed dormancy. Moreover, the conditions after buring favour the germination, emergence and early establishment of dodder in the field. The non-dormant seeds of dodder could germinate at temperatures of 5 to 30℃, and the time required for the germination decreased by increasing the temperatures. The germinating seedlings of dodder could emerge from up to 8 cm soil depth.

6. Host-Dodder Relationship

6.1. Objectives

Cuscuta japonica is a native species found all over japan. This species established its habitat in the natural landscape of the Geueral Coastal Meadow community in Hamaktshimizu Gensei-Kaen. This area is exceptionally beatiful and among the most famous scenic places.

However, the prolific growth of dodder in the coastal meadow community enables it to produce a large amount of seeds which can remain dormant in the soil for many years. The dispersal of these seeds to inland farming systems neighbouring to this coastal meadow community will cause a noxious weed problem in future. The present study is, thus, aiming at the following :

1. To list up host range of *C. japonica ;*
2. To test the susceptibility of some cultivated crops to *C. japonica ;*
3. To find what is a major host or a minor host of *C. japonica.*

6.2. Materials and Methods

The field observations were carried out in Koshimizu Gensei Kaen and its adjacent sand dune areas, stretching along the Okhotsk Sea, NE Hokkaido. The area is about 7. 5 ck in length and 100 m in width. The study area, as mentiomed already, is covered with the sand dune General Coastal Meadow community and the *Querucus mongolica* var. *grosseserrata* community. Most part of this area is represented by the General Coastal

Meadow cmmunity in which *Rosa rugosa* Thunb. is dominant and is followed by *Conioselinum kamtschaticum* Rupr., *Dianthus superbus* L., *Dracocephalum argunense* Fisch., *Galium verum* var. *trachycarpum* DC., *Geranium yesoense* Fr. & Sav., *Hemerocallis middendorffii* Trautv. et Mey., *Lilum duvricum* Kerl - Gawl., and *Malus baccata* var. *mandchurica* (Maxim.) C. K. Schn. In the General Coastal Meadow community *Cuscuta japnica* Choisy is often an important species, because of its parasitic character on members of the General Coastal Meadow community and sometimes disturbes the regeneration of the community after burning.

The lists of host plants as well as their relative susceptibility to dodder were compiled based on the ability of the dodder to attack, establish and regenerate on host. This was accomplished through field observations and experimental studies during the period from the year 1985 to 1987.

6.2.1. Field observations

Reconniassance survey was to locate the patches, where dodder was found to grow on plants. The patches were marked and a 1×1 m qaudrat was put on each of them. As the periodic recurrence of the dodder. The dodder made its appearance twice in the study area during the period of study ; the first was in 1986 where dodder found in sporadic patches in Yanbetsu ; the second was in 1987 following the grassland fires in Koshimizu Gensei-Kaen, where dodder might be more abundant than the previous year.

The plant species including the dodder-infected plants within each quadrat were recorded in July and August of 1986. The plants recorded in August are presented according to their frequency of occurrence as seen in Table 11. Since it was not possible to isolate the dodder on each plant in field conditions, the infected plants were evaluated based on visual observations which were supplemented by the following test criteria : i) checking the haustorial penetration to ensure firm attachment of dodder filaments (vines) to its host ; ii) relative increase in dodder stem diameter, and the elongation and growth of the stem, which is especially helpfull at the early stages of growth of dodder on the host ; and iii) the growth vigour of dodder when the growth of dodder was suppressed on non-suitable host plants. The assessment of the survival potential of dodder on the different host species was obtained by collecting five plants of each species infected by dodder three times in July, August and September of 1986. The sampling was carried out within and outside the quadrats. The host plants were clipped at the soil surface, then dodder filament was detached from its host plant and both were dried at 60 ℃ for two weeks to measure the dry weight. Other parameters measured include the dodder stem diameter in relation to that of its host and the number of capsules produced by dodder on the tested plants.

The host and non-host species were recorded twice in 18 patches, in August and September 1987. These plants are presented Table 12 and 13.

6.2.2. Experimental studies

Two experiments were carried out in 1986 and 1987. The experiments aimed at testing the susceptibility of some crop plants to dodder, and the damage caused by dodder on them ; and also aimed at estimation of the survival potential of the dodder on host species.

Table 11. Plant species recorded in 20 quadrants at Yanbets NE Hokkaido in August 1986, species arranged in order of frequency, and the dodder-infected plants are indicated by solid squares

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Galium verum var. *trachycarpum* DC.	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■
Rosa rugosa Thunb.	■	○	■	○	■	■	■	■	■		■	○	○	■	■	○	■	■	○	
Scutellaria strigilosa Hemsl.	○	○	■	○	■	■	■	■	■	○		○	■	○	■	○			○	○
Moehringia laterifolia L.		○	○	○	○	○	○	○	○	○	○	○			○	○	○			
Polygonatum humile Fisch.		○		○		○	○	○	○		○		○	○	○	○	■	■		
Rubus parvifolius L.			■	■		■	■	■		○	○	○			○	○	■			■
Sedum purpureum L.	■			○	○	○	■	■		○			○	○	■				■	
Lilium davuricum Ker.-Gawl.	■	○	■	○		○	■	○			○		○			○				
Poa pratensis L.	○	■			■	■		○	○	○				○	○				○	
Artemisia montana (Nakai) Paman.	■	■					■			■	○	○		○		○				■
Carex sp.			○		○	○	○			○	○	○	○		○					
Elymus mollis Trin.			■					○			○	○	○	○	○	○		○		
Geranium yezoense Fr. & Sav.			■	■							○	○	○			○			■	■
Lathyrus maritimus (L.) Bigel.		○			■	■			■							■	○	■		
Vicia japonica A. Gray.			■	■			■	■			■				■					○
Hieracium umbellatum var. *japonicum* Hara.	○	○	■					■				■				■			■	
Phleum pratense L.	■	○			○					○									○	○
Dianthus superbus L.		○				○		■			○	■	■							
Artemisia japonica Thunb.	■										■	○	■	■						
Allium tuberosum Rott.		■	■				○		○											○
Arabis glabra (L.) Bernh.				○		■	■	■						○						
Conioselinum kamtschaticum Rupr.										○		■				○	■			■
Dracocephalum argunense Fisch. ex Link.	■				○							○	■							
Inula salicina ver *asiatica* Kitam.			■							○	○									
Festuca rubra L.											○		○	○						
Phragmites communis Trin.										○										■
Malus baccata var. *mandshurica* (Maxim.) C. K. Schn.											○	■								
Solidago virga-auea var. *leiocarpa* (Benth) Miq.												○					■			

Table 12. Plant species recorded in 19 quadrants at Hamakoshimizu Genseikaen in August 1987, species arranged in order of frequency and the dodder-infected plants are indicated by solid squares

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Rosa rugosa Thunb.	■	■	■	○	■	■	■	■	■	■	■	○	○		■	■		○	■
Artemisia montana (Nakai) Pampan.	■		■	■	■	○	■	■	■	■		■	○	○	■		■	■	■
Galium verum var. *trachycarpum* DC.	■	■		○	○	■	■	■						■	■		■		■
Moehringia lateriflora L.	○		○	○	○	○	○		○	○	○				○			○	
Rubus parvifolious L.			■		■	■		○	○		■	○			■	○		■	○
Poa pratensis L.	○							○		■	○		○	○	○	■		○	○
Scutellaria strigilosa Hemsl.	○		○			○	■			○			■		■	○			○
Vicia japonica A. Gray	■				■	■	■			■			■	○	■			○	
Hemerocallis yezoensis Hara				■			■	■	■	■			○	○		■	■		
Vicia cracca L.		○			■	○		■	■		○						■	■	
Polygonatum humile Fisch.				○		○				○			○	○	○			○	○
Lilium davuricum Ker.-Gawl.	○		■	■				■		■			○				■		
Malus baccata var. *mandshurica* (Maxim) C. K. Schn				○	○		○					○			○		○		■
Conioselinum kamtschaticum Rupr.										■	■	■		■	■	○	■		
Elymus mollis Trin.	○				■	○	○												■
Stellaria radians L.			○			○						■				■			
Viburunum opulus L. var *calvescens* Hara.									■		○	○				■			
Potentila splendens willd.		○			■				○										
Festuca rubra L.			○					○											
Coeloplerum gmelinii (DC.) Ledeb.								■	■										
Phleum pratense L.		○	○																
Geranium yezoense Fr. & Sav.				■															
Chenopodium album L.												○							
Inula salicina var. *asiatica* Kitam.												○							
Hieracium umbellatum var. *japonicum* Hara.														■					
Achillea alpina var. *pulchra* Kitam.																		■	
Dracocephalum argunese Fsch. ex Link.																			○

Table 13. Plant species recorded in 18 quadrats at Hamakoshimizu Genseikaen on September 1987, species arranged in order of frequency and dodder-infected plants are indicated by solid squares

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Vicia cracca L.	■	■	■	○	■	■	■	■	■	■	■	■	○	■	○	■	■	■
Rosa rugosa Thunb.	■	■			■		■	■	■	■	■	■	○	■	■	■	■	■
Hemerocallis yezoensis Hara.		■	■	○	○		■	○	○	■	■	○	■	■		○	○	■
Galium verum var. *trachycarpum* DC.	■			■		○		○	■		■	○	■	■		■		■
Poa pratensis L.			■	○	■		○		○	○	■	○		■	○			
Rubus parvifolious L.					■	■	○	■		○					■		○	■
Scutellaria strigilosa Hemsl.								○	■	○		○	■	■	○			○
Elymus mollis Trin.		○	■			■	○					○	■		○			■
Artemisia montana (Nakai) Pampan.			■				■						■		■	■	■	
Achillea alpina var. *pulchra* Kitam.			■	■	■				■	○	■							
Sedum purpureum L.	■	○		■								■		■				■
Inula salicina var. *asiatica* Kitam.					■			■		■		○	■		○			
Hieracium umbellatum var. *japonicum* Hara.		■		■				○	○	■					○			
Allium tuberosum Rott.	○										■	■				■		○
Lilium davuricum Ker.-Gawl.					■					○	■			■			■	
Polygonatum humile Fisch.						○						○	○	○				
Phleum pratense L.	■				○									■		○		
Moehringia lateriflora L.						○							○			○		
Geranium yezoense Fr. & Sav.			■				○	○	■									
Vicia japonica A. Gray.				■	■	■												
Conioselinum kamtschaticum Rupr.					■	■	■								■			
Malus baccata var. *mandshurica* (Maxim.) C. K. Schn.	■							■						■				
Linaria japonica Miq.				○						○								■
Agrimonia pilosa Ledeb.								■										■
Lathyrus maritimus L. Bigel.						○						■						
Dianthus superbus L.				○														

a. *Susceptibility of some crop plants to C. japonica*

In this experiment 15 crop species belonging to 6 families were tested for their susceptibility to dodder. Seed and seedling used were obtained from commercial source (Sapporo Konoen) ; *Chrysanthemum coronarum* L., *Tagetes patula* L., *Brassica campestris* L., and *B. pekinensis* Rupr. were sown on 15 June in plastic planters filled with a 1 : 1 mixture of soil and vermiculite. As a fertilizer, Hyponex (N 6.5%, P 6%, K 19%) which was disolved in water at the rate of 1 g per litre and applied to them twice a week. The rest were grown in field plots under natural conditios. They were seeded on 15 May except for *Solanum melongena* L., *Cucumis sativus* L., and *Lycopersicon esculentum* L. were transplanted on 15 June 1986.

b. *Inoculation of dodder to host plants*

Dodder seeds used were collected from native places at Koshimizu Gensei-Kaen in the spring of 1985. Seeds collected were submerged in concentrated sulfuric acid solution (98%) for 30 min.; rinsed with water ; dried and kept in glass jars prior to the experiment. Some of them were sown together with host ; others were placed in moistened filter paper in petri dishes and incubated at 25 °C. When the seedlings reached 6 to 7 cm long they were inoculated to the test plants. The dodder seedlings were attached to small sample tubes plugged with moistened cotton in order to avoid drying up, and then placed beside the host. When dodder seedlings failed to attach in case of *Lycopersicon esculentum* and *Cucumis sativus,* they were brought into contact with young stems of dodder developed on different host species.

c. *Quantitative assessment to distinguish between major and minor hosts*

In this experiment six crop species belonging to two families, Solanaceae and Leguminosae were selected. Among those six species, five species were previously tested for susceptibility in the first experiment. These plants were raised in plastic pots filled with a 3 : 1 mixture of POT S (a commercial formula containing N 200 mg, P 500 mg, and K 200 mg per litre) and vermiculite.

The plants were raised as follows : i) Soybeans, peas and beans were planted in trays in the green house. Sixty seedlings were transplanted in pots (15 cm) one week later after emergence. From them, 30 plants were inoculated by dodder seedlings on transplanting ; ii) Potato seeds were swon directly in 60 pots of 20 cm in diameter. The seedlings were thinned to one seedling per pot one week later after emergence and half of them inoculated with dodder. The potato plants were removed from the pots to field plots six weeks later and Kept at wide spahing to ensure isolation of dodder plants ; iii) in egg plants 30 to 35 day-old seedlings were transplanted directly in 60 pots with 20 cm in diameter. Then half of them inoculated by dodder : iv) in tomatos 25 to 30 day-old seedlings were transplanted in pots and a part of them were inoculated by dodder. Young tomato seedlings which were one, two and three week-old were also tested for their susceptibility. During the first and second week of the experiment the plants were kept in a plastic house and then removed into outdoor conditions. The area was kept weed free and water was supplied when necessary. Number of days taken for attachment of dodder to its host were recorded. The parasitism of dodder was judged according to the following criteria : i) an increase in the diameter of seedlings which were immediately in contact with the host ; ii) changes in color of dodder stem from light green to yellow with reddish spots ; iii) elongation of the growing point on the host ; and iv) interruption of the connection of the seedling with the soil. When dodder get established and started to grow, the test plant was considered to be infected.

Percentages of susceptibility were calculated. In order to estimate decrease in yield of the tested plants due to infection the following were recorded : (i) the length of dodder filaments per host and (ii) the survival potential of dodder on the host species by harvesting plants (dodder and host) every two weeks. For this purpose 5 infected and 5 non-infected plants of eggplant, bean and pea were harvested. Dodder filaments separated from its host were measured and dried for determination of dry weight. Potato and soybean were harvested only once after maturity because of the limited number of infected plants. The survival potential of dodder on the different host species was estimated as follows :

Survival potential of dodder = (TDW of Dodder/TDW of its Host)×100

Host preference in dodder was also estimated by evaluating the decrease in yield caused by dodder on different host species ; percent susceptibility of the hosts ; the survival potential of dodder and the length of dodder filaments and the ability of dodder to

6.3. Results

6.3.1. Field observations

Table 11 shows plant species recorded in 20 quadrats in dodder infected communities at Yanbetsu in 1986. The plant species were arranged in order of frequency. Tables 12 and 13 show plant species recorded at Koshimizu Gensei-Kaen in 1987. These tables show that the most frequent hosts include *Rosa rugosa, Galium verum* var. *tachycarpum, Artemisia montana, Scutellaria strigilosa, Vicia cracca,* and *Hemerocallis yezoensis.* On the other hand, certain species, although found within the dodder-infected patches, were sometimes free from dodder. These include *Moehringia laterifolia, Polygonatum humile, Elymus mollis, Phleum pratense,* and *Poa pratensis.*

Fig. 7 shows the dry weight of dodder and the dry weight of its hosts as obtained three times during growing season in July, August and September 1986. Table 14 shows the stem diameter and the number of capsules of dodder in relation to different hosts. These show that dodder could grow and survive differently on various hosts. On hosts such as *Artemisia montana, A. japonica* and *Conioselinum kamtschaticum* dodder could attach and grow from seedling to reproductive stages, whereas on hosts such as *Dracocephalum argunense* and *Lathyrus maritimus* the parasite could grow for several weeks and then die before reproduction. The seedling of the parasite immediately after emergence could not establish on all hosts equally. For instance, the parasite has to grow up on other host, and attain a certain size in order to attack woody species such as *Rosa rugosa* and *Malus baccata.* However, in the case of monocotyledonous plants the pattern of parasitism was found to be different from the above mentioned dicotyledonous species. These plants can be parasitized by adult dodder growing on neighbouring dicotyledonous host. In this case haustorial penetration and yellowing could be found on the parasitized monocotyledonous hosts.

The above mentioned facts suggest that the pattern of parasitization of the host and

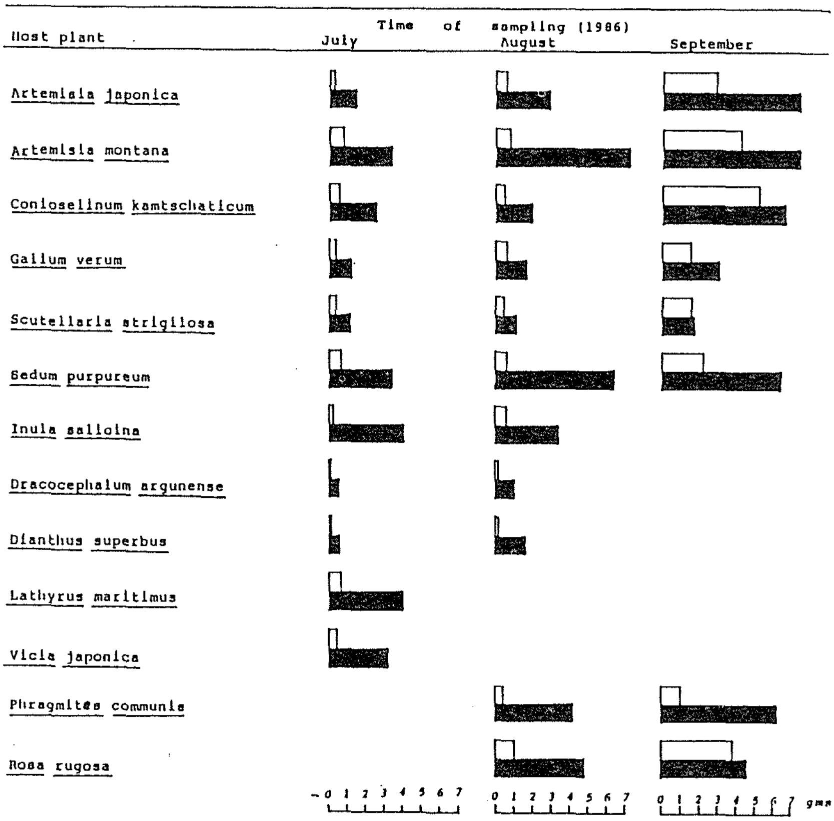

Fig 7. Dry welght varktlon of Japanese dodder in response to different host plants in three stages of growth during the year 1986. □, dodder dry welght ; ■, host plant dry welght (an average of 5 plants parasitized by dodder).

the suvival potential of the parasite vary significantly among various hosts. Accordingly, two groups of hosts were identified. Table 15 shows the first group of hosts which includes 30 dicotyledonous hosts. Table 16 shows the second group which includes 8 monocotyledonous hosts.

6.3.2. Experimental studies

a. *Crop plants tested for their susceptibility to dodder*

Table 17 shows 15 crop plants testd for susceptibility to dodder. Among these 7 species were parasitized. However, the parasite could grow and reproduce on only 4 hosts such as *Solanum melongena* and *Glycine max.* On the remaining 3 hosts the parasite could grow up until the flowering stage but it could not reproduce. On the other hand on 8 species the parasite could not establish itself. In some instances as in *Lycopersicon esculentum* and *Trifolium pratense* the parasite could attach and grow for 1-2 weeks and then die. As a result the tested crop plants were grouped into three groups based on the ability of dodder to attack and to survive on them.

Table 14. Dodder characters (stem diameter and number of capsules) in relation to different host species.

Host species	Stem diameter in mm* Host	Dodder	Number of capsules
Artemisia japonica Thunb.	2.41 ± .22	1.50 ± .30	180 ± 99
Artemisia montana Pampan.	3.80 ± .50	2.10 ± .60	271 ± 139
Conioselinum Kamtschaticum Rupr.	4.41 ± .89	2.70 ± .50	252 ± 120
Galium verum var. *trachycapum* DC.	2.38 ± .38	1.97 ± .83	97 ± 15
Rosa rugosa Thunb.**		2.46 ± .34	229 ± 80
Scutellaria strigilosa Hemsl.	2.20 ± .42	2.20 ± .34	54 ± 32
Sedum pureum L.	7.56 ± .47	3.16 ± .47	129 ± 60
Dianthus superbus L.	1.70 ± .40	1.60 ± .38	
Dracocephalum argunense Fisch.	1.66 ± .47	1.42 ± .24	
Lathyrus maritimus (L.) Bigel.	3.08 ± .47	2.21 ± .61	
Inula salicina var. *asiatica* Kitam.	3.40 ± .50	1.60 ± .20	
Rubus parvifolius L.	3.90 ± .72	2.90 ± .28	
Allium tuberosum Rott.	2.66 ± .22	2.01 ± .29	
Lilium davuricum Ker-Gawl.	5.13 ± .19	1.78 ± .29	
Polygonatum humile Firch.		1.43 ± .37	
Phragmites communis Trin.		1.88 ± .33	49 ± 16

* Measurement when first time collected.
** Rosa rugosa was sampled by collecting five twigs each 20cm. long from dodder-infected plants.

b. *Quantitative assessment to distinguish between crop hosts*

i. Susceptibility of the plants tested

Table 18 shows the percent infection and time which dodder required to establish on plants It revealed that eggplants, peas and beans were highly susceptible, and that potatos and soybeans were intermediately susceptible. While it revealed that tomato was completely unsusceptible. On some hosts dodder was able to reproduce. They were eggplant, potato, and soybean. Dodder, however, grew luxuriantly on eggplant and potato but was very small and its reproductive capacity reduced greatly on soybean. Dodder faied to reproduce on peas and beans in spite of their high susceptibility to it. Moreover, dodder grew rather slowly on them and it did not severely injures them as compared to eggplant and potato.

On the other hand potato and tomato were resistant to dodder seedling. In a case of potato which was intermediately susceptible, non-infected plants set off a sort of defense mechanism at the point of contact to dodder. The mechanism was the expulsion of the dodder and was caused apparently by the necrosis of the outer cortical layer of stem of the host around the point of contact. Consequently, dodder seedlings failed to establish on the plants. In another case of tomato which was completely free from dodder, dodder seedlings failed completely to establish itself on tomatoes at all stages of growth.

ii. Yield losses of the crops tested

The crop plants which infected by dodder suffered from losses in growth vigour and yield. Fig. 8 shows that the TDW of eggplant was significantly reduced during the different stages of growth. The average number of fruit per plant and the fruit yield per

Table 15. A list of host plants on which Japanese dodder grew and survived (first group)

Family	Scientific name	Japanese name
Caryophyllaceae	*Dianthus superbus* L.	Ezokawaranadeshiko
	Stellaria radians L.	Ezooyamahakobe
Chenopodiaceae	*Chenopodium album* L.	Shiroza
Celastraceae	*Celastrus orbiculatus* Thunb.	Tsuruumemodoki
	Euonymus sieboldianus Bl.	Mayumi
Campanulaceae	*Adenophora triphylla* var. *japonica* (Regel) Hara	Tsuriganeninjin
Caprifoliaceae	*Viburunum opulus* L. var. *calvescens* Hara	Kamboku
Compositae	*Artemisia japonica* Thunb.	Otokoyomogi
	Artemisia montana (Nakai) Pampan.	Ezoyomogi
	Hieracium umbellatum var. *japonicum* Hara.	Yanagitanpopo
	Inula salicina var. *asiatica* Kitam.	Kasenso
	Solidago virga-aurea var. *leiocarpa* (Benth.) Miq.	Miyamaakino-kirinso
Crassulaceae	*Sedum purpureum* L.	Murasakibenkeiso
Cruciferae	*Arabis glabra* (L.) Bernh.	Hatazao
	Capsella bursa-pastoris (L.) Medic.	Nazuna
Geraniaceae	*Geranium yesoense* Fr. & Sav.	Ezofuro
Labiatae	*Dracocephalum argunense* Fisch. ex Link.	Musharindo
	Scutellaria strigilosa Hemsl.	Namikiso
Leguminosae	*Lathyrus maritimus* (L.) Bigel.	Hamaendo
	Thermopsis lupinoides (L.) Link.	Sendaihagi
	Vicia cracca L.	Kusafuji
	Vicia japonica A. Gray	Hirohakusafuji
Ranunculaceae	*Thalictrum sachalinense* Lecoyer.	Akikaramatsu
Rosaceae	*Agimonia pilosa* Ledeb.	Kimimizuki
	Malus baccata var. *mandchurica* (Maxim.) C. K. Schn.	Ezonokoringo
	Rosa rugosa Thunb.	Hamanasu
	Rubus parvifolius L.	Nawashiroichigo
Rubiaceae	*Galium verum* var. *trachycarpum* DC.	Ezonokawaramatsuba
Umbelliferae	*Conioselinum kamtschaticum* Rupr.	Karafutoninjin
	Coelopleum gmelinii (DC.) Ledeb.	Ezonoshishudo

plant reduced by 98.0% and 94.4%, respectively (Table 19). In infected eggplant all flowers dropped and fruit yield was nilified. In some cases the parasite induced gall formation on the host stem.

Table 16. Plants on which Japanese dodder grew when they were associated with other more suitable dodder-parasitized plants

Family	Scientific name	Japanese name
Gramineae	*Elymus mollis* Trin.	Hamaninniku
	Phleum pratense L.	Oawagaeri
	Phragmites communis Trin.	Yoshi
	Poa pratensis L.	Nagahagusa
Liliaceae	*Allium tuberoum* Rott.	Nira
	Hemerocallis yezoensis Hara.	Ezokisuge
	Lilium davuricum Ker-Gawl.	Ezosukashiyuri
	Polygonatum humile Fisch.	Himeizui

Table 17. Three groups of hosts in response for dodder infection

Group	Dodder reaction to plants tested				
	twine :	attach :	grow :	bloom :	fruit
Group a					
1. *Cucurbita moschata* Dech. ex. Poier.	+	+	+	+	+
2. *Glycine max* Merr.	+	+	+	+	+
3. *Solanum melongena* L.	+	+	+	+	+
4. *Solanum tuberosum* L.	+	+	+	+	+
Group b					
5. *Brassica campestris* L.	+	+	+	+	−
6. *Brassica pekinensis* Rupr.	+	+	+	+	−
7. *Pisum sativum* L.	+	+	+	+	−
Group c					
8. *Chrysanthemum coronarium* L.	+	+	−	−	−
9. *Lycopersicon esculentum* Mill.	+	+	−	−	−
10. *Trifolium pratense* L.	+	+	−	−	−
11. *Tagetes patula* L.	+	+	−	−	−
12. *Zea mays* L.	+	+	−	−	−
13. *Zea rugosa* Bonaf.	+	+	−	−	−
14. *Cucumis sativus* L.	+	−	−	−	−
15. *Phleum pratense* L.	+	−	−	−	−

\+ indicates positive reaction.
− indicates negative reaction.

Table 18. List of plants tested, number of plants inoculated, percent infection and time required for dodder to establish on hosts

Plant name	No. of Plants tested	Infection (%)	Days to Establish
Eggplant *Solanum melongena* L.	30	100	5 to 6
Potato *S. tuberosum* L.	30	46.6	5 to 8
Peas *Pisum sativus* L.	30	100	7 to 8
Bean *Phaseolus vulgaris* L.	30	90	7 to 8
Soybean *Glycine max* Merr.	30	36.7	6 to 8
Tomato *Lycopericon esculuntum* Mill.	9	0	
〃 〃 One-, two-, and three-week-old seedlings	9		

Table 19. Reduction of fruit yield of eggplant in response to dodder infection

Treatment	Plant height (cm)	Aver. no. of fruit per plant	Aver. weight of fruit (g)
Control	36.8 ± 1.9	12 ± 3	267.0 ± 49.7
Dodder infected	22.6 ± 3.8	1 ± 1	14.9 ± 23.4
Reduction (%)	38.8	93	94.4

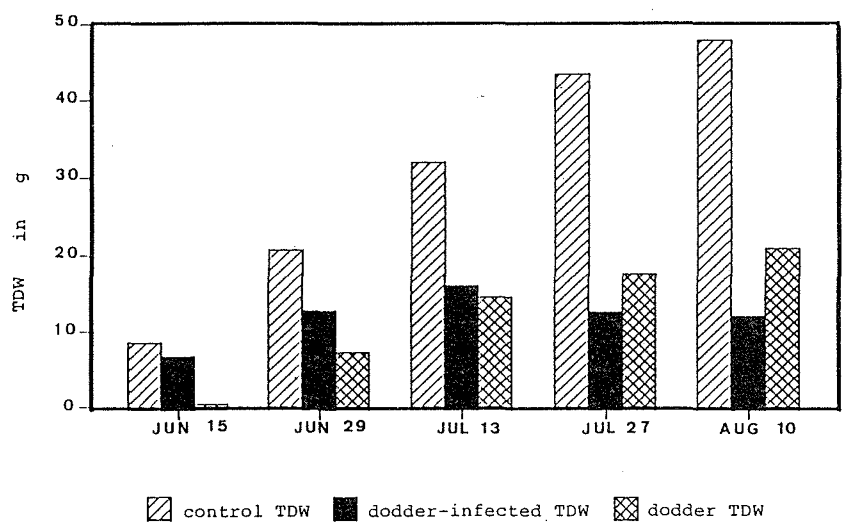

Fig 8. Effect of dodder infection on TDW yield of eggplant (*Solanum melongena* L.).

Table 20 shows reduction in yield of potatoes. The average number of tubers, weight of tubers per plant and the dry weight of shoots per plant were reduced by 41.7%, 66.2%, and 57.3%, respectively. Infected potatoes showed symptoms of leaf chlorosis in 3 to 4 weeks after the infection. Chloritioc leaves increased significantly in 8 to 9 weeks after then and accelerated senility of potatoes.

Table 20. Reduction of tuber yield and shoot dry weight of potato in response to dodder infection

Treatment	Aver. no. of tuber per plant	Aver. weight of tuber (g)	Shoot dry weight (g)
Control	12 ± 3	340.8 ± 22.8	17.9 ± 2.7
Dodder infected	7 ± 2	115.2 ± 40.2	7.7 ± 1.4
Reduction (%)	41.7	66.2	57.3

Among the plants tested, some of the legumes were not severely injured by dodder. In peas there was no significant reduction in TDW particularly in the first 4 to 6 weeks after infection as seen in Fig. 9. After flowering of peas dodder grew well on peas and reduced the TDW of peas by 16.6% which is significantly different at 5% level of probability (Table 21). In this case dodder stimualted gall formation around points of attachment on the stems.

Table 21. Reduction in pod yield of peas in response to dodder infection

Treatment	Aver. weight of pods
Control	33.7 ± 7.1
Dodder infected	30.9 ± 16.9
Reduction (%)	16.6

Fig. 10 shows the effect of dodder infection on TDW of beans at different stages of growth. The yield of beans infected reduced significantly. The average number of pods, and the average weight of pods per plant were reduced by 47.1% and 53.9%, respectively (Table 22). The severe reduction in yield was apparently due to the consistant shedding of flowers and immature pods (Table 23).

iii. The survival potential of dodder on the plants tested

The survival potential of dodder on a particular host could be defined as the index which examines the possibility of dodder to establish and grow on the host. It could also indicate whether dodder would reproduce on the host or not. The index could be expressed as the percent of the TDW of dodder divided by the TDW of its host. It was obtained for eggplants, peas and beans (Figs. 11, 12, and 13) at a two weeks interval. In case of potato and soybean it was obtained only once after maturity of the host, because only a limited number of the plants was successfully infected. In the case of potato this

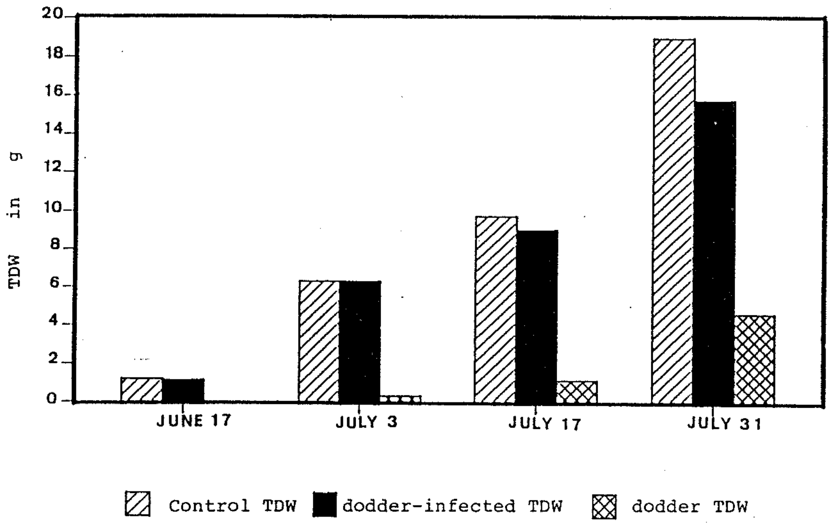

Fig 9. Effect of dodder infectio on TDW yield of peas (*Pisum satius* L.).

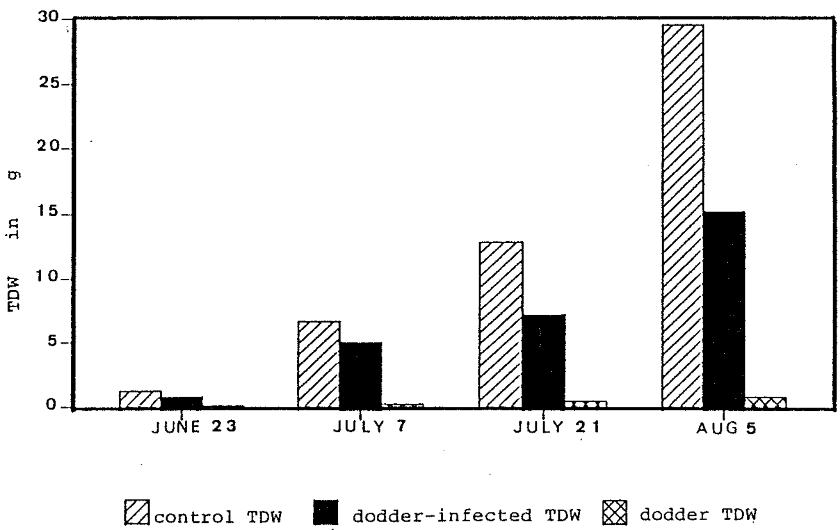

Fig 10. Effect of dodder infection on TDW yield on beas (*Phaseolus vulgaris* L.).

Table 22. Reduction in pod yield of bean in response to dodder infection

Treatment	Aver. No. of pods per plant	Aver. weight of pods per plant (g)
Control	17 ± 2	107.7 ± 18.6
Dodder infected	9 ± 4	49.7 ± 29.8
Reduction (%)	47.1	53.9

Table 23. Reduction in pod yield of soybean in response to dodder infection

Treatment	Plant hieght (cm)	Aver. No. of pods per plant	Aver. weight of pods (g)
Control	53.3	30 ± 3	21.1 ± 2.1
Dodder infected	53.0	21 ± 4	13.6 ± 2.4
Reduction (%)	0.6	30.0	35.5

ratio was calculated by considering the shoots dry weight instead of the TDW. Table 24 shows the survival potential and the approximate length of dodder filaments per host species. The results showed that the dodder grew luxuriantly on eggplant, and that produced very long filaments, i. e. 32 m in 6 weeks after infection. Dodder began to flower on 25 July and continued for 45 to 55 days. Although the hosts weakened and were about to die, the dodder set fruits and produced viable seeds on them except for the distal parts which were not fruiting and dying contemporaneously.

iv. Total length of dodder filaments

On potato dodder grew up successfully and produced long filaments i. e. 22.5 m per host plant. Dodder was successful in flowering, fruiting and producing viable seeds. On peas beans and soybean dodder produced short filaments. The maximum length of those filaments were ; 6.2 m, 2.9 m, and 3.1 m per host, respectively (Table 24). Dodder flowered and set fruits and produced seeds on soybean plants but failed to fruit on peas and beans because the hosts weakened and started to die. These results can be summarized as follows :

Table 24. The survival potential and approximate length of filaments of dodder (*Cuscuta japonica* Choisy) on different crop hosts

Host	Surval potential (%)	Length of filaments (m)
Eggplant	189.5	32
Potato	182.3	22.5
Pea	29.04	6.2
Bean	5.02	2.9
Soybean	6.12	3.1

(1) Plants tested can be arranged in a descending order of susceptibility, Eggplant > Pea > Bean > Potao >Soybean.

(2) Plants infected suffered from losses in growth vigour and in TDW. TDW of eggplant, potato, bean, soybean, and pea were reduced by 75%, 57.33%, 48.72%, 35.86%, and 16.6%, respectively.

(3) Dodder was able to establish, grow and reproduce on eggplant, potato and soybean, but its growth was terminated after flowering on pea and bean.

(4) The length of dodder filaments on eggplant was 32 m, 22.5 m on potato, 6.2 m on pea, 3.1 m on soybean, and 2.9 m on bean.

(5) The survival potential of dodder on different hosts were as follows ; eggplant 189.5%, potato 182.3%, pea 29.04%, soybean 6.12%, and bean 6.12%.

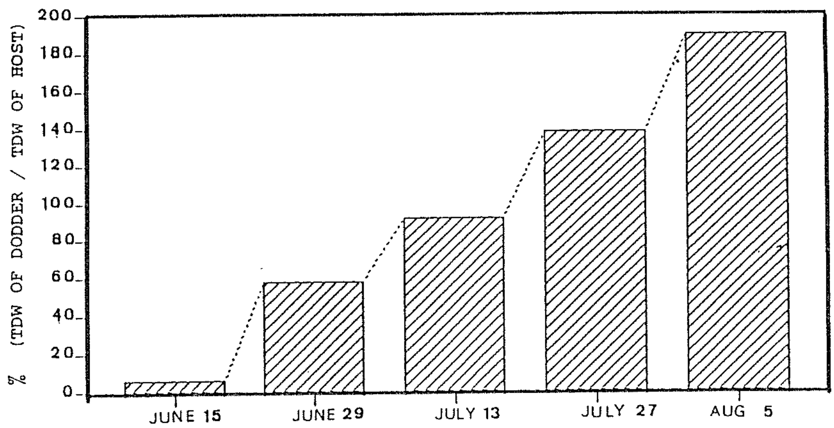

Fig 11. Survival potential of dodder on eggplant (*Solanum melongena* L.)

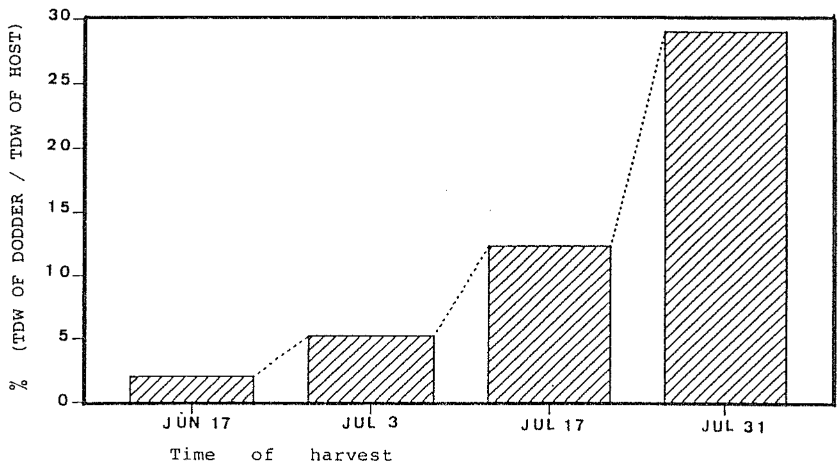

Fig 12. Survival potential dodder on pea (*Pisum sativus* L.)

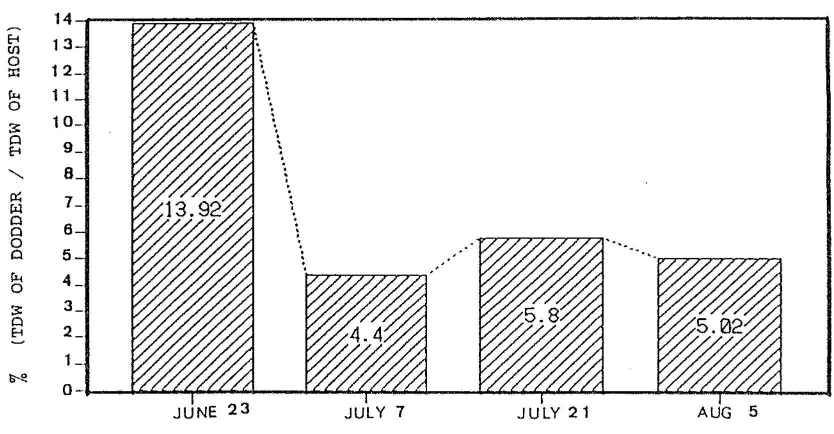

Fig 13. The survival potential of dodder on bean (*Phaseolus vulgaris* L.)

6.4. Discussion

6.4.1. Field observations

From the results mentioned already (Tables 11, 12, 13 and Fig. 7) two groups of host can be distinguished as follows :

i . The first group includes mainly dicotyledoneous plants including both herbaceous and woody species (Table 15). Although these plants provided good support and nutrients for dodder they were not equally susceptible for the survival of the dodder.

Herbaceous hosts were attacked in the course of growth by dodder. For instance dodder seedling could attach to herbaceous plants and establish on them. Host plants like *Galium verum* var *trachycarpum, Lathyrus maritimus, Rosa rugosa* (young stage), *Scutellaria strigilosa* and *Dracocephalum argunense,* were parasitized by dodder in the early growing season. While woody species such as *Rosa rugosa* (degenerative stage) and *Malus baccata* were parasitized by dodder which grew up luxuriantly on different hosts. But dodders frequently parasitized on the latest growth parts and youngest new leaves of the host. It suggests that the temporal and spatial distribution of the host and its ecological characteristics will determine whether plants belonging to this group can be parasitized or not. The facts mentioned above are in contrast to the supposition made by Gaertner (1950) that the age of host may provide mechanical obstruction to parasitism and the survival and reproductive capacity of the dodder depend on the physiological condition of the host plant. Sitkin (1976) concluded that the susceptibility of a particular host can vary according to age. He found that *C. campestris* could attack young tomato but not plants over 21 days old. The fact that dodder can germinate inside the capsule which hangs on its host (Zaroug and Ito 1987), can be responsible for the infection of woody plants if young seedlings of dodder are encountered with young shoots of hosts.

On the other hand, in some hosts such as *Lathyrus maritimus, Dracocephalum argunense* and *Vicia japonica* dodder was supported for several weeks by them. When completion of vegetative stage of the host, however, have finished the growth of dodder weakened and started to die. In case of *Inula salicina* var. *asiatica* it was observed that the growth of dodder weakened during the vegetative stage of the host. In this case it may be attributed to the biochemical incompatibility between the host and the parasite.

Table 14 and Fig. 7 show that dodder grew well and reproduced on the following host species : *Artemisia japonica, A. montana, Conioselinum kamtschaticum, Galium verum, Scutellaria strigilosa, Sedum purpureum* and *Rosa rugosa.* Because of their relative height and body strength these hosts behave as good supporters to dodder in the fruiting stage as compared to other hosts plants. From this it seemed to be reasonable to divide the hosts of the first group into two groups such as major hosts which sustain and support dodder throughout its biological cycle, and minor hosts which are parasitized mechanically or temporarily. The latter, however, are not necessarily of minor importance, since they play an important role in the survival of dodder early in the growing season which accelerates the prolific growth. Atsatt (1983) demonstrated that minor hosts were important to the maintenance of genetic variability.

ii . The second group is comprised of monocotyledons (Table 16). The members of this group could be parasitized by adult doder growing on neighbouring dicotyledoneous plants.

In this case, haustorial pentration was observed on hosts in the field. Sometimes yellowing of the infected parts of hosts recognized on the attacked plants. It was evident that the species of the second group were parasitized, but the pattern of parasitization was different from that on dicotyledoneous plants.

However, dodder seedlings immediately after emergence failed to attack monocotyledoneous plants listed in Table 16 that means they were free from the early establishment of dodders. Generally speaking monocotyledoneous plants seemed to be resistant to dodder's attack. Hegi (1927) reported that grasses were attacked by *C. sauveolens*, but the same species failed to attack grasses tested later by Gaertner (1950). Musselman (1987) demonstrated in connection to it that non of the dodder species could attack monocotyledoneous plants in Virginia U. S. A. In the case of gramineous species the resistance to dodder infection seemed to be due to the presence of mechanical barriers according to the following reports ; Furuya *et al* (1979) investigated the host range of *C. pentagona* and found that members of the Gramineae and Cyperaceae were not infected. Tsivion (1979) reported that Gramineae species were resistant to *C. campestris* due to the mechanical obstruction against haustorial penetratioin. But the haustorial penetration does not provide sufficient evidence for parasitism (Kuijt 1969). In the present study the haustorial penetration had been accompanied by yellowing of the infected parts which indicated that the parasite tapped some food from the infected tissues. Although the exact situation of the present observation showed that monocotyledoneous plants could be infected by dodders, the true parasitism on monocotyledoneous plants needed further investigation.

6.4.2. Experimental studies

a. *Susceptibility of some crop plants to dodder*

The plants tested for their susceptibility to dodder were classified into three groups in response to dodder infection (Table 17). Dodder infected successfully the plants of group a and group b. Dodder attached and grew from seedling to fruit stage on hosts of group a ; a dodder discontinued its growth shortly after flowering on hosts of group b due to either weakness or senility of hosts. Dodder attached and grew temporarily and died within 1 to 2 weeks on host species of group c.

Moreover, dodder showed a wide variation in growth vigour in response to the different host species of group a. Its growth was of high vigour on *Solanum melongena, S. tuberosum* ; medium and limited on *Cucurbita moschata* ; and weak on *Glycine max*. According to Gaertner (1950) *Glycine max* was not parasitized by 9 *Cuscuta* species and one variety tested by her.

On the other hand, dodder attached and infected red clover (*Trifolium pratense*) but it was dropped off along with the infected branches within 1 to 2 weeks after infection. On *Zea mays* and tomato (*Lycopersicon esculentum*) dodder attached but survived for about 5 to 7 days and then died. That was due to the death of the outer cortical layers of the stems and petioles of the infected plant around the attachment points of the host to dodder. The plants parasitized by dodder exhibited the following three symptoms :

(i) Stunted growth which was apparently due to the parasitism and physical damage caused by dodder, (ii) gall formation on stems and petioles of *Solanum melongena, Pisum sativum* and *Sedum purpureum* infected by dodder, and (iii) chlorosis of leaves in *Rosa rugosa* and

Solanum tuberosum.

b. *Discrimination between host species of dodder*

According to Gaertner (1950) succulent plants were frequently parasitized by dodder, and its survival and reproductive capacity were dependent on the physiological conditions of the host. This is also seemed to be true for the plants investigated under field conditions and accordingly two groups of host plant were identified. The first includes hosts which nourish and support the dodder throughout its biological cycle and are considered as major hosts, and minor hosts which determine the on-set and early establishment of dodder in the natural habitat. Dodder was frequently found to survive on the minor hosts for several weeks but its growth weakened and started to die when the vegetative growth of the host completed. The second group includes mainly monocotyledoneous plants which are known for their resistance against dodder. They were infected only when occurred in proximity of dodder growing on a suitable host.

The results obtained from experimental studies, where dodder had grown on each of the plants tested separately, showed the real differences in susceptibility among them and the variable survival and reproductive capacities of dodder on hosts. After the infection hosts showed a series of reactions from high susceptibility to dodder as seen in eggplants, peas and beans. Potatos and soybeans which were intermediately susceptible come to an entire resistance as in tomatos. It is significant that plants of the same genus Solanum were not equally susceptible. Among the plants tested certain species such as peas, beans and soybeans were susceptible in the sense that dodder established on them, but unsusceptible in the sense that dodder produced small filaments and its survival and reproductive capacities were reduced. Eventhough dodder plant was small it could grow, flower and set fruit on soybean when the growth of soybean had completely finished, because the latter was still green and can supply nutrients for the dodder. It suggests that the infection of a particular plant does neither provide sufficient information about its real susceptibility, nor about the survival and reproductive capacities of the dodder. Likewise the susceptible host which can support dodder until its reproductive stage is not sufficient for its utilization as a suitable host.

There are so far extensive lists of host plant for many *Cuscuta* species reported from different parts of the world, but the lack of discrimination between major and minor hosts depreciates their values. In this respect Khron (1934) quoted by Gaertner (1950) was the first botanist who classified the potential host species of dodder into three groups : i) good food providers ; ii) hosts on which dodder can survive ; and iii) hosts serving only to support dodder. Narayna (1956) observed that *C. hyalina* Roth. parasitized weeds and other small annual and pernnial herbs. He found the parasitism over a total of 42 species. He classified them into primary, secondary and tertiary hosts. Attst (1983) stated that a distinction must be made between the principal host which sustains the parasite and to which the gene pool is functionally adapted, and minor hosts that are sometimes utilized as encountered within each local region. He demontrated that this discrimination was important among the host generalists like *Cuscuta* spp.

As already described the hosts were not equally susceptible to dodder in both the field and in the experimental conditions. Moreover, dodder could not grow and reproduce on various hosts. The fact that dodder could grow equally on closely related hosts, as to be of the same family as seen in case of the Solanaceae and the Leguminosae. It is therefore seem necessary to discriminate between host species of *C. japonica*. For this purpose the following test criteria were adopted in small scale in experimental conditions as follows : (i) the variable susceptibility of host plants to dodder ; (ii) reduction in yield of the infected hosts ; (iii) the ability of dodder to establish and reproduce on different hosts ; (iv) the length of dodder filaments on its host ; and (v) the survival potential of dodder which can be estimated as a percentage of the TDW of dodder divided by the TDW of its host.

Each test criteria were assigned a score from 1 to 5. The host which get the lower score was considered as major host (Table 25). The host plants can be arranged in order of suitability as follows : Eggplant > Potato > Pea > Bean > soybean. The evaluation of these criteria as seen in Table 25 suggests that dodder can entablish and grow equally on closely related hosts. Additionally, it seems to prefer solanaceous species rather than leguminous ones. Nonetheless, both families included certain species which were found to be resistant to the same dodder species, namely tomato and red clover. A similar order can be obtained by using the survival potential of dodder, which suggests that this test criteria have the potential for the host discrimination in dodder. But many host plants need to be tested to verify the significance of using such criteria to evaluate and distinguish between host plant of dodder.

Table 25. Distinction between hosts of dodder (*C. japonica* Choisy by evaluating the percent reduction in TDW or shoot DW, percent susceptbility of hosts, survival potential of dodder, the length of filaments and ability of dodder to reproduce on different hosts

Host species	Reduction in TDW (%)	Suceptibility of hosts (%)	Survival potential (%)	Length of filament (m)	Ability to reproduce	Total scores
Eggplant	75 (1)**	100 (1)	189.5 (1)	32 (1)	1*	5
Potato	57.3 (2)	46.6 (3)	182.3 (1)	22.5 (2)	1	9
Pea	16.6 (5)	100 (1)	29.04 (2)	6.2 (3)	2*	13
Bean	48.7 (4)	90 (2)	5.02 (3)	2.9 (3)	2	13
Soybean	35.86 (4)	36.7 (4)	6.12 (3)	3.1 (3)	1	15

* 1 = reproduce, 2 = not reproduce
** Numbers in brackets indicate the score from 1 to 5, 1 = most preferable

The amount and length of filaments produced by dodder on a particular host species are of particular importance in determining the survival and reproductive capacity of the dodder, because dodder can accumulate sufficient nutrients and will be independent on its host in the last stages of growth. Singh *et al.* (1968) reported that the dry weight of three species of *Cuscuta* contained 10% starch. According to Singh (1970) the filaments can be separated into proximal and distal regions. The proximal region has an enzyme make-up functionally directed to synthesis of starch ; the distal region is more suited for metabolism of carbohydrates. Another distinctive feature of *Cuscuta* and other parasites seems to be the accumulation of phytic acid forming a reservoir of phosphate (Singh *et al.* 1963 ; Beg *et al.* 1968 ; Misra *et al.* 1970). These suggest that the dodder can efficiently accumulate nutrients and metabolite from its host. Wolswinkel (1974) demonstrated that *Cuscuta* can reach an efficiency of 100% in absorbing ^{14}C assimilates exported from an assimilating leaf of a fruiting host. He found that the draining action of *Cuscuta* which caused the death of the host in many cases, did not lead to self destruction of *Cuscuta*. He suggested that *Cuscuta* can accumulate an abundance of nutrient and metabolites in its long filaments which collected during the very intense absorption from the host and formed a stock for the future development of fruits. These strongly support the use of the criteria for the evaluation of major host plants of dodder above mentioned. On the major host plants dodder produced relatively long filaments, weakening the host plant, and consequently high value of survival potential. On minor host plants dodder produced a short filaments as in case of peas and beans where it flowered but failed to set fruits after the host beans where it flowered but failed to set fruits after the host completed its growth and started to die. Addtionally, the general growth vigour and losses in yield of minor hosts in response to dodder parasitism were relatively minor as compared to the major hosts.

6.4.3. Susceptibility and resistance of some hosts to dodder

Although it is difficult to interpret results on host range obtained from field observations only, a certain interrelated factors concerning this subject can be identified : (1) Spatiotemporal distribution of both the host and the parasite ; To explain how the spatial and temporal distribution affect the host susceptibility or host resistance to the dodder the following examples are available. Certain woody species such as *Rosa rugosa* (degenerative stage) and *Malus baccata* were parasitized only after the dodder grew on other hosts, and attained a certain length to enable it climb anew on those hosts. Dodder was able to establish only if a new shoots or leaves of the host are encountered with dodder. On the other hand, such plants as *Moehringia laterifolia* and *polygonatum humile* were more frequently enclosed with dodder patches but scarcely infected. Because their height and size was very small and escaped from dodder's elongation of stems and branches which are attaching to taller plants. That means a very small chance of those plants to encounter with dodder. (2) The stage of growth of dodder and hosts, Monocotyledoneous species are generally resistant to dodders (Furuya *et al.* 1979 ; Tsivion 1979 ; Musselman 1987). In this investigation monocots were scarcely infected by dodder seedlings. The latter were frequently found dying on *Elymus mollis, Poa pratensis* and *Phleum pratense* early in the growing season. However, these species were found to be infected when dodder grew on neighbouring dicotyledoneous plants. This is in contrast with what was reported by Gaertner that the susceptibility of certain plants varied according to their age. It was also supported by Sitkin (1976) who found young tomatoes were susceptible to parasitism by *C. campestris,* but old tomatoes were resistant. The circumstantial evidence of this observation, the haustorial penetration sometimes accompanied by yellowing of the infected monocot plants, indicates that they are parasitized. However, more studies remain to be done to confirm true parasitism. (3) Hypersensitivity as known in fungus is not commonly known in parasitic plants. Tsivion (1979) attributed the partial resistance of tomato plants against *C. campestris* to hypersensitivity. He demonstrated that when dodder came into contact with the stem of tomato the latter set off a reaction that killed the adjacent bark making it impossible for dodder to become established. Similar phenomenon was observed in this study when dodder came into contact with potato and tomato plants. But the potato was partially infected by dodder in spite of the hypersensitive reaction. In a case of tomato, dodder attached to a 2-week-old plants but failed completely to establish and grow. These facts indicate that tomato is resistant to *C. japonica*. In this respect Sitkin (1976) found that young tomato seedlings but not a 21-day-old were infected by *C. campestris*. He confirmed the earlier findings of Gaertner (1950) that the susceptibility of a particular host could vary according to age. On the contrary Dawson *et al.* (1984) reported that *C. campestris* would parasitize tomato at any stage of growth. It is particularly serious on yovng seedlings because they will die after infection.

7. Conclusion

7.1. Seed germination

Submerging the seeds in conc. sulfuric acid was the most effective method of the break of dormancy of seeds of *C. japonica*. The germination reached 99% in 15 min submersion. As the acid-pretreatment seems to dissolve the impermeable layers gradually the germination percentages increases gradually by the extension of the time of submersion of the acid. It indicates that impermeable layers are not restricted to a specific region such as the junction of the hypodermis and the palisade layers but are the whole layers of the epidermis, hypdermis and macrosclerieds of the seed coat.

Germination of the acid-pretreated seeds was influenced by the temperatures. The percentages of germination obtained were 58% at 5 ℃ in 15 days and 98% at 30 ℃ in 2 days. It was obvious that the time required for the germination decreased significantly with higher temperatures up to 30 ℃.

Effect of burial at various soil depths on seed dormancy of *C. japonica* was investigated. The seeds buried at 1, 5, 10 and 15 cm depths for one year lost impermeability from 2% to 24%. The loss of impermeability was higher at shallower than in deeper depths. Samples of the seeds which were recovered three months after burial and examined under Scanning Electron Microscope showed that part of the epidermis was removed depending on soil conditions. Thus, the removal of the hard seed coat seems to be effective on the break of dormancy of seeds during winter. The conditions showed pronounced effect at shallow soil depths.

In the burning experiment the dormant seeds which were placed artificially on the soil surface lost viability from 26% to 57% of seeds. The non-dormant seeds of which the seed coat was removed by acid-pretreatment lost viability by 87% of seeds. The seeds buried at 0.5 cm depth were not affected at 77 ℃ in burning the experiment. Dormant seeds which were exposed to heat-pretreatment at 85 ℃ for more than 30 min lost viability by 96% of seeds. The non-dormant seeds exposed to heat-pretreatment at 70 ℃ and 85 ℃ for more than 30 min lost their viability completely. From these facts it can be suggested that the hard seed coat can to some extend protect the embryo from burning effects. The seeds covered by soil, particularly those at 0.5 cm depth, could retain their viability after burning.

Percentages of germination of seeds buried at 0.5 cm depth were 2.6% to 5.7% for dormant seeds and 76% for non-dormant seeds in burning experiments. Percentages of germination of dormant seeds exposed to heat-pretreatment were 17% and 14% at 70 ℃ for

20 min and 85 ℃ for 10 min, respectively. Samples from the heat-pretreated seeds examined under light microscope and observed by naked eyes showed rupture of the seed coat. All the non-viable seeds which were heated for more than 30 min at 85 ℃ were always imbibed water. It indicates that heat-pretreatment ruptures the seed coat, and that improves the permeability and breaks the dormancy. But by extending the time of heat-pretreatment the seeds lost viability.

As a result, in *C. japonica* the process of the germination due to burning could be attributed to the following : i) the burning temperatures and heat-pretreatment can break dormancy of seeds and accelerate the germination particularly at the shallower depths ; ii) the non-dormant seeds buried in the soil can escape from the damage which might be caused by burning, and can germinate successfully in the post-fire recovery period,because during this period an increase in soil temperatures near the soil surface can accelerate the germination. It also provides the seeds with more heat energies (= high temperature) required for germination in burned areas than in unburned areas.

Temperatures required for the germination, and effect of soil depths on the dormancy are serviceable to interpret the phenological pattern of *C. japonica* in Hokkaido. As seen in Fig. 14 seeds on the soil surface or buried tend to lose the impermeability gradually in response to various environmental factors. Initiation of the germination begins in early spring. The seeds can remain in water absorption condition until soil temperatures rise to optimum levels for the germination. An increase in soil temperatures during late May and early June will accelerate the germination and seedlings emergence to above ground. The seedlings can survive for three weeks on ground, but they will die if they can not attach to a host. The seedlings which can attach to a host are tincted with red and increase in diameter. After vegetative growth flowering is from late July to September.

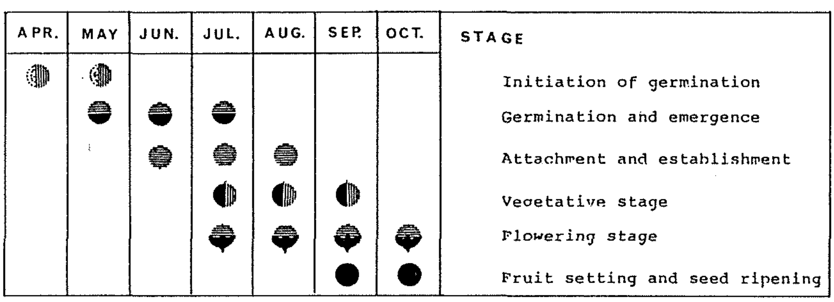

Fig 14. Phenology of *C. japonica* Choisy in Hokkaido

7.2. Host-dodder relationship in *C. japonica*

7.2.1. Some causes of host resistance and host susceptibility

Monocotyledoneous plants are generally resistant to dodders. In this investigation, monocotyledons were scarcely infected by dodder seedlings immediately after emergence. In particular, monocotyledoneous plants were attacked by dodder which grew up on neighbouring dicotyledoneous hosts. The haustorial penetration sometimes was accompanied by yellowing on the parasitized tissues provided evidence for parasitic relationship. These suggest that the mechanical barriers obstruct the establishment of haustoria of young dodder seedlings but not that of an adult dodder.

The phenomenon of hypersensitivity similar to that of fungus was observed when dodder came into contact with potato and tomato plants. However, potato (*Solanum tuberosum*) was partially infected in spite of this hypersensitive reaction. In case of tomato (*Lycopersicon esculentum*), dodder attached to a 2-week-old plant but failed to establish and grow on it. Another example was observed in case of red clover (*Trifolium pratense*) to dodder. The latter could parasitize and grew for about two weeks on red clover. The infected branches of red clover began to dry and led to starvation and the death of dodder. The reaction as already described has never been seen on such hosts in response to other dodder species. Thus it seems to be characteristic of *C. japonica,* which could be useful for identification.

7.2.2. Host range and discrimination between major and minor hosts of C. japonica

C. japonica parasitized 38 hosts belonging to 17 families in field conditions. These hosts were identified into two groups based on the pattern of parasitism and the survivals of dodder on them. The first group include dicotyledoneous species. As hosts of this group do not support dodder equally they are divided into major hosts including 6 species, and minor hosts including 24 species. On the major hosts, dodder will survive from seedling to fruiting stages. On minor hosts, dodder will survive for several weeks after infection and die before fruiting or attach to them later in its course of life cycle.

The second group is comprised of monocotyledoneous species which could be parasitized by adult dodder which grew up on neighbouring host plants.

There are so far extensive lists of hosts for several *Cuscuta* species reported from different parts of the world but the lack of discrimination between major and minor hosts depriciates their value. A discrimination between major and minor hosts can be made by using the following test criteria : i) the variable susceptibility of host plants to dodder ; ii) reduction in yield of the infected host ; iii) the ability of dodder to establish and reproduce on different hosts ; iv) the length of dodder filaments on its host ; and v) the survival potential of dodder which can be estimated as a percentage of the TDW of dodder divided by the TDW of its host.

Each test criteria was assigned a score from 1 to 5. The host which gets the lower score is considered as major host. The scores of 5 crop plants are as follows : eggplant 5, potato 9, pea 13, bean 13 and soybean 15. Thus the most perferable host, that is to say, major host is eggplant followed by potato. Dodder seems to prefer solanaceous species to leguminous ones. Nonetheless both families included certain species which were found to be resistant to the same dodder species, namely tomato and red clover.

On major hosts dodder produced relatively long filaments, and showed high value of survival potential. Whereas, on minor hosts dodder produced short filaments and failed to set fruits. Additionally, the general growth vigour and yield reduction of the minor hosts were relatively minor as compared to the major hosts.

Finally, Fig. 15 shows the behavior of dormant dodder seeds, that is, dispersed dodder seeds buried in the soil. The most common course of dodder seed in soils is to germinate in soils in the next year and consective years, and to emerge above the ground. After emergence, young seedlings can grow and fruit when they are successful in contact with major hosts but they can survive vegetatively when they attached to minor hosts. Among the seeds buried in the soil some are positioned in shallow depths but others are deeper. Seeds in shallow depths and those at depths within the maximum depth of seedling emergence of this species can emerge and look for a host. But seeds positioned deep in the soil can germinate and die owing to the lack of nutrients. Thus, there are 4 gates in order to complete dodder's life history as follows : (1) the ability of germination in soils ; (2) the possibility of emergence above ground ; (3) the chance of attaching to major hosts ; and (4) the guarrantee of sound growth given by hosts.

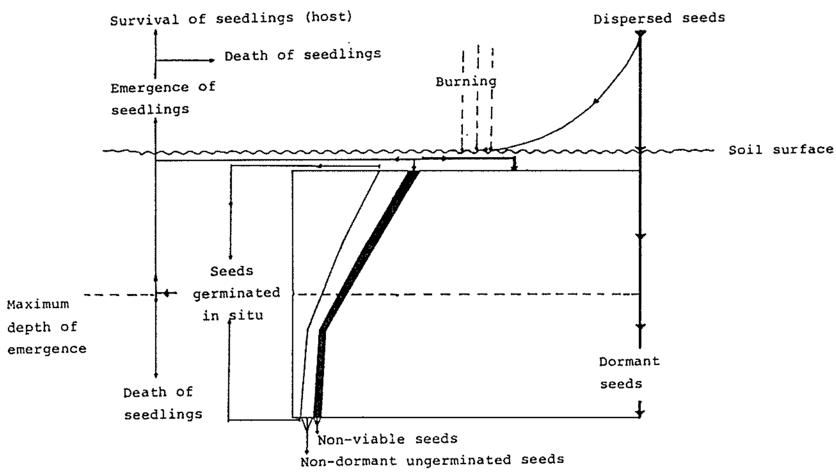

Fig 15. Behavior of dormant dodder seeds buried in the soil for one year, showing the non-viable, non-dormant and ungerminated, *in situ* germination of the seeds and the seedlings emergence.

Another course, although its occurence is small in chance, is the germination of seeds on the soil surface induced by burning. As a result, the emerging seedlings have an immediate chance to find a host and complete its life history. Generally speaking, the latter factor is more favourable to maintain the dodder population in an area than the former normal factors. This is one of the causes, which *Cuscuta* species are temporarily strongly harmful to crop plants in gardens and cultivated fields but are not members of common harmful weeds in pest lists in agiculture.

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References

Abu IRmaileh, B. E. 1979. Occurrence of parasitic plants in Jordan. In Proccedings Second International Symposium on Parasitic weeds, North Carolina 109-114.

Allred, E. E. and D. C. Tingey. 1964. Germination and spring emergence of dodder as influenced by temperature. Weeds 12 : 45-48.

Alpat'ev, N. M. 1969. Dodder a noxious weed. Zashchita Rastenii 14 (12) : 42-44. Abstracted in Weed Abstracts.

Asai, Y. 1975. On the North American dodder (*Cuscuta pentagona* Englm.), newly established in Japan. J. Jap. Bot. 50 (8) : 238-242 (in Japanese with English summary).

Ashton, F. M. and O. Santana. 1976. *Cuscuta* spp. (dodder) : A literature review of its biology and control. Bull. Div. of Agr. Sciences, Univ. Calif. No. 1880, 22 pp.

Atsatt, P. R. 1983. Host-parasite interactions in higher plants. In Encyclopedia of Plant Physiology, new series, vol. 12 C Physiological plant ecology III. Responses to the chemical and biological environment (edited by Lange, O. L. *et al.*) Berlin, Springer-Verlag, 519-535.

Barton, L. 1965. Dormancy in seeds imposed by the seed coat. ibid. vol. 15 : 727-745.

Beg, M. U., S. Parakash, M. Singh, K. K. Tewari and P. S. Krishnan. 1968. Biochemical aspects of parasitism by angiosperm parasites. III. Phytic acid and other forms of acid soluble phosphate in angiosperm parasite and hosts. Indian J. Biochem. 5 : 157-160.

Bellar, M. and S. Kebabeh. 1983. A list of diseases, injuries and parasitic weeds of lentiles in Syria (Survey 1979-1980). Lens 10 (1) : 30-31. Abstracted in Weed Abstracts.

Belyaeva, A. V., A. P. Cherkasna, L. G. Shpanova and R. A. Alfimova. 1978. Maleic hydrazide against dodder. Sakharrya Svekla 23 (3) : 37-39. Abstracted in Weed Abstracts.

Bhattacharya, P. K. 1978. Indian Cuscutaceae. Ind. J. For. (2) : 156-162.

Bloomfield, J. R. G. and I. B. Ruxton. 1979. The effect of farmyard manure on weed introduction and crop establishment during land reclamation in arid land agriculture (Saudi Arabia) ii. Effects of weed on crop yields. Joint Agr. Res. and Development Project Unv. College of North Wales. Bangor, U. K. Publication No. 87, 19 pp. Abstracted in Weed Abstracts.

Capderon, M. and A. F. P. Ozenda. 1985. About an unreported system leading to the expulsion of a parasite : *Cuscuta* on cotton-plant (*Cuscuta lupuliformis* Krock. on *Gossibium hirsutum* L.). C. R. Acad. Sc. Paris, t. 300, Serie 111 no. 6, 1985.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York, p 898-900.

Dawson, J. H. 1965. Prolonged emergence of field dodder. Weeds 13 : 373-374.

Dawson, J. H., F. M. Ashton, W. V. Welker, J. R. Frank, and G. A. Buchanan. 1984. Dodder and its control. U. S. Dept. Agr. Farmers Bull. No. 2276, 26 pp.

Dorovic, M. 1970. The use of herbicides for control of dodder in the Stiga region. Dok. Tehnol. Poljopr., Sveska 1/70, Separat (8) : 4pp.

Erdos, P. 1971. The host plants of *Cuscuta trifolii* Bab (*C. epithymum*) and *C. campestris* Yunck.

Botanikai Kozlemenyek 58 (3) : 145-151. Abstracted in Weed Abstracts.

Feinbrun, N. 1970. A taxonomic review of European Cuscuta. Israel J. Bot. 19 : 16-29.

Fisyunov, A. V. 1977. Parasitic weeds and their control. Somyakiparazity i bor'ba s nimi. Moscow, USSR, Rossel'khozizdat. 72 pp. Abstacted in Weed Abstracts.

Fujimoto, A. 1981. Host range and growth development of *C. pentagona* Engel. Weed Res. Jap. 26 Supp. (in Japanese).

Furuya, T., I Koyama and M. Takabayashi. 1979. Studies on Ecology and control of dodder (*Cuscuta pentagona* Engel.). The hosts and parasitic injury. Bull. Saitama Hort. Sta. 8 : 45-50. (in Japanese with English summary).

Furuya, T., I. Koyama and M. Takabayashi. 1980. Studies on ecology and control of dodder (*C. pentagona* Engel.). Ecological characteristics and the control. Bull. Saitama Hort. Sta. 9 : 33 -41. (in Japanese with English summary).

Gaertner, E. E. 1950. Studies of seed germination, seed identification, and host relationship in dodders *Cuscuta* spp. N. Y. Agr. Expt. Sta. Memoir No. 294, 56 pp.

Gaertner, E. E. 1956. Dormancy in the seeds of *Cuscuta europaea*. Ecology 37 : 389.

Gayed, S. R. 1986. Dodder in tobacco seedbed in Ontario Canada and its control. Canad.J. Pl. Sci. 66 : 421-423.

Gimesi, A. 1965. Dodder eradication with reglone. Outlook on Agr. 5 : 28-34.

Hadac, E. X. and J. Chrtex. 1970. Notes on the taxonmy of Cuscutaceae. Folia Geaobotanica and Phytotaxonomica 5 : 443-445.

Hadac, E. X. and J. Chrtex. 1973. Some further notes on the taxonomy and nomenclature of Cuscutaceae. ibid. 8 : 219-221.

Hassawy, G. S. 1973. *Cuscuta* species in Iraq : their hosts and seed germination. Proc. Eur. Weed Res. Coun. Symp. Parasitic Weeds, 282-289. Abstracted in Weed Abstracts.

Hegi, G. 1927. Illust. Flora von Mitteleuropa. Bd. V, Teil 3 : 2089-2111. Munchen.

Horowitz, M., Y. Regev, and G. Herzlinger. 1983. Solarization for weed control. Weed Science 30 : 170 -179.

Hutchinson, I. J. 1926. The families of flower of plants. lst ed. 622pp. Oxford Univ. Press. Oxford.

Hutchinson, I. J. 1973. The families of flower of plants, arranged according to a new system based on their probable phylogeny. 3rd ed. 968 pp. Oxford Univ. Press. Oxford.

Hutchison, J. M. and F. M. Ashton. 1979. Effects of dessication and scarification on the permeability of the seed coat of *C. campestris*. Am. J. Bot. 66 : 40-46.

Hutchison, J. M. and F. M. Ashton. 1980. Germination of field dodder (*Cuscuta campestris*). Weed Science 28 (3) : 330-333.

Iwata, E. 1964. Development of a dense thicket of shrubby lespedeza (*Lespedeza bicolor* Turcz.) following a forest fire. Ann. Rep. Coll. Liberal Arts, Univ. Iwate 23 (3) : 13-26.

Iwata, E. 1966. Germination behavior of shrubby lespedeza (*Lespedeza cyrtobotrya* Miq.) seeds with special reference to burning. Ecol. Rev. 16 (4) : 217-227.

King, L. J. 1966. Weeds of The World. New York Interscience Publ., Inc.

Kinzel, W. 1901. Die Keimung der Gattung *Cuscuta*. Landw. Vers. Stal. 55 : 255-266. Quoted by Gaertner (1950).

Krohn, V. 1934. Kurzer Bericht ueber *Cuscuta halophyta* Firies. Phytopath. Zeitschr. 7 : 505-514. Quoted by Gaertner (1950)

Kuijt, J. 1969. The Biology of Parasitic Flowering Plants. Univ. Calif. Rress. Brekeley and Los Angeles.

Mallik, A. W. and C. H. Gimingham. 1985. Ecological effects of heather burning ; ii. effects on seed germination and vegetation. J. Ecol. 73 : 633-644.

Mamluk, O. F. and H. C. Weltzien. 1978. Distribution and host range of some *Cuscuta* strains in the near and Middle east. Zeithschrft fure Pflanzenkrankheiten und Pflanzenschutz 85 (2) : 102-107.

Misra, P. C., P. N. Setty, D. V. Singh, P. K. Lal, P. N. Viswanthan, Y. R. Saxena and P. S. Krishnan. 1970. Heterogeneity in composition along the length of *Cuscuta* filaments. Physiol. Plant. 23 : 1025-1032. Abstracted in Weed Abstracts.

Movesesian, T. B. and K. A. Azarian. 1971. Pathological changes in cattle poisoned by dodder (*C. campestris* Yunck.). Biolgicheskii Shurnal Armenii 24 (7) : 67-70. Abstracted in Weed Abstracts.

Musselman, J. L. 1987. The genus *Cuscuta* in Virginia. Castanea in press.

Muthappa, B. N. 1973. Histopathology of a new parasite on coffee. J. Coffee Res. 3 (2) : 34-36. Abstracted in Weed Abstracts.

Narayana, H. S. 1956. Diffuse type of parasitism in *Cuscuta hyalina*. Science and Culture. 21 (8) : 447 -450.

Nemli, Y. and F. Ikiz. 1984. An investigation on the numerical taxonomy of some dodder species common in Turkey according to their seed and embroy characteristics. Doga Bilim Dergisi, Tarim ve Ormankcilik 8 (1) : 39-47.

Ohwi, J. 1983. Flora of Japan. New ed., rev. and enlarg. ed. 1121-1122. (in Japanese)

Philips, J. F. V. 1930. Fire : its influence on biotic communities and physical factors in south and east Africa. South African J. Sci. 27 : 352-367.

Rath, G. C. 1975. Host range of *Cuscuta chinensis* Lam. Science and Culture 41 (7) : 331-332.

Rogachev, L. D. 1969. Our experience in the control of dodder. Zashchita Rastenii, 14 (10) : 50-51. Abstracted in Weed Abstracts.

Sarpe, N., D. Halalau and M. Guta. 1973. Research on chemical control of dodder in lucerene and red clover. Proc. Eur. Weed Res. Coun. Symp. Porasitic Weeds. 289-295. Abstracted in Weed Abstracts.

Shamaev, M. I. and N. Y. Korzhentsevskaya. 1970. Dodder in retreat. Zaschi., Rast., 15 (9) : 42.

Singh, D. V., K. K. Tewari and P. S. Krishnan. 1963. Metabolisim of angiosperm parasites : 1. Phosphate partition in *Cuscuta reflexa* Roxb. and infested plants. Indian J. Exp. Biol. 1 : 207-209.

Singh, D. V. *et al.* 1970. Carbohydrate metabolism in *Cuscuta*. Phytochem. 9 : 1779-1785. Abstracted in Weed Abstracts.

Sitkin, R. S. 1976. Parasite host interactions of field dodder (*Cuscuta campestris* Yunck.). M. S. Thesis Cornel Univ. Abstracted in Weed Abstracts.

Stojanovic, D. and K. Mitatovic. 1973. Distribution, biology and control of *Cuscuta* species in Yugoslavia. Proc. Eur. Weed Res. Coun. Symp. Parasitic Weeds. 269-279.

Takabayashi, M., K. Nakayama, T. Furuya and I. Koyama. 1981. Distribution of dodder spp. and their parasitic damage caused by dodder. Jap. Pesticide Information No. 38, 3-9.

Tingey, D. C. and K. R. Allred. 1960. Breaking dormancy in seeds of *Cuscuta approximata*. Weeds 9 : 429-436.

Tsivion, Y. 1980. Resistance of tomato and bean plants to infection by *Cuscuta*. Abstracted in Weed Abstracts.

Viccer, J. 1981. South African Parasitic Flowering Plants. Juta Co. Ltd.

Villarias, J. L. 1978. Main weed problem in the Mediterranean basin : Proccedings of the Mediterranean Herbicide Symposium, Madrid Spain, Ministerio de Agricultura vol. 1 : 99-116.

Walzel, G. 1952. Clochicine-treated *Cuscuta*. Phyton. Ann. Rei. Bot. 4 : 137-143. Abstracted in Weed Abstracts.

Washitani, I. and A. Takenaka. 1986. 'Safe site' for the seed germination of *Rhus javanica* : a characterization by responses to temperature and light. Ecol. Res. 1 : 71-28.

Wolswinkel, P. 1974. Complete inhibition of setting and growth of fruits of *Vicia faba* L., resulting from the draining of the phloem system by *Cuscust* species. Acta Bot. Neerl. 23 (1) : 48-60.

Wright, H. A. and A. W. Bailey. 1982. Fire Ecology, United States and Southern Canada. John Willey & Sons, Inc. N., 501pp.

Yuncker, T. G. 1932. The genus *Cuscuta*. Mem. Torr. Bot. Club 18 : 113-331.

Yuncker T. G. 1942. A note on the precocious germination of dodder seed. Proc. Indiana Acad. Sci. 51 : 114-115.

Yunusov, S. and L. S. Badrtdinova. 1976. Species of *Cuscuta* L. in Tadzhikistan. Akadell Nauk Tadzhikskoi ssr 4 : 14-19. Abstracted in Weed Abstracts.

Zaroug, M. S. and K. Ito. 198. Notes on germination of Japanese dodder (*Cuscuta japonica* Choisy). J. Jap. Bot. 62 (5) : 140-144.

Zaroug, M. S. and K. Ito. 1988. Host nange and susceptibility of some cultivated plants to dodder (*Cuscuta japonica* Choisy) in Hokkaido. Weed Research. 33 (2) : 129-135.