Spatio-temporal consideration of soil conditions and site-specific management of nematodes

H. Melakeberhan · F. Avendaño

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Abstract Site-specific (precision) management (SSM) has potential for application in managing nematodes and soil conditions in environmentally meaningful ways. Successful application of SSM, however, may be dependent on how agronomically, biologically, and ecologically integrated the plan in question is. Otherwise, SSM risks falling into the "Tried but did not last" category. With this background and in addition to describing the concepts and principles of SSM, this presentation discusses the following interrelated points: (1) Case studies of spatio-temporal analysis of soybean cyst nematode (*Heterodera glycines*) infestations, soil conditions and crop yield in managed ecosystems. Among the critical factors to an accurate and sustained application of SSM are understanding (i) the temporal structure and (ii) the spatial structure of the attribute in question, and (iii) establishing cause-and-effect relationships in the prevailing conditions. New approaches to temporal structure analysis when balancing the purpose of SSM application and nematode biology (as it relates to life stages), population density in soil and root tissue (to determine threshold), and damage functions (physiological stress of the plant during the growing season) are outlined. (2) Application of the concept of fertiliser use efficiency (FUE) to identify soil conditions when managing soil fertility. Defined as increase in host productivity and/or decrease in plant-parasitic nematode population density in response to a given fertiliser treatment, the FUE model recognizes variable responses and identifies four categories of interactions necessary for integrated management decision-making options that account for agronomic, economic, ecological and environmental and pest management issues. (3) Approaches to changing soil conditions in agro-biologically integrated ways. By incorporating nematode community structure (an excellent indicator of soil bio-ecological changes), soil nutrient amendments and crop yield, we have described a modification of the

H. Melakeberhan (🖂)

Agricultural Nematology Laboratory, College of Agriculture and Natural Resources, Michigan State University, East Lansing, MI 48824, USA e-mail: melakebe@msu.edu

F. Avendaño Department of Plant Pathology, Iowa State University, Ames, IA 50011, USA e-mail: avendano@iastate.edu

FUE model to identify and monitor changes in soil conditions, thereby creating the necessary bridges to disciplinary and cross-disciplinary gaps and interactions.

Keywords Biological indicators · Cause-and-effect relationships · Daily nematode population density · Fertiliser use efficiency · Nematode community structure · Nematode population density · Proof-of-concept · Soil nutrients · Spatial structure · Temporal structure

Introduction

Meeting the food, fiber and living environment needs of the increasing world population in a limited space and with many biological, technological, ecological and conflicting socioeconomic restrictions is a global challenge. The challenge is further complicated by physical degradation of soils, requiring many forms of amendments (Bumb 1995; Fink et al. 1999; Baligar et al. 2001; Good et al. 2004). For example, over 140 million metric tonnes of fertiliser (total N-P-K) per year are applied globally to improve nutritionally depleted soils (Anon 2006). Moreover, the increase of pesticide application from 50,000 t/ year in 1945 to 2.5 million t/year in 2005 (Sundquist 2007) has added to the biological and chemical degradation of soil, creating many long-term agro-environmental challenges (Wickham et al. 1997).

Balancing the production challenges facing agriculture with the projected increase in world population to 9 billions and decrease in arable land to 0.07 ha per person by 2050 will require more efficient use of finite resources (Sundquist 2007). In this, site-specific management (SSM) can play a significant role. However, SSM will require a spatiotemporal understanding of the soil environment and the approaches being applied to achieve desired agro-biological changes and, most significantly, will require considerable knowledge and disciplinary gaps to be bridged. For example, plant-parasitic nematodes cause an estimated \$100 billion annual crop loss globally (Sasser and Freckman 1987), and their impact on bio-fuel crops, an emerging enterprise, is yet to be determined. As they are not the only biotic yield-limiting factor, approaches beyond the science of nematology may be required. Breeders often try to develop products with specific traits, such as high yield or resistance to a particular biotic or abiotic factor, and all are likely to be grown in fields where unaccounted for limitations will affect the desired results. Breeders can benefit by interacting with other disciplines and working in a more integrated fashion. Similarly, soil scientists may look at physical and chemical constraints while overlooking biological constraints, so missing an integral component of continually changing soil conditions. The changes required will involve all disciplines in making fundamental changes of thinking and adopting integrated cross- and multi-disciplinary approaches, to the benefit of all. These approaches include characterising soil conditions and changing them efficiently in integrated ways. In this manuscript, our focus is not to make an exhausted review of the topics, but to highlight factors that need critical consideration if the potential of SSM is to be fully realized and sustained. Using plant parasitic nematodes as examples, the following interrelated points will be discussed: (1) Case studies of spatio-temporal analysis of soybean cyst nematode (SCN, *Heterodera glycines*), soil conditions and crop yield in managed ecosystems; (2) Application of Fertiliser Use Efficiency (FUE) to identify soil conditions when managing soil fertility; (3) Approaches to changing soil conditions in agro-biologically integrated ways.

Site-specific management of plant-parasitic nematodes and requirements

The first symposium on the application of SSM in nematology and plant pathology was held at the joint meeting of the Society of Nematologists and the American Phytopathological Society in 2001 in Salt Lake City, Utah, USA, and all papers presented there were published in the Journal of Nematology 34:185–231 (Evans et al. 2002; Melakeberhan 2002; Morgan et al. 2002; Nutter et al. 2002; Oudemans et al. 2002; Royle and Lathrop 2002; Thomas et al. 2002). Since then, more publications in the subject area than can be listed here have appeared (Avendaño et al. 2003, 2004a, b, c; Farias et al. 2002). The reader is referred to these for details of the diversity of studies, organisms, crops and methods employed. Given soil physical and chemical heterogeneity (Marschner 1995) and that soil dwelling plant-parasitic nematodes have patchy distributions, the conditions for the application of SSM to the management of nematodes seem appropriate. Successful application of SSM, however, may depend on how agronomically, biologically, and ecologically integrated the plan in question is. Otherwise, SSM risks falling into the "Tried but did not last" category. Among the factors critical to an accurate and sustained application of SSM are understanding (i) the temporal structure and (ii) the spatial structure of the attribute in question, and (iii) establishing cause-and-effect relationships among the prevailing conditions (Melakeberhan 2002).

Temporal structure

Because plant-parasitic nematodes have limited mobility on their own, they meet one of the requirements of SSM (Pierce and Sadler, 1997). However, considering SSM based on nematodes' limited mobility without carefully weighing the purpose of SSM application on one hand (based on what we know and anticipating future advances) and the complexity of the nematode in question on the other can lead to inadequate decisions. Depending on the value of the crop, the purpose of SSM application may be to adversely affect the nematode in question, to compensate for nematode-induced stress during the growing season (e.g. N side-dressing), or both. Nematode complexity includes biology (as it relates to life stages), population density in soil and root tissue (to determine damage thresholds), and damage functions (physiological stress of the plant during the growing season). From the nematode biology point of view, a treatment may not be effective unless it is applied at the appropriate time for the nematode in question. For example, if the problem is a cystforming nematode and the potential treatment is effective against vermiform stages, one needs to know at what stage the nematode will be at the time of treatment application.

How and when nematode population density threshold level is determined, which is a function of nematode reproduction, is another challenge. The standard approach to determining nematode population density is described as follows (Barker et al. 1985):

$$R_f = P_f/P_i$$

where R_f = reproduction factor, P_i is the initial and P_f is end of season nematode population density. If the ratio is >1, the nematode population density has increased and vice versa. The P_f/P_i ratio has limitations because it gives only an estimate of the difference in nematode population density between the start and the end of the season. It does not account for when and what levels of nematode population densities (NPD) occurred during the growing season (Fig. 1) to cause crop yield or quality loss. NPD is defined here as the number of nematodes of all stages per unit weight (g) of root plus per unit volume (100 ml)



of soil at each sampling time. NPD increase and the R_f were greater in Year 1 than in Year 2, possibly leading to different management decisions. The R_f values, however, do not account for the differences in population density peaks and nor do they explain the difference in yield between years. Moreover, increase in NPD over a growing season can vary considerably with soil type (Fig. 2). A more accurate NPD analysis, therefore, needs to incorporate frequency of sampling and root and soil populations separated by soil types. If mid-season remedial treatments are available, knowing when the NPD peaks occur should be helpful to making SSM applications.

While determining NPD over time provides more information than the P_f/P_i ratio, relating it to the physiological stress an infected plant suffers is a challenge. In part, this has to do with the lack of quantifiable and/or predictable damage threshold levels, which

Fig. 2 SCN cyst population density in soil samples collected at approximately monthly intervals during the soybean growing season in a field in Shiawassee Co., Michigan. Soil texture determined on subsamples collected at planting (DAP 0) was used to classify samples based on the sand content in the soil sample (%). Data are from Avendaño (2003)



are further confounded by the lack of an integrated understanding of host-nematode interactions under the prevailing conditions (Melakeberhan 1997, 2004). For example, plant-parasitic nematodes obtain all of their energy requirements from the host (Atkinson 1985). Thus, the physiological stress a nematode-infected plant suffers is a function of the NPD over time in the prevailing conditions (Ferris et al. 2004). This raises the challenges of measuring the season-long physiological impact on the host and how the information can be used in SSM. One approach is to measure daily nematode population density (DNPD) as an indicator of nematode damage functions and the host's carrying capacity over the growing season (Melakeberhan 2007). DNPD is calculated as follows (Melakeberhan 2007):

 $DNPD = \left(\sum NPD \text{ at all sampling dates/number of days between first and last sampling}\right).$

DNPD assumes that the first sampling occurs at planting time and has several advantages over other approaches. First, it provides a better estimate than the P_f/P_i ratio of a host's carrying capacity during a growing season and better interpretation of the numbers. For example, DNPD and R_f values were higher in Year 1 than in Year 2, as was yield (Fig. 1). With DNPD, one can tell how many nematodes were actually present during the growing season. Second, by incorporating NPD, DNPD shows the seasonal picture and detailed interpretation of the conditions. For example, it is possible that the occurrence of NPD peaks during the pod formation stage in Year 2 and later in Year 1 may have contributed to yield differences between the years. Moreover, knowing the DNPD and when the population density peaks occur, one can make more accurate decisions as to when potential preventative and/or remedial SSM treatments may be applied. Third, DNPD provides a foundation upon which further modifications (e.g. environmental conditions) may be incorporated to develop predictable damage threshold models, important decisionmaking tools. With regard to the example in Fig. 1, it is likely that the difference in yield between Years 1 and 2 had other confounding factors, in which case the incorporation of possible remedies for the confounding factors should lead to better decision-making for the prevailing conditions.

Spatial structure

Assuming that economics justify it, SSM will be applicable if the plant-parasitic nematode distribution has a well-defined structure, which, in turn, is a function of sampling design, frequency of nematode distribution, and any interpolated distribution map (Avendaño et al. 2004a, c; Evans et al. 2002). Traditional sampling schemes are to collect a predetermined number of samples along a zig-zag line and to determine the average infestation level from a composite sample (McSorley 1998; Melakeberhan 2002), a process that undermines a key component of SSM—nematode spatial variability. Economics usually dictate that traditional bulk sampling continues, but point or site-specific sampling would be better for accurate application of SSM. Using a previously described sampling plan (Avendaño et al. 2003), we demonstrate the difference in value of information obtained by traditional and geostatistical analysis of SCN cyst density from 109 soil samples (Fig. 3). Traditional sampling would have provided only the average number of cysts/100 cm³ of soil, which was 14.5, high enough to warrant a decision to apply a control treatment. The point samples that were collected could be sorted by frequency of distribution, generating additional information. SCN cysts were not detected in 19% of the samples, 54% had up to



15, and 27% had 30 or more cysts/100 cm³ of soil (Fig. 3). The next step is to determine the spatial structure of the nematode distribution. There are several statistical tools that can be used to make a spatial analysis of the data; geostatistics is just one that has been successfully applied to the study of plant parasitic nematodes (Avendaño 2003; Evans et al. 2002). Kriging, the mapping of the nematode distribution structure through interpolation, is the final step in a geostatistical analysis to determining the pattern of the problem in the field (Fig. 4a). It is clear from this data set that there is spatial structure (Fig. 4a) that may justify SSM rather than blanket treatment. Using such analyses to identify whether or not SSM is applicable may simply depend on understanding the principles behind the science and having the means to obtain a sufficient number of samples and the necessary computer and software. Whether or not SSM application will be sustained, however, may depend on establishing cause-and-effect relationships beyond disciplinary boundaries.

Establishing cause-and-effect relationships

As Avendaño (2003) clearly documented, it is rare that a single factor is 100% responsible for what is visible or may be identified as a cause of a problem in question under field conditions (Fig. 4). This leads to the need to distinguish between correlations and causeand-effect (as in Koch's postulates) relationships. In addition to establishing the SCN cyst spatial structure (Fig. 4a), Avendaño (2003) collected data on soybean yield (Fig. 4b) and normalized difference vegetative index (not shown), a physiological indicator of plant health (Royle and Lathrop 2002). The correlation between SCN and yield parameters suggested that the main cause of yield variation was SCN, the remedy for which the use of resistant cultivars in a rotation system is the obvious recommendation. However, there was the additional problem of the association of yield loss with poor plant health. It was not until after an analysis of the US Geological Survey (USGS) maps (Fig. 4c; Anon 2003) that the problem was found to be deep and structural. The low yield and high SCN population density were over nutritionally depleted and poorly drained Berville loam and Newaygo sandy loam close to a deep drainage ditch, whereas the high yield and low SCN population density occurred over richer Brookston loam. There are two points worth noting here: (i) the problem cannot be solved without simultaneous consideration of the soil conditions and SCN, and (ii) the soil conditions would not have been clearly identified without consulting USGS soil maps. It was evident from this data set that a simple

(2003)

Fig. 4 SCN population density and soybean yield data were collected from a soybean field in Shiawassee County, Michigan. Scales on the axes represent geographic location of the field (43.13 degrees North and 84.04 degrees West). Geostatistics were applied to analyze the data and to map the spatial distribution of the two variables. (a) SCN cyst population density at planting was spatially structured and ranged from 0 to 120 cysts/ 100 ml of soil collected within the 250 m \times 250 m area indicated by blue flags in the vield map. (b) Seed vield was recorded with a yield monitoring system mounted on the combine as soybean was harvested. Data are from Avendaño (2003). (c) Three distinct soil types can be identified in the soil classification map for this field: Berville Loam (BVL), Newaygo Sandy Loam (NSL) and Brookston Loam (BSL). Map digitized by F. Avendaño from the USGS soil classification map of Shiawassee County (Soil Survey Division

Staff 1993)



cause-and-effect relationship could not be established, but that there was a complex relationship involving the effects of soil physical and chemical characteristics on the nematode and the plant, disturbing the host-parasite relationship, thus demonstrating the need to look beyond limited horizons (Wallace 1978). Though seemingly appropriate for the delineated SCN distribution and yield maps, SSM would not have been successful without simultaneously addressing the SCN problem and the soil conditions. When such limitations have been clearly delineated, it becomes possible to test the efficiency of potential soil and nematode management options.

Fertiliser use efficiency and changing soil conditions

Because many agricultural soils are degraded, some forms of soil amendments and/or technology application will always be needed. These include changing the plant to fit the soil or vice versa (Baligar et al. 2001; Fink et al. 1999; Good et al. 2004; Loneragan 1997; Tillman 1999). In the case of biotic limitations, it may be relevant to change the soil and/or

the plant to manage the biotic limitation (Hussey and Williamson 1998). Most of the approaches to addressing soil-driven biotic or abiotic problems have strong disciplinary focus and are primarily based on parallel models. For example, an agronomist/soil scientist and a nematologist may apply fertiliser to increase yield, but their primary focus would be abiotic and biotic yield-limiting factors, respectively. In order to deal with multiple soil limiting factors and to better apply SSM in sustainable ways, multi-faceted and integrated models are needed. One such model is that of fertiliser use efficiency (FUE; Melakeberhan 2006). FUE is defined as increase in host productivity and/or decrease in plant-parasitic nematode population density in response to a given fertiliser treatment (Melakeberhan 2006; Fig. 5).

FUE model-the idea and proof-of-concept

When fertiliser is applied to affect plant growth, nematode population density, or soil deficiencies, alone or in combination, there is an increased, decreased, or unchanged response for none, some, or all factors, leading to linear conclusions with possible unintended consequences. The idea behind the FUE model is that the responses are variable and that the management decision-making options that account for agronomic, economic, ecological and environmental issues can be identified by subjecting the data to an integrated analysis (Melakeberhan 2006; Fig. 5). For example, by expressing the host productivity and nematode population data on the same scale (standardized as percent of control) and plotting the relationships, the FUE model identifies four efficiency categories (Melakeberhan 2006; Fig. 5). If the controls represent 100%, standardized data points above the 100% line on the respective axes would mean that host productivity (Fig. 5, Boxes A & B) and nematode population density (Fig. 5, Boxes B & D) have increased. The data points within a box may vary greatly from host to host or nematode to nematode, which allows further separation within a category. Best case scenario under nematode (and



Number of plant-parasitic nematodes as % of control

Fig. 5 Four hypothetical categories of FUE derived from host productivity/nematode/nutrient interactions. Data points that fall above the controls (100%) will show an increase in host productivity (A & B) and numbers of nematodes (B & D). Data points in Box A would be the best-case scenario, and in Box D would be extremely unsatisfactory. Data points in Boxes B and C provide a choice of what the priorities of fertilizer application should be—improving host productivity or suppressing nematode numbers, respectively. Modified from Melakeberhan (2006) with permission from Brill

other pest) infestation would be if the data points fell in Box A, where the host productivity is increased and the nematode population density decreased. If data points fall in Box D, the worst-case scenario, the result of fertiliser application would be completely undesirable, expensive, and perhaps damaging to the environment. Data points that fall in Boxes B and C are half-efficient, and would need to be complemented by other means of suppressing nematode population density and improving host productivity, respectively.

Using *H. glycines* resistant ('Bryan'; Boerma et al. 1991), susceptible-tolerant ('G88-20092'; Boerma et al. 1993) and susceptible-intolerant ('Tracy M') soybean cultivars against *Meloidogyne incognita* (root knot nematode) and *Pratylenchus penetrans* (root lesion nematode) and treating with no nutrients, full-strength Hoagland Solution (HS), and HS without N (HS-N), a proof-of-concept was published (Melakeberhan 2006). A tolerant and an intolerant cultivar allow equally easy reproduction of the nematode, but the former does not suffer yield loss. Bryan has a limited resistance to *M. incognita* (Hussey et al. 1991). The study was conducted under glasshouse conditions and terminated 25 days after inoculation with 15,000 eggs and mixed vermiform stages of *M. incognita* and *P. penetrans*, respectively. Nutrient application improved photosynthesis (and hence physiological efficiency) of all of the cultivars, more so with HS than with HS-N, but differed in its effects on the nematodes (Fig. 6). Nutrient treatment suppressed population densities of



Fig. 6 Proof-of-concept on the relationships among changes in photosynthetic rate, *Meloidogyne incognita* and *Pratylenchus penetrans* population densities, and FUE in Bryan, G88-20092 and Tracy M soybeans after receiving either full-strength Hoagland Solution (HS, solid squares) or HS-N (open squares). Broken lines represent the respective controls (100%). Data points less than 100% on the X-axis and more than 100% on the Y-axis, represent high FUE. Reproduced from Melakeberhan (2006) with permission from Brill

M. incognita and *P. penetrans* in Tracy M and was more effective for the former than the latter nematode in G88-20092. The effect of nutrient treatment on Bryan was mixed for *M. incognita* and of no benefit for *P. penetrans*. Under the experimental conditions, no data points fell in Box D and few in Box C (Fig. 6), suggesting benefits of nutrient treatment in suppressing nematode population density and/or improving host physiology in the susceptible-intolerant variety. The results provide the proof-of-concept needed for field tests.

The FUE model is also applicable to other biotic limiting factors, with many crossdisciplinary benefits. For example, current procedures for the selection of crop cultivars are mostly based on identifying narrow genetic/agronomic traits for a specific purpose. But the reality is that the durability of selected traits may be affected by many factors not taken into account in the selection process. What the FUE model provides is a basis upon which integrated selection can be employed. For example, a breeder and/or an agronomist would be able to make a better and potentially more sustainable selection if they understand the interactions that result in the data falling in Boxes A and B (Fig. 5) than if they simply look at one parameter (increased yield/host productivity). Another example would be how a crop protectionist makes IPM recommendations by looking at Boxes B and C. Thus, by identifying the four categories of FUE, the model creates a road map for cross- and multidisciplinary applications of soil amendment-based management practices that account for economic and environmental impacts.

Approaches to changing soil conditions in agro-biologically integrated ways

In addition to an affirmative proof-of-concept, the FUE model identifies management decision-making options, based on observed interactions, that account for agronomic, economic, ecological and environmental issues (Fig. 5). With the ability to identify soil conditions comes the option of changing soil conditions and biologically monitoring the efficiency of the changes in space and time. An example of agro-ecological application of the FUE model is to consider soil nutrient management and nematode community structure (NCS). Nematodes represent four out of five multi-cellular animals on the planet; they are the engine that drives soil nutrient cycling and are excellent indicators of agro-ecological changes (Bongers and Ferris 1999; Ferris et al. 2001; Fiscus and Neher 2002; Neher and Olsen 1999). Many ecological conditions have been described by analysing NCS as trophic groups (carnivores, omnivores, herbivores, bacterivores, fungivores, or predators). Analysis of NCS is an important biological monitoring tool when imposing soil treatments such as nutrient (organic or inorganic) amendment to change soil conditions in favour of increasing crop yield and improving soil conditions in integrated and ecologically sound ways. A modification of the FUE model is proposed herein (Fig. 7), to develop agrobiologically sustainable soil nutrient management using NCS as a biological driver. Let us assume that soil amendments (organic or inorganic) are applied and NCS, soil parameters (SP) (nutrients, pH, % organic matter) and crop yield are measured. Responses of herbivores to the soil amendments can be analyzed using the FUE model (Fig. 5). Using a modification of the FUE model, the relationships among nematode trophic groups (TG, excluding herbivores), SP and yield can be described as follows:

Percent yield = $((yield in amended soil)/(average yield in non-amended soil)) \times 100.$



Numbers of trophic group as % of control

Fig. 7 Modified FUE model applied to assess the effect of soil amendment on the relationships between nematode trophic groups (TG, excluding plant-parasites) and yield or soil parameters (SP). Data points that fall above the controls (100%) will show an increase in host productivity (E & F) and numbers of nematodes (F & H). Data points in Box F would be best-case scenario, in Box G would be worst-case scenario or environmental hazard, and those in Boxes E and H provide a choice of improving TG or yield, respectively. After Melakeberhan (2006)

Percent TG = $((TG \text{ number in amended soil})/(average TG \text{ number in non-amended soil})) \times 100.$

Percent SP = ((SP value in amended soil)/(average SP value in non-amended soil)) \times 100.

By plotting the relationships, four categories of interactions can be identified (Fig. 7). The differences between Figs. 5 and 7 are that the positions of the best- and worst-case scenario boxes have moved one box clockwise in the latter. In Fig. 7, data points that fall in Box F will be ideal and those in Box G would be worst-case. Data points that fall in Boxes E and H will require complementary treatments to improve the numbers of nematodes of the various trophic groups or host productivity and/or soil conditions, respectively. This modified FUE model links nematology and cross-disciplinary gaps in the testing and development of agro-biologically sustainable soil nutrient management using NCS as a biological driver of changes of soil conditions. Such an approach is likely to be appealing to a broad range of disciplines.

Conclusions

The potential for SSM of biotic and abiotic yield-limiting factors remains high, especially when considering the increasing demands for healthy and sustainable crop production in agro-ecosystems that have so many limitations. In order to help expand and sustain the application of SSM, we have described three intertwined themes: (1) Considerations for best application of SSM in managing plant-parasitic nematodes, with three critical subcomponents; these include understanding the temporal structure of nematode populations as it relates to life stages, damage threshold (population density) and damage functions (physiological stress on a plant) during a growing season; a second aspect is understanding the spatial structure of the attribute in question, and a third is to establish cause-and-effect relationships of the prevailing conditions; often, the latter will require looking beyond disciplinary perimeters and failure to consider any one of the components when making decisions about SSM application may lead to wrong conclusions. (2) Mechanisms to measure FUE when managing soil fertility, a routine practice in crop production systems; the FUE model identifies four categories of interactions that account for agronomic, economic, environmental, and nematode (pest) management impacts, all of which are integral parts of SSM, thus creating a road map for cross- and multi-disciplinary applications when considering soil nutrient amendment practices. (3) The need for improving soil health is not in question, but how to improve it is a challenge; by incorporating the FUE model and NCS, an agro-biologically integrated way of changing soil conditions is described.

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