This is to certify that the

thesis entitled
THE ROLE OF 7-OXABICYCLO[2.2.1]
HEPTANE-2,3-DICARBOXYLIC ACID
(ENDOTHALL)
IN ANNUAL BLUEGRASS (*POA ANNUA* L.) CONTROL IN TURF

presented by

ALFRED J. TURGEON

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Crop & Soil Sciences

William F. Meggitt
Major professor

Date September 3, 1971

O-7639

ABSTRACT

THE ROLE OF 7-OXABICYCLO[2.2.1]HEPTANE-2,3-DICARBOXYLIC ACID (ENDOTHALL) IN ANNUAL BLUEGRASS (*POA ANNUA* L.) CONTROL IN TURF

By

Alfred J. Turgeon

Experiments were conducted to evaluate the potential of 7-oxabicyclo[2.2.1]heptane-2,3-dicarboxylic acid (endothall) for controlling *Poa annua* L. infestations in *Poa pratensis* L. and *Agrostis palustris* Huds. turfs. The absorption, translocation and metabolism of endothall and the effects of endothall on photosynthesis, respiration and transpiration were studied to determine whether they contributed to selectivity among these 3 grasses.

Foliar applications of endothall to single-plant sand cultures of the 3 turfgrass species produced a selective growth suppression of *Poa annua* at certain rates and frequencies of application. Field spraying of the herbicide produced variable results which were highly dependent upon the season of application.

Root applications to plants in sand culture resulted in a selective kill of *Poa annua* within a certain concentration range of the herbicide. A granular formulation of endothall provided selective control of *Poa annua* in some field and greenhouse studies. Variables affecting this response included: watering frequency prior to application, the nature of the underlying soil, and plant variability within the *Poa annua* species.

The selectivity of endothall in turf was attributed, in part, to differential absorption and metabolism of the herbicide from root applications and the greater sensitivity of the physiological systems of *Poa annua* to endothall.

Following foliar sprays of endothall, a reduction of photosynthesis and an increase in respiration were observed in *Poa pratensis* and *Agrostis palustris*. These effects disappeared within 48 hr. Conversely, the photosynthetic activity of *Poa annua* was considerably below normal 48 hr after treatment. Root applications resulted in a continuous decrease of photosynthesis in *Poa annua*, with little effect on the other grasses. Transpiration was severely reduced in *Poa annua*, and to a lesser extent in *Poa pratensis*, from root applications of endothall. In contrast, foliar sprays caused no significant effect on transpiration water loss by all 3 turfgrass species.

THE ROLE OF 7-OXABICYCLO[2.2.1]HEPTANE-2,3-DICARBOXYLIC ACID (ENDOTHALL) IN ANNUAL BLUEGRASS (*POA ANNUA* L.) CONTROL IN TURF

By

Alfred J. Turgeon

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Sciences

1971

ACKNOWLEDGMENTS

To my wife, Jean, for her continued encouragement and assistance in the preparation of this manuscript;

To Dr. D. Penner for his advice and assistance in the laboratory investigations that constituted an important part of the research;

To Dr. J. Beard for his council through the Doctoral program;

To Drs. P. Rieke, R. Kunze and J. Vargas for their participation on my graduate committee and their suggestions thererelating;

And to Dr. W. Meggitt, major professor, constructive critic, and friend;

I wish to extend my most sincere appreciation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I. INTRODUCTION

Annual bluegrass (*Poa annua* L.) is a low-growing plant that provides a dense, vigorous turf under relatively low cutting heights. It survives reasonably well on compacted soils and is well adapted to moist, shaded conditions. Although it is almost never planted intentionally, it frequently comprises the major component of such turfgrass communities as golf course greens, tees and fairways.

Poa annua is generally considered to be a weed. Its profuse seedhead production under a wide range of mowing heights and its sensitivity to climatic extremes make it an undesirable grass for turf use.

Considerable research has been devoted to finding a suitable procedure for controlling *Poa annua*. A large number and variety of chemicals have been evaluated for their phytotoxic effects on this plant species, and many have been described as offering some promise for its control; yet *Poa annua* remains a widespread and perplexing problem for the turfgrass manager.

The herbicide 7-oxabicyclo[2.2.1]heptane-2,3-dicarboxylic acid (endothall) was introduced over 2 decades ago and has been useful as a defoliant, desiccant, aquatic herbicide and for preemergence weed control in certain crops. Prior to the development of 2-(2,4,5-trichlorophenoxy)propionic acid (silvex) and 3,6-dichloro-*o*-anisic acid (dicamba), endothall was used for the control of white clover (*Trifolium* *repens* L.) and knotweed (*Polygonum aviculare* L.) in turf. In addition, endothall was reported as having some selective action on *Poa annua*.

The objectives of this study were to determine the nature and basis for the selectivity of endothall in turf and its potential and practical role as a control for *Poa annua*. Various foliar application rates and root treatments of endothall were used to determine the range of selectivity. Climatic and soil conditions, plant variability, and methods of application were studied to determine their relationship to the phytotoxic effects of this herbicide.

Absorption, translocation and metabolism of endothall by *Poa annua* and 2 turfgrass species were studied to determine whether they contributed to selectivity. The effects of endothall on photosynthesis, respiration and transpiration were examined to determine how these physiological processes might be involved in selective action.

II. LITERATURE REVIEW

The Plant - Annual Bluegrass (Poa annua L.)

Description: Hubbard (1959) included all known characteristics of the species in the following description:

> A loosely to compactly tufted annual or short lived perennial, 3-30 cm. high. Culms erect, spreading, or prostrate, sometimes with a creeping base and rooting at the nodes, smooth. Leaves green, hairless; sheaths compressed, keeled, smooth; ligules thinly membranous, 2-5 mm. long; blades with abruptly pointed or blunt hooded tips, 1-14 cm. long, folded or opening out and 1-5 mm. wide, weak, often crinkled when young, minutely rough only on the margins. Panicles ovate or triangular, open and loose, or somewhat dense, 1-12 cm. long, pale to bright green, reddish or purplish; branches mostly paired or solitary, spreading, smooth, bare and undivided in the lower part; pedicels 0.3-4 mm. long.
>
> Spikelets ovate or oblong, 3-10 mm. long, 3-10 flowered, readily breaking up beneath each lemma at maturity. Glumes persistent, pointed, keeled; lower lanceolate to ovate, 1.5-3 mm. long, 1-nerved; upper elliptic or oblong, 2-4 mm. long, 3-nerved. Lemmas overlapping, semi-elliptic or oblong and rather blunt in side view, 2.5-4 mm. long, keeled, 5-nerved, membranous and with broad delicate tips and margins, sparsely to densely hairy on the nerves below the middle, or hairless. Paleas slightly shorter than the lemmas, with hairy or hairless keels. Anthers 0.7-1.3 mm. long. Grain enclosed by the lemma and palea. Ch. no. 2n=28.

Origin and Distribution: Tutin (1952) postulated that Poa annua arose from a cross between Poa infirma H.B.K., an annual species, and Poa supina Schrad., a creeping perennial. This is believed to have occurred in Europe during the Quaternary glaciation. Hitchcock (1935) stated that Poa annua is found in a wide variety of habitats from Newfoundland and Labrador to Alaska, south to Florida and

California, and at high altitudes in Tropical America. Its occurrence has also been recorded in Australia, South America, North Africa and North Asia (Gibeault, 1970). Tutin (1952) observed that it is usually limited to areas of human habitation. Hovin (1957) postulated that it was introduced to America by the early Spanish explorers.

Reproduction: The propagation of Poa annua is primarily by seed (Beard, 1970; Harper, 1965; Hawes, 1965; Sprague and Burton, 1937). Renney (1964) observed that a single plant produced over 360 seeds between May and August in western British Columbia. Recent investigations into the perenniality of some biotypes by Gibeault (1970) suggest that vegetative propagation by stolons may also be operative in the survival and spreading of the plant.

Hovin (1958) observed that Poa annua is almost always self-pollinating but that by growing the plant in maximum day temperatures of 28.0 ± 1.6 C and 20.0 ± 1.2 C minimum night temperatures, the anthers could be shrivelled and made nonfunctional. Cross-pollination then produced 96% hybrids in the F_1 generation. Koshy (1969) reported that "sexual reproduction in Poa annua combines an efficient mechanism of pollen liberation and stigma exsertion which promotes cross-pollination and self-incompatibility." He concluded that self- and cross-pollination are equally probable in terms of the timing of pollination, since pollen liberation does not occur in the closed floret. He also observed that seed formation can proceed following pollination even when the panicles are removed from the plant on the same day pollination occurs. Hence, the remarkable efficiency of seed formation contributes substantially to the success of *Poa annua* as a weed.

Youngner (1959) determined that flowering was not governed by day length and only slightly affected by temperature within the range of 10 to 27 C. Consequently, seed production may occur throughout the entire growing season. It has been widely observed, however, that seedheads are most abundant in spring.

Seed Germination: Cockerham and Whitworth (1967) reported that freshly produced *Poa annua* seed, in New Mexico, were dormant. These required several weeks aging and temperatures below 27 C during the day and nighttime temperatures of 10 to 21 C before germination would occur. Tutin (1957) observed that seed of var. *reptans*, a perennial biotype, germinated soon after production but that an annual variety usually required a 3-month ripening period before germination would take place.

Germination of *Poa annua* normally takes place in late summer or early fall, with spring germination occurring in some areas (Harper, 1965). Engel (1967) found that alternating temperatures of 30 C day and 20 C night resulted in higher percentage germination than 30 C day and 10 C night, or constant temperatures of 19 C and 30 C. Also, comparisons of dark-germinated seeds with those receiving 8 hours of light per day revealed significantly higher germination when the seeds were exposed to light. These results were supported by Neidlinger (1965), who also demonstrated that light was essential for optimum germination.

Growth: Harper (1965) reported that seedling *Poa annua* plants develop quite rapidly and produce thick stands despite the lack of creeping stems. Furthermore, growth might occur during late fall, winter and early spring as long as the soil remains unfrozen.

Juhren *et al*. (1957) measured the growth rate of *Poa annua* under various temperatures, photoperiods and light intensities. They determined that optimum growth occurred at 26 C day temperature and 17 C night temperature with a 16-hr photoperiod and high light intensity. Sprague and Burton (1937) concluded from experiments in New Jersey that continuous light shade was more favorable to *Poa annua*, in summer, than full sunlight. They attributed this to the cooler temperature and higher humidity associated with the shaded environment. Hawes (1965) observed that the optimum soil temperature for root growth of *Poa annua* was approximately 16 C. At this temperature the plants had a distinctly horizontal growth as compared to a more vertical development at 32 C. Beard (1970) reported that optimum shoot and root growth occurred at approximately 15 to 21 C and 10 to 15 C, respectively.

Youngner (1959) showed that the growth and survival of *Poa annua* were highly dependent upon continuous availability of soil moisture. Observations of this type have led to the common belief that *Poa annua* is a typically shallow-rooted plant. Sprague and Burton (1937) determined, however, that shallow rooting was a response to compacted soil conditions and that, with a more favorable soil structure, *Poa annua* produced roots comparable to those of Kentucky bluegrass (*Poa pratensis* L.) and colonial bentgrass (*Agrostis tenuis* Sibth.).

Susceptibility to Environmental Stress: *Poa annua* is inferior to perennial turfgrasses in its hardiness to heat stress (Beard, 1970). Temperatures as low as 40 C might cause a direct high temperature kill of the plant and even lower temperatures may result in injury if the plants are also subjected to a moisture stress (Beard, 1968).

Low temperatures might also be especially injurious to *Poa annua* (Beard and Olein, 1963). This results from mechanical disruption of the protoplasm by ice crystals during winter and early spring. Ice crystal formation is largely dependent upon the hydration level of the plant tissue. Even if direct low temperature kill does not occur, the roots of *Poa annua* might be injured sufficiently to limit the water uptake capability of the plant so that rapid transpiration in spring might cause desiccation and death.

Beard (1970) reported that the relative tolerance of *Poa annua* to submersion was inferior to bermudagrass (*Cynodon dactylon* L. Pers.), bentgrass, zoysiagrass (*Zoysia* Willd.) and Kentucky bluegrass. Also, it had a much higher wilting tendency than most other turfgrasses where there was a deficit or excess of moisture. Drought and wear tolerance were also poor.

Bobrov (1955) found that *Poa annua* was very susceptible to smog in Los Angeles, California. This might be of considerable significance in urban industrial areas where atmospheric pollution might reach phytotoxic levels. Injury appeared as a light brown band between the tip and midsection of the leaf blades. Microscopic examination revealed chloroplast disintegration, plasmolysis and dehydration of mesophyll cells in the leaf tissue.

Diseases to which *Poa annua* is susceptible include: anthracnose, *Helminthosporium* leafspot, *Fusarium* snow mold (Sprague and Evaul, 1930), *Septoria* leafspot, *Fusarium* root and crown rot, dollar spot, brown patch, red thread, *Ophiobolus* patch, rust and leaf smut (Couch, 1962). There is evidence that some fungicides are less effective on *Poa annua* than on bentgrass for the same diseases. McCullough (1953) found that *Poa annua* required much higher rates of mercury fungicides for snow mold control than did bentgrass.

Subspecies Variability: *Poa annua* is generally considered a short-lived plant, completing its life cycle within one growing season (Harper, 1965). Goss (1965) reported that it may live as a perennial provided no climatic extremes are encountered. McCullough (1953) determined that *Poa annua* is a biennial in the Alberta region of Canada. Tutin (1957) observed both annual and perennial growth forms in England. Hovin (1957) noted that perennial biotypes form secondary tillers on the upper nodes of the culm and produce more tillers per plant than the annual forms. Timm (1965) reported that most samples collected in Europe were perennial or biennial. These were procumbant and had a strongly fibrous root system, while the annual types were erect and exhibited a less extensive rooting habit. He proposed the following subspecies designations: *annua* (var. *typica* Beck.), for the upright-growing annual types; *reptans* (var. *reptans* Hausskn.), for the creeping perennial type; and *aquatica* (var. *aquatica* Aschers.), for those plants found on ditchbanks and adjacent to bodies of water. Since cross-pollination between the upright annual and the creeping perennial is possible, many intermediate forms probably occur.

Although Hovin (1957) concluded that the most common type of *Poa annua* in the United States was the upright annual, Gibeault (1970) found a high proportion of perennial types in samples collected in Oregon and Washington. He determined that the presence of annual or perennial subspecies in a turf could be correlated with the watering regime. Areas that were watered infrequently or not at all would have mainly annual types, while the perennial subspecies could be anticipated in more frequently irrigated turfs.

Cultural Control: Weed control in turf is based primarily on a comprehensive program of cultural practices designed to maximize the competitive ability of the desired turfgrass species. Furgeson (1959) proposed that greens should be fertilized when *Poa annua* is weakest in comparison to bentgrass, and that irrigation water should be supplied infrequently but thoroughly to favor deep rooting of the desired species. He also recommended periodic alleviation of soil compaction and disease and insect control. Engel (1967) suggested that late summer overseeding could help some bentgrasses gain a head start over Poa annua. Schery (1968) noted that the correct choice of turfgrass varieties is an important competitive control for Poa annua. Musser (1961) suggested withholding spring fertilization until the bentgrass or Kentucky bluegrass has initiated growth. Conversely, late summer or fall fertilizer applications should be made before Poa annua begins to make its vigorous cool weather growth. Sprague and Burton (1937) reported that turf made strongly acid by the use of acid-forming fertilizers did not allow entry of Poa annua because of the low tolerance of this species for high acidity. They cautioned, however, that bentgrass also suffered from high soil acidity and that intentional reduction of pH was unsatisfactory as a means of controlling Poa annua.

Chemical Control: Attempts to control Poa annua with chemicals began over 40 years ago. Sprague and Burton (1937) reported that applications of lead arsenate greatly reduced the abundance of Poa annua in creeping bentgrass turf. Daniel (1955) reported that calcium arsenate, lead arsenate and sodium arsenite were effective in removing Poa annua from Kentucky bluegrass and colonial bentgrass turfs. He further indicated that arsenic toxicity was inversely related to the soil phosphorus level. Engel and Aldrich (1960) reported substantial reductions in *Poa annua* from successive applications of sodium arsenite in combination with 2,4-dichlorophenoxyacetic acid (2,4-D).

Injury to bentgrass turf has been observed following application of arsenic compounds (Daniel, 1955; Cornman, 1964). Engel *et al*. (1968) reported that the quality of bentgrass fairway turf was often reduced to 50% of normal from calcium arsenate. Also, late summer applications were generally more damaging than mid-spring applications.

Goetze (1956) found that fall applications of 1-butyl-3-(3,4-dichlorophenol)-1-methylurea (neburon) gave excellent control of *Poa annua* with no sustained injury to the desirable bluegrass turf. Mruk and DeFrance (1957) reported fair to moderate control in athletic field turf with disodium methanearsonate (DSMA), isopropyl *m*-chlorocarbanilate (chlorpropham) and neburon. Several copper compounds showed promise for the control of *Poa annua* without objectionable turfgrass injury in tests by DeFrance and Kolett (1959).

Fluorophenoxyacetic acids were reported to induce sterility in *Poa annua* for 4 to 6 weeks (Anderson and McLane, 1958). Also, 1,2-dihydro-3,6-pyridazinedione (maleic hydrazide) reduced the number of *Poa annua* seedheads but also seriously reduced the bentgrass content of the turf and allowed a substantial increase in white clover (Engel and Aldrich, 1960). Goss (1964) found that dimethyl tetrachloroterephthalate (DCPA), *O*-(2,4-dichlorophenyl)*O*-methyl isopropylphosphoramidothioate (DMPA), a,a,a,-trifluoro-2,6-dinitro-_N_,_N_-dipropyl-_p_-toluidine (trifluralin), _O_,_O_-diisopropyl phosphorodithioate _S_-ester with _N_-(2-mercaptoethyl) benzenesulfonamide (bensulide) and _N_,_N_-dimethyl-2,2-diphenylacetamide (diphenamid) effectively inhibited either germination or subsequent growth and development of _Poa annua_ seedlings. His results indicated that overseeding with desirable grasses should be delayed at least 12 weeks after application of these materials. Gibeault (1967) observed that DCPA, trifluralin, bensulide and _N_-butyl-_N_-ethyl-a,a,a,-trifluoro-2,6-dinitro-_p_-toluidine (benefin) effectively controlled _Poa annua_ that was artificially introduced into sea-marsh turf (_Agrostis palustris_ Huds. and _Festuca rubra_ L.). Cornman _et al_. (1964) reported injury to bentgrasses with DCPA and DMPA but not bensulide. Furthermore, _Poa annua_ control was reduced when these materials were applied to soils with high phosphorus levels (Juska and Hanson, 1967).

The list of herbicides that have, at times, shown promise for the control of _Poa annua_ is extensive. Continued evaluation of these materials, however, has often produced inconsistent results (Engel _et al_., 1968). Further testing of these herbicides in specific use situations is necessary to clarify their respective roles in the control of _Poa annua_.

The Herbicide - Endothall

Applications to Turf: Nutter _et al_. (1951) observed a temporary discoloration of turf from endothall applied in

October at the rate of 1.1 kg/ha. Varying the spray volume from 94 to 1870 l/ha (10 to 200 gal/A) did not significantly affect the degree of discoloration. Higher application rates produced correspondingly greater turfgrass injury. Simmons and DeFrance (1953) reported temporary but severe turfgrass discoloration from endothall applied in July at 2.2 kg/ha. They also concluded that varying the spray volume from 234 to 1870 l/ha did not influence the degree of discoloration. Jagschitz (1954) observed that creeping bentgrass (Agrostis palustris Huds.) developed greater discoloration than Kentucky bluegrass and that mowing the grasses before application generally increased the degree of discoloration. Presumably, this would allow greater penetration of the herbicide into the fresh wounds of the turfgrass leaves. Recently, Turgeon and Meggitt (1971b) reported browning of Kentucky bluegrass from endothall applied at rates of 2.2 and 4.5 kg/ha; however, the turf had completely recovered 4 weeks after application.

Engel and Aldrich (1960) reported profound differences in turfgrass discoloration depending upon the season of application. Severe injury resulted from most fall applications of endothall to bentgrass turf, while only slight injury was observed after spring applications. In addition, they made spring applications of endothall for 4 consecutive years to a bentgrass fairway having a uniform distribution of Poa annua. A series of 2 or 3 treatments, at 0.56 kg/ha, was applied at 2-week intervals each spring. This resulted in a 37% reduction in Poa annua the first season and a 62% reduction at the close of the fourth season when compared to the untreated check. The corresponding increase in bentgrass was 37% and 55%.

Absorption: Poland (1952) suggested that the highly polar nature of endothall limits its penetration into plant surfaces. Maestri and Currier (1958) noted that maleic hydrazide enhanced penetration of endothall. They attributed this response to the surfactant and/or humectant effect of the maleic hydrazide formulation. Tischler et al. (1951) found that the addition of a surfactant to the spray solution increased the effectiveness of endothall. Stahler (1950) observed a considerable increase in the activity of endothall with the addition of ammonium sulfate.

Translocation: Linder (1951) found that injury from foliar-applied endothall was confined to the sprayed portions of oat (Avena sativa L.) and bean (Phaseolus vulgaris L.) plants. Application of endothall to the soil, however, resulted in complete kill of these plants. He interpreted these observations as evidence of little or no basipetal translocation, although acropetal transport of the herbicide was possible. Maestri and Currier (1958) showed that, at certain concentrations, endothall prevented basipetal movement of ^{14}C-maleic hydrazide in barley (Hordium vulgare L.). More recently, Maestri (1967) reported essentially no translocation of ^{14}C-endothall in bean plants, but rapid apoplastic and some symplastic movement in cucumber (Cucumis *sativus* L.) plants. Thomas (1966) reported that ^{14}C-endothall moved from treated leaves in a symplastic pattern in pondweed (*Potamogeton nodosus* Poir.) and water-weed (*Elodea canadensis* Gray). Furthermore, Belonsov (1960) observed that radioisotopes of phosphorus and sulfur applied to the leaves of cotton (*Gossypium hirsutum* L.) plants moved to the ripening capsules at a faster rate when endothall was sprayed on the leaves.

Metabolism: Hiltibran (1962) employed a flax-seed (*Linum usitatissimum* L.) bioassay to determine endothall residue in aquatic systems. He reported that applications to achieve up to 10 ppm in field water tanks could not be detected after 60 hr. He also observed that the addition of mud and plant debris hastened the disappearance of endothall in aquaria. This suggests that endothall degradation is related to the presence of microorganisms. Horowitz (1966) observed that endothall residues persisted longer on dry than on moist soils. In addition, he reported that successive applications of endothall resulted in a faster degradation of the herbicide in soil. This is in agreement with some established principles of microbial decomposition of herbicides as defined by Kearney and Kaufmann (1969). An initial application of some herbicides stimulates microbial population growth in a pattern illustrated by a sigmoidal curve. Subsequent applications intercepting a point at which the microbial population is large are degraded more quickly, as more microorganisms capable of using the herbicide as a substrate are present.

The incorporation of degradation products of endothall into carbohydrates was reported by Freed *et al*. (1961). This was determined in tests with beet (*Beta vulgaris* L.) and spinach (*Spinacia oleracea* L.) plants. Montgomery and Freed (1964) have shown that plants, fish and soil microorganisms can completely metabolize endothall. Although the main degradation product in microorganisms was carbon dioxide, the radioactive label was found in various biochemical components in the plants and fish. They suggested that the first point of attack on the endothall molecule was probably the endoxo bridge, with subsequent formation of organic acids containing hydroxy or keto functional groups.

Physiological Effects: A continuous decrease in the photosynthetic activity of young apple (*Pyrus malvus* L.) plants treated with endothall was reported by Rakitin and Imamaliev (1959b). The chlorophyll content of the leaves also decreased, although higher endothall concentrations lessened the chlorophyll destruction. Maestri (1967) observed grana disintegration and chloroplast shrinkage following endothall treatment.

Hall (1952) observed that respiration of detached cotton leaves decreased for about 2 hours following endothall application and then increased to about twice the rate of the control. Currier (1953) found a marked increase in respiration of *Elodea* leaves treated with endothall. Maestri and Currier (1958) reported that endothall increased respiration in root tips and leaf segments of barley. In apple tree leaves treated with endothall, Rakitin and Imamaliev (1959b) observed increased respiration accompanied by an increase in the activity of oxidative enzymes.

Dunning (1958) concluded that endothall stimulates callose formation in either parenchyma cells or in the sieve elements. Maestri (1967) observed that endothall induced callose formation in beans and cucumber in the time sequence: epidermis, veinlet endings, spongy mesophyll and vein parenchyma, and palisade cells. This sequence generally correlates with the presumed path of endothall in the leaves. Following root applications, endothall promoted callose deposition in sieve tubes in the leaves.

Rakitin and Imamaliev (1959b) reported a considerable increase in the content of monosaccharides and a decrease of disaccharides and starch in applies treated with endothall. Also, there was evidence of a conversion of organic phosphorus to an inorganic form in the endothall-treated plants. The authors further stated that endothall caused an accumulation of inorganic nitrogen in the leaves, followed by a decrease in all forms of nitrogenous substances. Mann *et al*. (1965) suggested that protein synthesis might be inhibited by endothall.

Currier and van der Zweep (1956) observed cytoplasmic swelling and streaming in plasmolyzed leaf cells of *Elodea* treated with endothall. Maestri (1967) also reported accelerated protoplasmic streaming in *Elodea* and suggested that this might be due to the higher respiratory rates caused by endothall.

Cell membrane permeability changes are suggested by the observations of Rakitin and Imamaliev (1959a), as the ability of apple leaves to retain water decreased and transpiration increased during the first day following spraying with endothall. Afterwards, this effect reversed--leaf water content increased and transpiration decreased. Maestri (1967) reported other membrane effects due to endothall, including ion leakage, modified tonoplast plasmolysis, water loss and browning of leaf tissue. He also suggested that endothall is probably bound to the membranes by ionic interactions, resulting in a general molecular disorder and a disturbance of cell compartmentation.