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BIOLOGY AND MANAGEMENT OF EARLY DYING OF POTATOES

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DISEASE ETIOLOGY

Background

Premature vine death and declining yields are a long-standing problem in many areas where potatoes have been in production for several years. This syndrome, called potato early dying (PED), occurs in both nonirrigated and irrigated production areas of the United States. It is especially important in irrigated areas of the central, southern, and western states (53, 57, 72, 75, 77). Common synonyms for this disease include early maturity wilt, early die, and verticillium wilt.

In long-established potato production areas, especially in the north-central states, the Red River Valley of North Dakota and Minnesota, and in Idaho, PED has developed slowly over many years. Growers often do not realize that their yield expectations are low and consider early maturity a "normal" situation on their land. The recognition of PED in long-established production areas has been complicated by the trend over the last 10–20 years of increasing yields due to improved cultivars, cultural practices, and pest controls. In many

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cases PED may not have caused notable declines in yield over time, but rather has prevented the increases in yield that could have been realized from investments made in cultural improvements and pest controls (77).

In contrast to the above situation, growers in the newly irrigated areas of the Pacific Northwest, with large investments in land and irrigation systems, have recognized the problem more quickly than those who have dealt with it on a chronic basis for many years (72, 77). After high initial yields on these "virgin" soils, the early dying pattern often has developed quickly with subsequent croppings.

To assess critical needs of the US potato industry, the Potato Association of America conducted a survey of growers and research personnel in 1984. Both groups rated PED as the most important disease currently limiting commercial potato production (64). A more recent survey ranked PED as the most important disease of both seed and commercial potato crops and as the second most important yield constraint to potato production in North America (84).

Symptoms and Effects on Yield

Nonvisual symptoms of PED occur several weeks before the appearance of visual symptoms and include reduced net photosynthesis and transpiration and increased leaf surface temperatures during sunny days compared with healthy plants (2). The most common disease symptoms—acropetal progression of chlorosis and necrosis of leaves followed by premature defoliation—are indistinguishable from natural senescence. These symptoms sometimes occur on only one side of the plant or on individual leaves (42). Vascular browning is often prominent in the bases of affected stems, and necrosis of the vascular ring develops in tubers of some cultivars. Advanced symptoms usually do not appear until the tuber-bulking stage. PED is evident within a field as early maturity of isolated plants, groups of plants, or, in severe cases, an entire crop (16, 52, 79).

The effect of PED on yield is highly variable and lowered yield is not always associated with foliar symptom development (79). Yield is limited by reduced photosynthesis as well as early senescence (3). Unfortunately, there are few reliable estimates of yield reduction due specifically to PED, and most reports are qualitative rather than quantitative. Reported yield reductions range from very slight (48, 79) to 30–50% (8, 16, 66, 72, 78, 82). In a two-year study in Minnesota, yields were 12% lower than the potential because of PED, which was reported as an average for three cultivars (48).

Pathogens and Disease Interactions

Soilborne fungi of the taxon *Verticillium* are the primary causes of PED in the different potato-growing areas of North America. Two different species are involved in the disease in different areas; *Verticillium dahliae* Kleb and *V. albo-atrum* Reinke and Berthold. In some regions root-lesion nematodes, namely *Pratylenchus penetrans* (Cobb) Filipjev & Schuur. Stekh., interact with *V. dahliae* as a critical component of this disease. Although numerous other biotic and abiotic factors may cause potato plants to die prematurely, only *Verticillium* species alone or in combination with *Pratylenchus* species can cause premature death associated with the symptoms described above. Thus, this paper focuses on *Verticillium* and *Pratylenchus.*

Verticillium dahliae is the more widespread of the two species and predominates in the north central states and the Pacific Northwest where average summer air temperatures frequently exceed 25°C. Both *V. dahliae* and *V. albo-atrum* are involved in PED in more northern production areas, such as Maine and the Red River Valley, and in the winter production areas of Florida, where average air temperatures are cooler during the growing season (77). These two species of *Verticillium* have an extensive host range that includes many trees, ground covers, shrubs, vines, vegetable and field crops, herbaceous ornamentals, and many weeds (6, 52, 59). Plants regarded as resistant or immune include ferns, gymnosperms, many monocots (including grasses, lilies, irises, orchids, and palms), and one group of dicots, the cactus family. In addition to susceptible plants on which these fungi, following infection and colonization, can reproduce, many symptomless crop and weed species can maintain these fungi at low populations on the roots (52, 58).

Verticillium has generally been considered relatively uniform in its ability to infect a wide range of host plants, but more recent evidence indicates that distinct populations occur within species and vary in their pathogenic capabilities. Pathotypes of *V. dahliae* were first identified on cotton (81). More recently, several subgroups of *V. dahliae* have been identified using vegetative compatibility analysis (43, 73, 88), including two distinct pathotypes on potato (44).

Root-lesion nematodes are migratory endoparasites, i.e. they enter root tissues but move freely through soil from root to root. All stages persist in soil in the absence of host plants, but fourth-stage juveniles and adults are the primary overwintering forms. Nematodes hatch as second-stage juveniles and molt three times before becoming adults and reproducing. Juvenile and adult nematodes feed on root surfaces and burrow into the root cortex (55).

Many species of *Pratylenchus* have been described, but four are commonly found on potato in North America (*P. crenatus, P. neglectus, P. penetrans,* and *P. scribneri)* (4, 50, 90). These nematodes have wide host ranges, including vegetable, forage and fruit crops, and many weed species. Some hosts favor large increases in nematode populations whereas others support only limited reproduction.

Although *Pratylenchus* species (especially *P. penetrans*) can affect potato growth and development directly in some cases if soil populations are high (23, 29), their importance in PED is due to their ability to interact with *Verticillium*. Synergistic interactions between fungi that cause wilts and nematodes are well documented for several crops (5, 54, 60, 71, 83). Detailed field microplot studies on PED conducted in Ohio (57, 74, 78) and Wisconsin (51, 53) have demonstrated conclusively the involvement of root-lesion nematodes in PED. Data from studies in Ohio over the past 10 years have shown consistent patterns in which *V. dahliae* and *P. penetrans* interact synergistically. Together they cause severe symptom development and yields are significantly lower at population densities that have little or no effect with each pathogen individually.

Evidence also indicates that this interaction is specific to certain species of *Pratylenchus, P. penetrans* being the most important (74). Recent studies with several isolates of *V. dahliae* representing two distinct pathotypes on potato indicate further that only certain strains of the fungus may be involved in the interaction (D. D. Botseas & R. C. Rowe, unpublished data).

The mechanism of the *Verticillium-Pratylenchus* interaction in PED is unknown. A general assumption has been that root wounding as a result of nematode feeding provides entry into the stele for fungal pathogens, thus bypassing host defenses to fungal infections (54, 71). This assumption seems reasonable, especially with nematodes such as *Pratylenchus* that physically injure roots while feeding, penetrating, and moving through root tissues (55). However, the fact that the interaction occurs with some species of *Pratylenchus* and not others, despite the fact that they all feed and reproduce in the cortex of potato roots, casts some doubt on the root-wounding theory. Interactions between these two pathogens are probably more complex and involve modifications in host physiology that affect resistance of the plant to infection by *Verticillium*. Split-root studies have demonstrated the synergistic interactions in mint (28) and potato (R. C. Rowe, unpublished data) even when fungal and nematode pathogens were physically separated on halves of the same root system. Moreover, current histological studies using an immunostaining technique (36) indicate that infection of potato by *V. dahliae* is not spatially associated with root wounds caused by nematode feeding (J. H. Bowers & R. C. Rowe, unpublished data).

Overall evidence from several pathosystems indicates that fungal-nematode interactions are most likely biological rather than physical in nature. A current hypothesis is that certain *Pratylenchus* species in their feeding alter the physiology of the potato plant in a manner that favors infection and/or vascular colonization by *V. dahliae*.

Although *Verticillium* is the primary pathogen in PED, other organisms also have been associated with this syndrome. Interestingly, the importance of associated pathogens may differ in various potato production areas. Under sprinkler-irrigated conditions, a connection with the soft rot bacteria (*Erwinia carotovora*) (72a) and *Colletotrichum coccodes* (45b, 68a) has been established. In potato, *E. carotovora* causes blackleg and aerial stem rot. The disease can result in premature death of the foliage that is distinguishable from PED by the completely hollowed pith of the dead vines (77). In some areas, *E. carotovora* also has been associated with systemic vascular infection that may result in symptoms similar to PED (72a, 72b).

C. coccodes is known to cause black dot of potato. Symptoms include development of abundant, small, black sclerotia on senescent and dead potato roots, stolons, and stems. Foliar symptoms of yellowing and wilting have been attributed to infection and rot of below-ground stems and roots (15a). Infection of below-ground tissues by *C. coccodes* has been discounted by some researchers as playing a significant role in PED (18, 51, 77). Recently, foliar infections have been reported from greenhouse studies (45a, 62a). Foliar inoculations with conidia caused sunken, dark necrotic lesions on stems, leaves, and petioles. This pathogen may play a more important role as a foliar pathogen of potato than previously recognized.

Environmental Influences

The development of PED is affected by external abiotic factors including temperature and moisture. Temperature appears to be the most significant factor. Geographical distribution of the pathogens, development and severity of PED, and effects of PED on yield all relate to temperature during the potato-growing season.

Potatoes grow optimally within a temperature range of 18–20°C. The optimum range for growth of *V. dahliae,* however, is 21–27°C (52, 80). Reflecting these temperature optima, disease severity in potatoes infected with *V. dahliae* tends to increase as the mean air temperature rises from 20 to 28°C (66). Symptom development was arrested when the temperature was lowered from 20 to 13°C (66). In the field, temperature effects on symptom development and yield have been demonstrated by comparing results over different seasons or different locations. In a multilocation study in Ohio (79), yields were 24 to 37% lower for potatoes grown in fumigated microplots infested with than without *V.dahliae* when the average July-August temperature was 24°C. However, *V. dahliae* in the same experimental design had little effect on tuber yield when the average July-August temperature was 20°C. Using correlation analysis on data collected over eight years from Ohio microplot studies, Francl and co-workers (31) showed that periods of high temperature (average >24°C) during early emergence and early tuber bulking were correlated with lower yields from infected plants as compared with noninfected controls. In two warm production areas of Colorado, a negative relationship was observed between yield and population densities of *V. dahliae* in soil, but a similar relationship could not be demonstrated in a cool growing region, though the crops were infected (66).

Influence of soil moisture on development of potato diseases caused by *Verticillium* species is just as clear as that of temperature. McLean (61) reported that verticillium wilt in Idaho occurred earlier and symptoms were more severe in moderately resistant potatoes during a wet growing season than in a dry season. Davis et al (22) showed that disease incidence was greater when wilting-point stress on the crop was delayed until mid-August than when moisture stress on the plants was applied in late June. In field microplot studies in Oregon, severity of PED increased with an increase in soil moisture content under both a long-season and short-season environment (8). In a later field microplot study, irrigation treatments were applied either early or midseason to determine the effect of soil moisture status on severity of PED. Disease severity was greater in treatments with excessive compared to optimal or deficit early season moisture treatments. Midseason soil moisture status had no effect on symptom expression (9). Vascular diseases in general are favored by soil moisture and evapotranspiration conditions that result in rapid unrestricted flow of water—and conidia of the pathogen— through stems and leaves of the plant (12a).

Soil water pressure does not appear to play a direct role in the infection process. In greenhouse studies, potato roots (cv Russet Burbank) became colonized over a wide range of soil water pressures. Gaudreault et al (35) concluded that soil water pressures of −0.03, −0.08, and −0.15 MPa had no differential effect on root colonization; i.e. there was no significant effect on number of epidermal or cortical root infections per unit of root length. Water may have an effect, however, on movement of conidia of *V. dahliae* from the microsclerotia to the root surface. Menzies & Griebel (62) and Farley et al (27) demonstrated that microsclerotia multiplied by sporulation when soil was air-dried and remoistened. Under field conditions, microsclerotia of *V. dahliae* may germinate and sporulate several times, thus causing an increase in the population size of the pathogen.

MANAGEMENT STRATEGIES

Severity of PED that develops in a given crop is a function of populations of *V. dahliae* and associated pathogens such as *P. penetrans* in the soil at planting, susceptibility of the cultivar, and favorability of the environment to disease development. Management tactics for this disease thus are aimed at reducing the populations of these pathogens in soil, altering the efficacy of these inocula, or changing the susceptibility of the host.

No single practice will provide complete control of PED. Thus, effective management strategies must emphasize integrated crop management systems in which several decisions are implemented throughout multiple-year, rotational cropping programs. Most management decisions must be made before potatoes are planted. Potential components of integrated systems include pesticides (primarily fumigation), cultural methods (crop rotation, green manures, fertilization, irrigation, vine removal), and host resistance and other biological controls (88). Appropriate strategies will vary from region to region and will be dictated by climate, soil characteristics, availability of irrigation, market requirements of cultivars grown, and overall economics of production.

Soil Fumigation

Soil fumigation has been used effectively for many years to control verticillium wilt in several crops including potato, strawberry, tomato, eggplant, melon, and mint. The soil fumigants chloropicrin and metham-sodium are effective in controlling PED (1, 17, 21, 24, 68). To a limited degree, PED is suppressed by nonfumigant nematicides such as aldicarb and ethoprop (78, 82), but these products have no direct effect on *Verticillium*.

Soil fumigation is accomplished in two ways. Some fumigant materials are injected into the soil using a shank-injection applicator, plow-sole applicator, or blade applicator. On coarse-textured soils where water infiltration rates are high, metham-sodium products are applied in water directly through sprinkler irrigation systems (1). Due to effectiveness and ease of application, this technique became a common practice during the past decade for the control of PED in the Pacific Northwest and some irrigated production areas of Wisconsin and Michigan. Yield increases of 5–10 tons/ha have been reported for the Pacific Northwest (21). If done correctly, soil fumigation is highly effective in reducing populations of nematodes and soilborne fungal pathogens, controlling weeds and soilborne insects, and, thereby, improving market quality of harvested tubers. These biocidal effects may carry over into other crops and thus provide benefits for several seasons.

Despite these advantages, soil fumigation is expensive and concerns have been raised regarding applicator and food safety, nontarget effects, and environmental protection. Specific issues not fully researched include potential contamination of ground water, drift of sprinkler-applied products, destruction of beneficial soil microorganisms, and incompatibility with some cultural and biocontrol practices. Because of the first two concerns, soil injection of metham sodium rather than application through sprinklers is becoming more common. Government regulations of fumigants will likely increase and thus future management programs for PED will probably rely less on these pesticides and more on host plant resistance, cultural manipulations, and biological control with microorganisms.

Crop Rotation

Crop rotation is practiced to some extent in most potato production areas to improve soil structure and fertility and for management of pathogens and pests. Several crops that are grown in rotation with potatoes do not serve as hosts of *Verticillium;* these include cereals, corn, grasses, onion, carrot, bean, pea, and asparagus. Although watermelon and mint, which are highly susceptible, are grown in some potato production areas, they are seldom, if ever, grown in rotation with potatoes. Unfortunately, root-lesion nematodes also have a wide but different host range than *Verticillium* among potential rotational crops. Alfalfa, corn, soybeans, and wheat will host large populations of certain species of *Pratylenchus* (23, 29, 55).

The effectiveness of short-term (two- to four-year) rotations in potato production as a strategy for managing PED is limited by the fact that microsclerotia of *V. dahliae* can survive in soil for at least eight years in the absence of susceptible hosts (52). The population of microsclerotia in soil may decline each year due to microbial activity, but whenever a susceptible crop is produced, new microsclerotia are formed abundantly within host tissues as diseased plants die. A four-year study in Ohio of 15 fields in a two-year, wheat-potato rotation showed a general pattern of a 30–60% increase in soil populations of *V. dahliae* (based on dilution-plate counts) during years in which wheat was grown. An equivalent decline was noted the following year when potatoes were again planted (45). The increase in soil populations in the crop following potatoes was attributed to the decay of colonized potato tissues containing microsclerotia and the release of these propagules into the soil, where they could then be detected by dilution-plate counts.

There is considerable disagreement concerning the value of crop rotation as a management tool for *Verticillium* (1, 6, 41, 45, 68). Inconsistent effects of rotation may be due to the fact that soil populations of *V. dahliae* vary widely among production areas. Long-term rotations away from a susceptible crop will lead to lower populations of viable microsclerotia, but short-term rotations in areas with high populations may not reduce populations of the fungus below thresholds necessary to prevent significant crop loss.

Irrigation Management

Where potatoes are grown under irrigation, the amount and timing of water can be managed to suppress the severity of PED. Although soil moisture must be maintained at 80–90% available soil water following tuber initiation, to optimize growth and prevent tuber disorders, there is some flexibility for water management during early vegetative growth of a potato crop. The amount of applied water can be reduced early in the season to minimize water use by the crop without sacrificing tuber yield or quality. In field studies conducted in Oregon and Wisconsin (10) with the moderately resistant cultivar Russet Burbank, disease severity in mid-August was two- to fourfold less with irrigation treatments that supplied 75 or 100%, compared to 125%, of estimated water use by the crop from planting to tuber initiation. In Oregon, irrigation management also increased tuber yield (10). Thus, early season irrigation management can be an effective component of integrated disease management.

Host Resistance

The most efficient, effective, economical, and environmentally sound means of managing PED would be to plant resistant cultivars. Immunity to this disease has not been reported in *Solanum tuberosum*. Although a few of the most widely grown potato cultivars have some resistance to *Verticillium*, most commercial cultivars are susceptible. Several possible mechanisms of resistance may be present in germplasm. Root-graft experiments with the resistant cultivar 'Reddale' indicated that root infection but not colonization of the vascular tissue was inhibited (37, 38). Efforts are now underway in several US Department of Agriculture and state agricultural experiment station breeding programs to develop commercial potato cultivars with resistance to *Verticillium* (13, 15, 20, 70). Introduction of additional new sources of resistance into different fertile lines of *S. tuberosum* would be useful to breeding programs. There are noncultivated tuber-bearing *Solanum* species with resistance to *Verticillium*. They include *S. berthaultii, S. chacoense, S. sparsipilun*, and *S. tarijense* (14). Research aimed at transferring genes from these diploids to tetraploid potatoes is ongoing (11, 12).

In developing PED-resistant potato cultivars, it would be of interest to know whether resistance to both *Pratylenchus* and *Verticillium* is essential. Microplot studies in Ohio have shown that genotypes exhibiting resistance to *Verticillium* in the absence of *P. penetrans* were more susceptible to PED in the presence of the nematode in some seasons (76; T. A. Wheeler & R. C. Rowe, unpublished data). When breeding for PED resistance, it may be advisable to screen germplasm against both pathogens. Several isolates of both organisms should be used to ensure selection of germplasm that will maintain resistance in many areas.

Biological Control

Little is known about biological control of PED and other diseases caused by *Verticillium*. Nonetheless, the effectiveness of some cultural practices is rooted in effects on the community of resident soil microorganisms, the host, and interactions between the two. The benefits of crop rotation depend on the naturally occurring soil microorganisms to destroy or hasten the death of microsclerotia. Microbial antagonists of *Verticillium* added to soil have been tested for potential use as biocontrol agents with varying success (33, 34, 56). To date, effectiveness of these agents introduced into soil at planting for control of PED has not been encouraging (86), but future research may lead to useful products. One promising line of research is the selection of antagonists that inactivate the microsclerotia before the microsclerotia can infect the plant (49). The rationale for this approach is founded in an understanding of the epidemiology of PED. Microsclerotia of *V. dahliae* germinate and germ tubes infect potato root tips (69) as well as the cortical tissue along the length of the root at anytime during the growing season. Because of the large fibrous root system, the difficulty of protecting moving infection courts, and the long period during which roots may become infected, it is unlikely that PED will be suppressed by biological agents that operate by protecting the growing root from infection.

PED is suppressed following green-manure treatments that effect a change in the activity and composition of the natural soil microflora. This suppression has been demonstrated following production of a green-manure crop and the plowdown of that crop (19). Davis et al (19) have shown that several green manure crops (corn, oats, peas, rape, rye, and sudangrass) suppressed PED compared to a weed-free fallow. Sudangrass, however, was the most effective green manure in reducing both numbers of root infections and soil populations of *V. dahliae*. In addition to the effect on *V. dahliae*, there was a significant increase in total microbial activity in the soil and an increase in root colonization by the soilborne saprophyte *Fusarium equiseti*. The working hypothesis of these investigators is that suppression of PED with green manures is a form of biological control.

One problem with the green-manure strategy is that PED has been suppressed only after two years of green-manure culture. One year of green manuring is not enough. In fact, a three-year period of green manuring is even better in reducing disease severity and increasing tuber yield and quality (19). At present, this cultural strategy is not economically viable for management of PED. Research aimed at decreasing this time frame to one year of green manuring, perhaps by integrating this practice with other management strategies, is a high priority.

DEVELOPMENT OF IPM SYSTEMS

Improved control of PED will require the use of an integrated management program in which most elements are implemented before the crop is planted. Development and use of high-quality cultivars with resistance to both PED pathogens will be the foundation of this program. Multiyear rotational cropping schemes and/or the use of appropriate cover/green-manure crops will play a significant role in suppressing this disease. Use of soil fumigants and nematicides are likely to be continued, although in a more limited role.

Cultural practices will be an important component of IPM. Planting and harvest dates can be timed to minimize yield effects in some situations. For example, cultivars grown for an early market can be harvested while still green, thus escaping the full effects of PED. Careful irrigation and fertility management also will be significant. Vine removal or burning may be appropriate to minimize incorporation of new *Verticillium* microsclerotia into soil (25), although this is likely to be limited because of adverse environmental impacts.

Timely implementation of management practices for PED requires that some estimate of potential effects of disease on yield be available before the crop is planted. Traditionally this has been done by considering the disease and crop history of a given planting site and then basing control measures on past experience. To allow growers to approach management options from a more informed basis, various yield-loss risk-assessment systems have been developed to serve as decision aids (30, 31, 46). These are based on the fact that incidence and severity of PED are related to preplant population densities of *Verticillium* and *Pratylenchus* (30, 65, 66) and to various environmental factors (18, 31, 32, 48).

Growers may be advised to implement control measures if soil samples contain pathogen populations that exceed action threshold values (30, 65, 66, 90). Although there is some variability in published threshold values, they fall in the range of 5–30 cfu/cm^3 air-dried soil for *V. dahliae* alone. In the presence of sufficient populations of *P. penetrans* to cause an interaction (10–20 vermiforms/100 cm^3 soil), the threshold for *V. dahliae* drops to 2–13 cfu/cm^3. These thresholds are currently in use in some situations as decisions aids in determining the need for soil fumigation. Beyond simple thresholds, various yield-loss risk-assessment models have been developed that quantitatively relate preplant populations of one or both pathogens directly to projected yields or yield-loss categories (30, 90).

Both action thresholds and risk-assessment models rely on accurate estimates of the pre-plant populations of both pathogens and will require knowledge about environmental conditions during the crop season. Unfortunately, these estimates can be compromised by sampling errors during collection of soil samples (26) and by the assay method used to evaluate population densities of the pathogens. Spatial patterns of both organisms in soil are typically clustered or aggregated (7, 39, 47, 55, 67, 85), and considerable work is still needed to ascertain appropriate sample number and collection technique, and timing necessary to develop reliable population estimates. Current indirect assay techniques for *Verticillium* rely on propagules of the fungus growing on plates of a selective agar medium (40, 63). Accuracy of these techniques depends on the method of placing the soil on the plates (wet sieving, dilution plating, Anderson sampler) and on potential microbial interactions on the agar surface (65, 85). Development of quantitative, direct assays for *Verticillium* in soil based on serological tests or use of DNA probes may, in the future, improve the accuracy of population estimates.

Research in several key areas will continue to improve integrated management systems for PED. These include:

Development of rapid, economical, and reliable soil assay methods for PED pathogens;
Improved accuracy of action thresholds and/or yield-loss risk-assessment models;
Development of horticulturally acceptable potato cultivars with resistance to *Verticillium* and possibly *Pratylenchus*;
Discovery of new fungicides or nematicides with specific activity against PED pathogens;
Development of new and improved cultural practices and an understanding of the effects of cultural practices and soil type on infection efficiency and disease development;
Identification and enhancement of biological control agents; and
Evaluation of integrated practices for management of PED.

PED is a complex disease that is presently controlled by fumigation, planting of cultivars with moderate resistance, and management of fertility and irrigation. Our understanding of PED is steadily improving and with continued research directed toward the above goals, implementation of viable IPM systems using improved management techniques should be possible.

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