THEMATIC ARTICLES

The Occurrence and Economic Impact of Plasmodiophora brassicae and Clubroot Disease

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Abstract The significance of *Plasmodiophora brassicae* Woronin and clubroot disease which it incites in members of the family Brassicaceae is reviewed as the focus for this special edition of the Journal of Plant Growth Regulation. This is a monographic treatment of recent research into the pathogen and disease; previous similar treatments are now well over half a century old. Vernacular nomenclature of the disease indicates that it had a well-established importance in agriculture and horticulture from at least the Middle Ages onward in Europe and probably earlier. Subsequently, the pathogen probably spread worldwide as a result of transfer on and in fodder taken by colonists as livestock feed. It is a moot point, however, whether there was much earlier spread by P. brassicae into China and subsequently Japan as *Brassica rapa* (Chinese cabbage and many variants) colonized those lands in archaeological time. Symptoms, worldwide distribution, and economic impact are briefly described here to provide a basis for understanding subsequent papers. Clubroot disease devastates both infected field and protected vegetable and agricultural Brassica crops. Particular importance is placed on recent reports of crop losses in tropical countries, albeit where the crops are grown in cooler altitudes, and in the Canadian prairie land canola crops. The latter is of enormous importance because this crop is the single most important and essential source of vegetable oils used in human foodstuffs and in industrial lubricants where mineral oils are inappropriate.

Keywords Plasmodiophora brassicae Clubroot disease · Vernacular nomenclature · Symptoms · Worldwide distribution · Economic impact

This special edition of the Journal of Plant Growth Regulation focuses in detail on the more recent research into the microbial plant pathogen Plasmodiophora brassicae, which is the causal agent of clubroot disease in members of the family Brassicaceae. This is the first monographic treatment, albeit of limited scope, in over 50 years. An Acta Horticulturae (No. 706) contains a previous series of review papers and Plant Protection Science 45(1) (2009) contains the abstracts from a conference held in 2008.

Introduction

The association of P. brassicae with the gross distortion of growth in its hosts makes this an entirely appropriate subject for a digest of current research findings in the Journal of Plant Growth Regulation. Clubroot disease has been known on cultivated brassicas in Europe at least as far back as the 13th century and quite possibly much earlier to Roman times and has been ascribed to many causes. The early 19th century Scottish view that it resulted from ''unsatisfactory soil conditions or unbalanced fertiliser practices'' was, in the absence of microbiological knowledge, an entirely reasonable assertion. Recent considerations of the ecology of the organism make an association of epidemics of P. brassicae with unbalanced host nutrition a quite tenable view. In 1873, the Russian biologist M. S. Woronin commenced studies of the disease in St. Petersburg and five

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Fig. 1 Professor Geoffrey Richard Dixon, Guest Editor

years later identified Plasmodipophora brassicae Woron. as the causal agent of clubroot disease (Woronin [1878](#page-8-0)). Woronin's interest was quite possibly stimulated by the ravages of clubroot disease in cabbage crops in that part of Russia. More than a century of subsequent study has unraveled much concerning the biology and host-pathogen relationships of P. brassicae and the Brassicaceae, briefly reviewed by Dixon ([2006\)](#page-7-0) (Fig. 1). As is very evident from the ensuing chapters, much is still unknown, not least the true taxonomic status of the microbe, its full life cycle, interactions with hosts, and means of controlling a disease that is of considerable and increasing economic significance.

Vernacular Names

Common names for the disease are listed in Table [1.](#page-2-0) In countries such as Belgium and Germany the multiplicity of names probably indicates a considerable degree of regionality and localization reflecting the distinctly separate dialects used by farmers and growers living in historically separate states. The naming also reflects the relative importance of the crops affected. In northern Europe cabbage was the major crop grown and hence diseased by clubroot, whereas further south in France cauliflower was of greater importance. Colonists from Europe took their names for this disease with them to the New World and at the same time the pathogen was exported in animal fodder such as swedes (*Brassica napus*) and turnips (*B. rapa*) used as sustenance for their beasts. It is possible that P. brassicae reached China and Japan much earlier as ancestral forms of B. rapa moved from southeastern Europe, establishing Chinese cabbage and all its associated variant forms (Dixon [2007\)](#page-7-0).

In southern Europe the disease was viewed as a form of plant ''hernia,'' whereas further north as ''club foot,'' a term exported by German and Scandinavian colonists with their crops. In recent years the disease has generally been referred to as "clubroot" as opposed to "club root." This reflects a desire for uniformity in the nomenclature of diseases stemming from European Union rules relating to crop cultivar assessment.

Crop Hosts

All members of the family Brassicaceae are thought to be potential hosts for Plasmodiophora brassicae and within them it is able to complete both the root hair and cortical stages of its life cycle (see Kageyama and Asano, this issue). Cultivated crops appear to be especially susceptible. This includes all varieties (sensu Bailey [1961](#page-7-0)) of B. oleracea, the Occidental Cole vegetables (Brussels sprout, cabbages, calabrese/green broccoli, cauliflower, culinary and fodder kale, kohlrabi); B. rapa (syn. B. campestris), including turnip, turnip rape, sarson, and the enormous range of Oriental variants which provide leaf and root vegetables such as Brassica rapa var. pekinensis and B. rapa var. chinensis (Chinese cabbages); B. napus, including swede (rutabaga), oil seed rape, and fodder rape; and seed, condiment (mustard), and vegetable crops derived from B. carinata, B. nigra, and B. juncea. Related genera such as radish (Raphanus), cruciferous weeds, for example, Sinapis, and decorative ornamentals including stocks (Matthiola spp) and wallflower (Cheiranthus cheiri) can be infected. The scientific model and rock garden plant Arabidopsis is also susceptible. Very few studies of infection have been done outside the genera Brassica, Raphanus, and Arabidopsis in the past 50 years and reliance is largely placed on the knowledge gathered by Colhoun ([1958\)](#page-7-0) and Karling [\(1968](#page-7-0)). Raphanus is credited with possessing a greater degree of resistance compared with Brassica but this may solely reflect a lower frequency of virulences in current pathogen populations. Certainly, where radish crops are grown intensively clubroot disease rapidly becomes a major problem for crop producers. Glasshouse radish crops grown in what was East Germany during the 1960s and 1970s were reported as being extensively diseased (H. Bochow, personal communication), and field crops in Florida in the US are also reputed to be susceptible to the pathogen. Of the few recent studies of P. brassicae on wild host populations,

Table 1 Common names for clubroot disease^a

^a After Karling [\(1968](#page-7-0))

probably the most extensive was that of Mats Gustafsson (personal communication). Despite intensive searching in the Mediterranean centers of origin of several Brassica hosts, the microbe was difficult to locate. These results lead to speculation that it may be a ''disease of cultivation.'' This concept suggests that increasingly intensive cultivation of brassicas and related crops provided conditions under which the pathogenic microbe could thrive and where it is less subject to predation by antagonistic organisms. In Japan Tanaka and others ([2006\)](#page-7-0) found clubroot on the cruciferous weed Cardamine flexuosa (bitter cress) in Hokkaido, Aomori, and Okinawa. The pathogen appears to be spreading because these authors comment on its presence as new records in isolated island prefectures, including Sado (Niigasaki), Oki (Shimane), Mishima (Yamaguchi), Tsushima, Iki and Goto (Nagasaki), Koshiki (Yakushima) and Tanegashima (Kagoshima). The host C. flexuosa is possibly an alien weed of cultivation having possibly originated in southern Europe.

Disease Cycle

Primary stages of the life cycle have been recorded in root hairs and epidermal cells of some noncruciferous hosts in the families Papaveraceae, Poaceae, and Rosaceae, for example (Colhoun [1958;](#page-7-0) Karling [1968\)](#page-7-0). The significance of these infestations in offering additional opportunities for reproduction by P. brassicae is untested. These infections may simply be chance encounters providing no reproductive avenues for P. brassicae; alternatively, they could be part of biological systems as yet unrecognized and unevaluated in terms of adding to the ultimate inoculum potential (sensu Garrett [1956\)](#page-7-0) of this microbe. The pathogen persists in soil as apparently very durable resting spores and is reputedly capable of remaining viable and dormant for at least 20 years (see Dixon, this issue). It is possible to speculate that wild hosts outside the Brassicaceae might offer means of maintaining this durability. This is only speculation. Yet P. brassicae is so enigmatic that it is only thanks to Dr Anne-Charlotte Wallenhammar's comparatively recent studies that its long-term dormancy characteristics have been quantified (Wallenhammar [1996](#page-7-0)).

In the disease cycle, primary infection of the root hairs by zoospores formed from the resting spores leads to the deformation and curling of the root hairs (Samuel and Garrett [1945\)](#page-7-0) and possibly some root "epidermal" cells. Thereafter, secondary zoospores are a vehicle for cortical infection which results in typical galling and clubbing of the main root systems. Symptoms vary according to whether the host produces a fibrous root system or the ''root'' is composed of mainly a swollen hypocotyl as in swede and turnip. In both cases the net results are similar and root tissues become deformed and composed of massively disrupted cells filled with secondary plasmodia and eventually release vast numbers of resting spores. A survey of current thinking concerning the life cycle of P. brassicae is given in detail in Kageyama and Asano (this issue) and

the interaction of this microbe with the soil environment in Dixon (this issue).

Symptoms

Infection of seedlings may lead to plant death but invasion in later growth stages rarely kills. Infected plants typically exhibit reversible, foliar wilting when under slight soil moisture stress. As the disease progresses the leaves become reddened, chlorotic, necrotic, and abscise. Plants become stunted and flowering is accelerated, with the formation of poor-quality curds or spears in cauliflower and calabrese (green broccoli) and small unthrifty hearts in Chinese cabbage. Heavy-framed plants such as Brussels sprouts become physically unstable and crops may lodge badly. Seed number and oil quality are depressed in oil seed and turnip rape crops, whereas the roots of swede and turnip exhibit contusions and excrescences on their surfaces. Crop consistency is impaired as a consequence of erratic maturity. Yield, quality, palatability, and storability are reduced and land capital value is diminished (Dixon [1974,](#page-7-0) [1981](#page-7-0), [1984](#page-7-0), [2007\)](#page-7-0). The physiologic and biochemical effects of P. brassicae are described in detail in Ludwig-Müller and others (this issue). The root malformations produced may be confused with the symptoms of insect damage, especially that of the turnip gall weevil (Ceutorhyncus pleurostigma), and on swede and turnip, with the hard swellings of uncertain origin, termed colloquially as ''hybridization nodules.''

Handling

Plasmodiophora brassicae cannot be cultured axenically. Galls containing resting spores may be stored at -20° C for several years with minimal loss of viability. When required, the galls are brought to room temperature and macerated either mechanically or with a pestle and mortar. The resultant suspensions are filtered through nylon or muslin sheets removing host debris and then centrifuged at approximately 3,000 rpm for 10 min. This yields pellets of resting spores that are free from macromaterial. The supernatant liquid is decanted and discarded. Resting spore pellets are resuspended in sterile water and recentrifuged until clean preparations, free from starch granules, are obtained. Inoculum may be applied directly to seedling roots by dipping them; it may be mixed with compost into which seed or seedlings are placed; or aliquots of standardized concentration of spores (normally 10^4 – 10^6 resting spores ml^{-1}) may be applied to the surface of compost in which seedlings will be grown (Dixon [1976a](#page-7-0)). Inoculated test plants should be maintained at a basal temperature of

 $20-25$ °C for up to 6 weeks at which time galling symptoms will be apparent and may be assessed by the method of Dixon ([1976b\)](#page-7-0). Worldwide physiologic specialization was analyzed by Toxopeus and others ([1986\)](#page-7-0). On the microgeographic scale there is substantial physiologic variation, whereas on the macroscale it is more limited and reflects the dominant species of Brassica most commonly cultivated in a particular geographic region.

Economic Significance

Plasmodiophora brassicae is widespread throughout the world. The disease is especially prevalent in mild, moist, temperate areas; these areas may be mountainous parts of tropical countries. Epidemics are developing quickly as the dietary and industrial significance of Brassica crops are increasingly appreciated and concomitantly the intensity of cultivation rises. It is thought that movement of the pathogen from Europe resulted from transport of diseased animal fodder taken by colonists traveling to America, Australasia, and other similar centers of settlement. Occurrence of P. brassicae in countries such as China and Japan may be a good deal more ancient. The pathogen might have accompanied ancestral B. rapa types moving from the Fertile Crescent in what is now Turkey, Iraq, and Iran to Asia.

Disease incidence surveys have been published by the Commonwealth Mycological Institute (CMI) and more recently by the European Plant Pathology Organisation (EPPO) (Table [2\)](#page-4-0). In those countries where brassicas are popular crops, clubroot disease has been identified for many decades. More recent unpublished information indicates the presence of P. brassicae in countries such as Indonesia, Java, and Zambia. One of the problems associated with the historical record of clubroot incidence is its relative simplicity of diagnosis. Quite frequently the incidence goes formally unrecorded because laboratory assays are not required to confirm an outbreak.

There are several European reports of what appears to be clubroot disease in the 16th and 17th centuries; and some illustrations of cruciferous plants by noted herbalists and artists appear to have root swellings that might represent symptoms elicited by P. brassicae on the roots. The Agricultural Revolution in the 18th century encouraged the use of root crops such as the turnip, and as part of the Norfolk four-course rotation their use possibly increased the incidence of disease. The frequency of reports increases substantially in 19th century Europe as agriculture increased to feed burgeoning populations serving the Industrial Revolution. Urbanized Victorian populations demanded both Brassica vegetables and meat from animals sustained over winter with cruciferous fodder. In the latter

Table 2 List of countries [based on data from the Commonwealth Mycological Institute, Egham, Surrey, UK (Commonwealth Mycological Institute [1977](#page-7-0)), Anon ([1987\)](#page-7-0) and the European Plant Pathology Organisation, Paris, France (Anon. [1996](#page-7-0))]

Table 2 continued

Guangdong: present Guangxi: present Hong Kong: present Hubei: present Hunan: present Jiangsu: present Jiangxi: present Taiwan: present Yunnan: present Zhejiang: present India: widespread Israel: present Japan: present Korea, DPR: present Korea, Republic: present Malaysia: present Peninsular Malaysia: present Philippines: present Sri Lanka: present Turkey: present Africa Angola: present South Africa: present Western Hemisphere Argentina: present Brazil: present Rio Grande do Sul: present Sao Paulo: present Canada: widespread Chile: present Guyana: present Mexico: present Puerto Rico: present Trinidad and Tobago: present USA: widespread Alaska: present Hawaii: present Venezuela: present Oceania Australia: present New South Wales: present Queensland: present South Australia: present Tasmania: present Victoria: present Western Australia: present New Zealand: present Papua New Guinea: restricted distribution part of the 19th century, disease incidence was being noted quiet widely in North America and Australasia, presumably as a result of spread along with colonization of the midwest and west coast of North America and movement from coastal centers into the inland fertile areas in Australasia. In northeastern Europe, where cabbage represented a significant part of the diet and was conserved in a pickled form (sauerkraut) to carry populations through the winter, the disease appeared to have reached severe epidemic proportions. By the first half of the 20th century clubroot was recognized as a major constraint to the production of cruciferous vegetables on all continents. In rural areas where sheep still formed a major segment of the agrarian economy, the effects of clubroot disease were devastating. In northeastern Scotland, for instance, swede and turnip formed the backbone of winter fodder supplies and Morrison ([1977\)](#page-7-0) estimated that 50% of the acreage was infested with *P. brassicae*. The social significance of clubroot in that area led to early attempts in the 1930s to breed for resistance. This resulted in swede (B. napus) cvs. Wallace and Bruce which even today retain good ''field'' resistance.

In Asia, crops of Chinese cabbage in all its variant forms, which are of major importance in the diet of local people, has been and still is at serious risk from this pathogen. The importance of this pathogen is demonstrated by the intensive breeding of resistant Chinese cabbage cultivars from the 1960s onward at the National Institute for Vegetables, Ornamentals and Tea (NIVOT) in Japan (see Siemens and others, this issue; Piao and others, this issue; Diederichsen and others, this issue). Breeding has been supplemented by a successful joint industry-government search in Japan for agrochemicals competent to control the microbe. More recently, in the Republic of Korea breeding year-round Chinese cabbage cultivars has been accompanied by the search for clubroot resistance. Here there is a significant parallel between Chinese cabbage (B. rapa) and European heading cabbage (B. oleracea var. capitata) in the Korean pickle kimshi, which was originally used to carry the population through the winter months. Clubroot disease in China is recognized as a major cause of depressed yield of their vast Brassica crops such as Chinese cabbage (Daowang and others [2004](#page-7-0)). Recently, Jing and others ([2008\)](#page-7-0) quantified losses of oil seed rape in China; there is 17% loss of young growing plants and 15% at maturity with 10.2% loss of yield. They report significant losses of plant height, numbers of siliquae, and seed production.

Clubroot is now found throughout the world wherever Brassica crops are grown and is assessed as the major source of disease-induced loss. The severity of infestation and symptom expression increases with the intensity and frequency of crop production. The only scientifically valid worldwide attempt to establish the frequency of infestation

Table 3 Results from a worldwide survey of crop losses caused by clubroot disease⁸

Country	Average % Country infection		Average $%$ infection
Australia	6	Japan	5
Canada	0.11	Netherlands	10
Czechoslovakia	-10	New Zealand	15
Denmark	5	Norway	12
England	6	Poland	4
Finland	4	Scotland	48
France	3	Sweden	1
Germany	8	United States of America	-10
Ireland	17	Wales	45

 a From Crête [\(1981](#page-7-0))

was made by Crête [\(1981](#page-7-0)). His survey looked at infection in individual Brassica crops. High levels of infestation ($>10\%$) were recorded in *B. oleracea* in Australia, Canada, Czechoslovakia, Finland, Germany, Ireland, Netherlands, Norway, Poland, Scotland, and Wales; in B.rapa in Germany, New Zealand, and the United States; and in B. napus in Finland, New Zealand, Scotland, and Wales. In total, Crête's survey (summarized in Table 3) covered 6 million hectares of Brassica and related crops and found an overall mean infection of 11%. This concurs with the general estimate of in-field losses to individual crop pathogens of $10-15%$

The only subsequent surveys have been those of private and public plant breeders used in setting objectives for their programs of work. These indicate that producing clubrootresistant cultivars is rated highly important (see Diederichsen and others, this issue) in terms of satisfying the demands of crop producers. Nonetheless, this task is beset with substantial scientific and technical problems.

The disease is becoming substantially important to emerging economies as the following statement about India demonstrates: ''Club root disease is the main constraint for oilseed rape and mustard cultivation in Eastern part of India mainly in West Bengal bordering Bangladesh and sporadic occurrence in Orissa states where yellow sarson Brassica campestris (B. rapa) var. yellow sarson has been found to be highly susceptible. Clubroot disease is also a serious problem on cruciferous vegetables in Darjeeling Hills in the eastern Himalayan region and the northeastern region states like Manipur, Meghalaya, Mizoram and Arunachal Pradesh bordering China. Bangladesh and China are now both considered high risk zones for clubroot disease'' (from Dr. Indrabrata Bhattacharya, 2008, personal communication). In Nepal, clubroot disease has been observed since 1993 (Timila and others [2008\)](#page-7-0). Severe and widespread outbreaks have been seen since 2004 in

Treatment	Yield	Overall return $(\mathcal{E}_{\text{sterling}})$
Return/ha in the absence of clubroot	1635 crates @ 40p 654.00	
Return/ha if clubroot present	832 crates @ 40p 332.95	
Return/ha if clubroot present and controlled (cost of control with mercurous chloride $= \text{\pounds}46.48/\text{ha}$) 1180 crates @ 40p 472.00		

Table 4 Historic estimate of yield and financial losses to cauliflower crops caused by clubroot disease

Source: D. J. Harrison, unpublished data (1973); Agricultural Development and Advisory Service (ADAS), Lincolnshire, England. Taken from Dixon ([1981\)](#page-7-0)

Bhaktapur, Kathmandu, Lalitpur, and the Palung Valley. The disease is especially severe in the Kathmandu Valley and the Palung/Dama area of Makwanpur District. Cauliflower appears to be the crop most at risk, with 40% overall loss to clubroot. In some parts of the country, production was reduced from 5–6 metric tonnes per household plot of 1500 $m²$ prior to 2004 to 300 kg per plot. A report from Indonesia (Cicu [2006](#page-7-0)) comments on the serious nature of clubroot disease but fails to quantify it. This reinforces the report of Yamada and others ([2004\)](#page-8-0) for West Java, Indonesia.

Possibly of greatest concern from an international financial perspective is the recently reported outbreak of clubroot in Canadian canola crops (B. napus) which has raised the political profile of this problem, especially as legislation now prohibits cultivating this valuable crop on infested land for 5 years. This disease has been known about for many years in the vegetable crops near Toronto, Montreal, and Newfoundland (for example, see McDonald and others [2004](#page-7-0); Belec and others [2004\)](#page-7-0). Reports of infection in oil seed rape from the area near Quebec (Pageau and others [2006\)](#page-7-0) indicated the susceptibility of the canola crop. Testing cultivars indicated that losses due to clubroot in grain yield were 80, 91, and 85% in an Argentinian-derived cultivar over the 1998–2000 seasons and 69, 96, and 89% in Polish cultivars in the same period. Clubroot has now reached the Great Plains which has 6 million ha of canola (oil seed rape) (mostly B. napus with B. rapa to a lesser extent). Appreciable losses in yield of canola are reported by Tewari and others ([2005\)](#page-7-0) in Alberta. Previously, Donald and Porter ([2003\)](#page-7-0) indicated the upsurge in importance of oil seed rape $(B. napus)$ to Australia's broadacre agricultural economy $(\hat{\mathcal{S}}_{\text{Au}})$ 545 million), indicating the risks posed by clubroot based on the losses sustained in that country's field vegetable brassicas. These authors estimate clubroot causes losses of at least 50% (1.6 t ha^{-1}) in diseased crops of oil seed rape in Australia.

As with other soil-borne and foliar diseases, evaluating losses in agricultural broadacre crops are relatively straightforward because they result in direct reductions in grain yield that can be measured quantitatively (for example, from Large and Doling [1962](#page-7-0) to Madden and others [2008\)](#page-7-0). Losses to horticultural crops are frequently not as easy to measure (Dixon [1981](#page-7-0), [1984\)](#page-7-0). There may be direct losses that can be assessed, for example, where there are agrochemicals available to provide disease-free crops (see Table 4). The data provided here are historic but provide a view of the impact of clubroot on yield, even where a pesticide was used. Because mercurous chloride is now banned on the grounds of preventing pollution of the environment with mercury, no attempt has been made to bring the figures up to date either agronomically or financially.

Disease may also result in crop rejection because of blemishes such as residual and untrimmed tumors on the roots of swede or turnip. A crop may also be rejected because disease has delayed maturity and hence it is out of phase with the requirements of the supermarket buyer. Disease may also cause loss of quality in terms of appearance and size leading to downgrading. The incidence of clubroot in a field may kill out a portion of the plants resulting in luxury growth by those remaining and as a consequence crop heads mature erratically and are of unacceptably variable sizes. Clubroot disease complicates the planning of crop rotations and machinery movements, making land management more difficult and expensive. Once established, this soil-borne pathogen reduces the asset value of the land that previously was highly prized for field Brassica production, causing a direct reduction in the wealth of a holding. Where land is rented for crop production, the presence of clubroot reduces the owners' opportunities for leasing to other farmers and growers.

Sources of Information

The International Clubroot Working Group (ICWG) was founded in 1975 and published newsletters until 1985; thereafter, reports from its meetings have been contained in the Cruciferae Newsletter. Meetings of ICWG are usually arranged in conjunction with Brassica Symposia of the International Society for Horticultural Science (ISHS) and Crucifer Genetics Workshops, International Horticultural Congresses, or International Congresses of Plant Pathology.

Fig. 2 International workshop of scientists interested in ''Plasmodiophorids and Related Organisms,'' held 23 August 2008 at the Jolly Hotel, Torino, Italy, under the aegis of the International Clubroot Working Group (ICWG) prior to the 9th International Congress of Plant Pathology (ICPP)

Recently, there has been an upsurge in interest in research leading to free-standing meetings such as those held in London (2006) and Turin (2008) (see Fig. 2), especially where other "Plasmodiophorid Organisms" such as Spongospora and Polymyxa species are included. Abstracts of the Turin meeting have been published in Plant Protection Science 44(1) 2009. Seed of the European Clubroot Differential (ECD) Series, which was developed by ICWG in 1975, is available on request from The Genebank, Warwick University Horticulture Research International (Warwick-HRI), Wellesbourne, Warwickshire CV35 9EF, UK.

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