

## Plant Population Viability Analysis in Conservation Biology: A Review

**Summary.** In this report we review the role of population viability analysis (PVA) in plants. PVA is widely used to assess the population persistence of small populations for different management scenarios and is therefore one of the most powerful and pervasive tools in conservation biology. However, plant PVAs are relatively scarce and computer-aided, plant-specific PVA tools are currently not available. On the base of a selected literature review we summarize typical features of plant PVA and show that plant life history traits such as dormancy, periodic recruitment or clonal growth are crucial model components. Moreover, we emphasize the particular importance of buffer mechanisms, density dependence and genetics as these aspects may modify the assessment of persistence time and thus potential management decisions.

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## 1 Introduction

Population viability analysis (PVA) is widely used to assess the population persistence or extinction risk of small populations for different management scenarios and is therefore one of the most powerful and pervasive tools in conservation biology (e.g. Burgman et al. 1993). Based on field-collected demographic data, the viability of a population is usually assessed by means of computer modeling tools, including a variety of packaged modeling programs (e.g. RAMAS©GIS; Vortex; PATCH; Meta-X). However, until now, there is no real census on the definition of a PVA and its application has ranged from qualitative, verbal processes to sophisticated, spatial-explicit simulation models (Reed et al. 2002). Particularly for plants, the definition and application of PVA is relatively opaque. This may be the reason why recent reviews of PVAs have included only few plant studies (see Boyce 1992; Beissinger & Westphal 1998; but see Menges 2000) and animal PVAs are apparently more common. Is it really true that plant PVAs are scarce? What are typical features of plant PVAs? Are any plant PVA computer tools available? Moreover, what are future challenges and approaches for population viability analysis in plants? To answer the latter questions we will provide a selected literature review in this report. Based on twelve recent plant PVA studies we summarize current knowledge and assess plant PVA as a tool in conservation biology. We show that particular aspects of plant life history are crucial for model precision and that the consideration of buffer mechanisms, density dependence and genetics may modify the assessment of persistence time and thus potential management decision.

Plant PVAs are principally different from animal PVAs. Whereas animal PVAs are often based on age-classified matrices, most plant PVAs are stage or size-classified (so called Lefkovitch matrix models). In stage or size-classified matrix models each plant individual is subject to a stage or size class with a certain transition probability of reaching the next class. For plant matrices this applies to life-history stages such as dormant seeds, seedlings and flowering plants. In other words, in the PVA model plant individuals have a certain probability to emerge from a seed bank, become adults and, eventually, reach the reproductive stage, i.e. produce seeds for the next generation. Particularly for plants, the process of deriving these probabilistic values from empirical data and generating quantitative predictions has revealed many challenges to both plant ecologists and modelers.

However, which quantitative criteria are used for the assessment of population persistence? The earliest plant PVA calculated the finite rate of increase, ( $\lambda$ ), for aged-structured data derived from Scots Pine (*Pinus sylvestris*) forest (Usher 1969). The finite rate of increase is the exponential rate of population growth in a density-independent, deterministic environment (Menges 2000). A lambda of 1 projects a stable population, larger values represent growing populations, smaller values project declining populations. More recently, Nantel et al. (1996) used the concept of minimum viable populations (MVP) to assess extinction risk of the American ginseng (*Panax quinquefolium*) and wild leek (*Allium tricoccum*), two plant species which have declined and gone extinct because of overharvesting in Canada. Given an assumption of the maximum risk to be tolerated (e.g. less than 5% risk of extinction in 100 years), a MVP will forecast extinction. However, using MVP in nature conservation may lead to wrong management decisions or even non-action. Reed et al. (2002) suggested that PVA should not be used to determine minimum population sizes, because critical sizes may be sensitive to small errors in demographic data,

and most models are not accurate enough to make such precise predictions. Therefore, more often mean time to extinction or the probability of extinction have been used to assess viability of plant populations.

## **2 Case studies of plant PVA**

Is it really true that plant PVAs are scarce? As pointed out by Menges (2000) the answer, of course, depends on the definition of a PVA. Surprisingly, in his review Menges found 95 plant PVA studies when the term PVA was broadly defined. However, in this review we will focus on selected case studies in order to emphasize particular challenges in plant PVA. Therefore, we have chosen twelve recent case studies for the period 1998-2003. Of these studies, seven are based on North American species, three are from Europe and one each from Australia and Asia (see Table 1; six notable plant PVA studies are presented in detail in the following section).

### **2.1 *Saxifraga cotyledon***

Dinnetz & Nilsson (2002) analyzed population dynamics of *Saxifraga cotyledon*, a rare, long lived herb of fragmented habitats at high latitudes. Based on a five year demographical study they used both deterministic and stochastic matrix simulations to estimate population growth rates and extinction risks for one small and one large subpopulation. None of the two subpopulations were found to suffer from high extinction rates, because plant individuals were capable of vegetative reproduction when environmental conditions were severe. Surprisingly, if population sizes were small, demographic stochasticity was of minor importance for the risk of extinction. These results are opposite to the general assumption that demographic stochasticity may increase extinction risk in small populations (Menges 1998).

### **2.2 *Gentianella campestris***

Lennartson & Oostermeijer (2001) applied transition matrix models to evaluate the effects of environmental stochasticity and different methods of grassland management on dynamics and viability of a Scandinavian population of the biennial *Gentianella campestris*. They concluded that traditional grassland management, i.e. mid-July mowing followed by autumn grazing, is more favorable for this plant than the methods that prevail in Scandinavia today. In a subsequent paper, Lennartson (2002) demonstrated that reduced population viability of *Gentianella campestris* may also result from disruption of plant-pollinator interactions through reduced pollination in small and isolated habitat fragments.

### **2.3 *Hudsonia montana***

By using both a deterministic and stochastic size-based matrix model Gross et al. (1998) studied the effect of burning and trampling on the viability of populations of Mountain golden heather (*Hudsonia montana*). This threatened North Carolina shrub

species suffered major population declines due to the suppression of natural fires and increased trampling by bikers and campers. Even though neither increased burning nor trampling reduction alone can reverse *H. montana*'s decline, a judicious combination of both management strategies may have a positive effect on population persistence. The authors suggest that even with limited data available, population viability tools such as matrix models may support decision-making in nature conservation.

Table 1: Overview of twelve selected plant PVA studies for the period 1998-2003.

Reference	Species	Ecosystem	Management / thread	Variable of risk analysis
Damman & Cain (1998)	<i>Asarum canadense</i>	North American woodlands, eastern Ontario (Canada)	Forestry	Extinction risk, mean time to extinction
Dinnézt & Nilsson (2002)	<i>Saxifraga cotyledon</i>	Alpine habitat, Scandinavia	Environmental / demographic stochasticity	Finite rate of increase ( $\lambda$ ), extinction risk
Enright et al. (1998)	<i>Banksiana hookeriana</i>	Mediterranean shrublands (South-western Australia)	Fire	Finite rate of increase ( $\lambda$ )
Gross et al. (1998)	<i>Hudsonia montana</i>	Mountain forests, North Carolina (USA)	Burning, trampling	Finite rate of increase ( $\lambda$ )
Hof et al. (1999)	<i>Platanthera praeclara</i>	Western tallgrass prairie, North Dakota (USA)	Drought, flood	Population density
Kaye et al. (2001)	<i>Lomatium bradshawii</i>	Prairie, western Oregon, Washington (USA)	Fire	Stochastic growth rate ( $\lambda_s$ ), extinction probability
Lennartson & Oostermeijer (2001)	<i>Gentianella campestris</i>	Grassland, Scandinavia	Grazing, mowing, environmental stochasticity	Extinction probability, Finite rate of increase ( $\lambda$ )
Lennartsson (2002)	<i>Gentianella campestris</i>	Grassland, Scandinavia	Fragmentation	Extinction risk, Mean time to extinction
Menges & Dolan (1998)	<i>Silene regia</i>	Mid-western, south-eastern prairie (USA)	Fire	Finite rate of increase ( $\lambda$ ), extinction probability
Nantel et al. (1996)	<i>Panax quinquefolium</i> , <i>Alium tricoccum</i>	Deciduous forests, southern Ontario / Québec (Canada)	Harvest	Finite rate of increase ( $\lambda$ ), minimum viable population size
Quintana-Ascencio et al. (2003)	<i>Hypericum cummulicola</i>	Xerix Florida scrubland (USA)	Fire	Mean time to extinction, extinction

Shimada & Ishihama (2000)	<i>Aster kantoensis</i>	Riverside habitat	Flood	probability Extinction frequency
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## 2.4 *Hypericum cumulicola*

Quintana-Ascencio et al. (2003) performed a population viability analysis for the fire-dependent Florida Rosemary scrub *Hypericum cumulicola*. Stochastic and deterministic matrix population models based on six censuses and data from several germination and seedling survival experiments were used to compare demography and extinction probabilities under different fire regimes. The authors found that the simulations were particularly sensitive to estimates of survival in the seed bank. As suggested by other studies, seed banks are a key phase of plant life histories, since they may buffer environmental variation and reduce extinction risk (see also 3.1).

## 2.5 *Lomatium bradshawii*

Kaye et al. (2001) examined the effects of fire on population growth rate and extinction probability of the rare prairie plant *Lomatium bradshawii*, an endangered species of western Oregon and Washington prairies. Using data from mapped plants in two populations subjected to different fall burning frequencies over a six-year period, Kaye et al. constructed stochastic transition matrix models to evaluate the effects of fire on the viability of populations. They found that burning every two or three years had a positive effects on population viability, while extinction probability in the absence of fire declined to near certainty.

## 2.6 *Asarum canadense*

Damman & Cain (1998) combined empirical data based on a 7-year-long study with a simulation model in order to investigate the relative impact of reproduction and survival on the persistence of populations of the North American woodland herb, *Asarum canadense*. Genets of *A. canadense*, like those for all clonal plants, are potentially immortal. Damman & Cain, however, found that few genets live more than 100 years, even under superior environmental conditions. The simulations also indicated that the dynamics of ramets and genets differ highly: while in early successional forests population of both ramets and genets declined in the course of time, the number of ramets decreased and the number of genets increased in mature forest stages.

## 3 The importance of plant life history in plant PVA

Many aspects of plant life history can present obstacles when obtaining empirical data and generating population projections. Based on this literature review, we give four examples of plant life history characteristics which we found to be crucial for population viability analysis in plants.

### **3.1 Seed dormancy**

Seed banks are characteristic for many, mostly annual, plant species. They are a reserve of viable seeds in the soil that hold seeds dormant until a later germination season. As seed banks buffer environmental variation and therefore reduce extinction risk they have to be considered explicitly in population viability analysis (see also section 4.1). However, data on seed dormancy are often fragmentary, even for plant species with longer time series of empirical data. For example, Kalisz & McPeck (1992) created experimental seed banks to obtain two years of data on the annual *Collinsia verna*. Subsequently, they then used simulations to examine what proportion of the demographically-favorable year would be required for long-term population viability. Quintana-Ascencio et al. (2003) studied *Hypericum cummulicola*, a fire-dependent plant with a persistent seed bank endemic to the Lake Wales Ridge, Florida (U.S.A.) (see also 2.4). The authors found that 50% reduction of *H. cummulicola* seed survival significantly increased projected extinction risk. In most cases, however, data on seed dormancy are lacking, and simulation scenarios have to be based on theoretical assumptions. For example, Gross et al. (1998) assumed that seeds of *Hudsonia montana*, a threatened North Carolina shrub, may be viable for up to 10 years. They computed an annual seed survival rate (0.512) that produced a small probability (0.001) of a seed surviving 10 years in the soil. Although this is a reasonable approach, the authors failed to include the variability in seed survival. Based on this literature review the latter critique seems to apply to many other studies of plant population viability analysis where seed dormancy is an important life history trait.

### **3.2 Plant dormancy**

Dormancy of adult individuals occurs in many perennial and facultative biennial plant species. Plant dormancy (i.e. the time before adults enter the reproductive stage) presents a challenge in population viability analysis, because a wide array of studies are based on short-term empirical data and most likely inflate mortality rates (Lesica & Steele 1994). The PVA of Shimada & Ishihama (2000) was conducted for *Aster kantoensis*, a facultative biennial plant of gravelly river floodplains. Seedlings of this composite grow up to the rosette stage in the fall. They overwinter at this stage, and some of them grow to flowering stage in the second-year fall, although others stay at the rosette stage for one more year or a few years. Long durations of the rosette stage contribute to an increase in extinction probability, because *A. kantoensis* does not produce a seed bank and the establishment of seedlings requires new colonization events by flood-induced seed dispersal. The duration of plant dormancy also becomes important when dormant plants reproduce vegetatively. For example, Dinnétz & Nilsson (2002) reported that rosettes of the perennial, alpine *Saxifraga cotyledon* produce daughter rosettes which may survive the mother plant. Such evolutionary strategies, typically for harsh environments, may present an obstacle for modelers because if empirical data are lacking the precision of PVA models may be strongly affected.

### **3.3 Periodic recruitment**

Periodic recruitment of seedlings is a common life history trait in plants. Many plants with episodic recruitment depend on disturbance events creating superior environmental conditions for the long-term persistence. Disturbance events such as fire or flooding enable e.g. certain seed dispersal strategies or increase nutrient availability for plants. Enright et al. (1998) presented a PVA for *Banksia hookeriana*, a highly serotinous, fire-killed (non-sprouting) woody shrub. Mature cones of this species normally remain attached to the plant throughout their life. Recruitment events are strongly linked with fire frequencies, because most seeds are released by fires causing the follicles on cones to open. Fire plays also an important role in the population dynamics of *Silene regia*, an endemic prairie perennial of the mid-western and south-eastern USA (see Menges & Dolan 1998). Management of fire regimes promoted more frequent seedling recruitment and reduces extinction risk. For plants with periodic recruitment modeling constant recruitment rates, as found in most studies, does not capture the natural variation. Consequently, episodic recruitment has to be considered explicitly in PVA, e.g. by constructing matrices representing years with and without recruitment (see Menges & Dolan 1998).

### **3.4 Clonal growth**

Clonal reproduction of perennial plants can present a difficult task for plant population models. Ramets, i.e. single units of clonal growth forms that reproduce vegetatively, can have different demographic parameters. For wild ginger *Asarum canadense*, a common understorey herb in the North American forests, Cain & Damman (1997) and Damman & Cain (1998) found that ramets in late successional forest habitat often survived better and flowered more often than ramets in early successional forest stages. However, despite the extensive spatial and temporal variation in demographic parameters, relatively few empirical studies of clonal plants consider sufficiently long time spans and information from enough sites to provide an estimate of temporal and spatial variation (but see e.g. Falinska 1995). Yet, this is important for model parameter estimates in PVA. Otherwise different scenarios of ramet variation have to be tested. Data collection and modeling are most practical at the ramet level because genets (genetic individuals as a product of an independent colonization event) can not always be identified (Menges 2000).

## **4 Challenges and new approaches**

As shown above, plant life history characteristics create some difficult challenges which should be obeyed in order to improve the precision of plant PVA models. Moreover, particular methodological issues and modeling approaches are of major importance for the outcome of plant PVAs. For example, the type of density dependence that is modeled is crucial since this will affect population projections and potential management decisions: if a local population is able to overshoot the long-term average of the habitat carrying capacity this will have positive effects for population persistence. The same principle accounts for the consideration of buffer mechanisms. Since the consequences of buffer mechanisms are often neglected, we will discuss them explicitly in the following section.

#### **4.1 Complexity or simplicity ? The importance of buffer mechanisms**

The stochastic population models, which are used in PVA, are often difficult to parameterize and test because empirical data are usually poor. It has therefore been argued that simple models with less parameters should be preferred instead of more realistic and therefore complex models (e.g. Beissinger & Westphal 1998). Simple models necessarily ignore many processes of their real counterpart so that the assessments of extinction risk they produce have to be weighted very carefully. Nevertheless, it is argued that these assessments are still useful for two reasons. Firstly, PVA does not aim at absolute assessments of extinction risk, but at relative ones (Burgman & Possingham 2000). If we compare two management scenarios and the error of the assessment of extinction risk is of the same order of magnitude for both scenarios, we might still identify the better management option. Secondly, simple models tend to overestimate extinction risk because they ignore mechanisms that in the real population might decrease extinction risk. Nevertheless, such overestimations are considered conservative (e.g. Conner & White 1999) because they are on the “safe side”. In other words, one can be sure that one is not too optimistic about the ability of a population so that one will not opt for non-action in situations where management would have been critical.

However, these two arguments may be incompatible with each other and “conservative” (i.e., pessimistic) assessments of extinction risk are not necessarily conservative. This is in particular so if buffer mechanisms exist in the real population. Buffer mechanisms are mechanisms which reduce environmental noise, i.e. year-to-year variation in the population’s growth rate. With buffer mechanisms, conservative assessments of extinction risk may lead to non-action in situations where actions would have been worthwhile. To illustrate this point, consider a simple model, which does not, and a more complex model of the same population, which does include a certain buffer mechanism. In the simple model, environmental noise is thus higher than in the more realistic model. Higher environmental noise causes a higher risk of extinction (e.g. Lande 1993), so that the extinction risk predicted by the simple model is higher than that of the more realistic model. However, reduced environmental noise does not only change extinction risk in a given situation but also the functional relationship between extinction risk and habitat capacity. With high environmental noise, increases in habitat capacity only slightly reduce extinction risk because environmental variation still can lead to population sizes so small that demographic noise causes extinction. With low or none environmental noise, however, even small increases in habitat capacity may lead to a substantial decrease of extinction risk. For larger habitat capacity, a simple model of course is still pessimistic and thus “conservative”, but the comparative, relative assessment of extinction risks for small and large habitat capacity in fact is not necessarily conservative. The more complex model which includes buffer mechanisms correctly predicts a significant positive effect of increasing capacity, whereas the simple model only predicts a marginal positive effect. Hence, the seemingly “conservative” model thus may lead to non-action. Thus, the claim that simple models combine both relative and conservative assessments of extinction risk is not necessarily true.

Based on the above considerations it is critical to consider buffer mechanisms. The question is: do we know mechanisms that limit the environmentally induced variation of demographic parameters? For example, are there safe sites in the habitat where individuals are less affected by environmental variation (McLaughlin et al. 2002;

Greene 2003)? How important is seed dormancy for a plant population? Dormant seeds can buffer environmental variation, because they are in a “sit and wait” positions, i.e. seeds will germinate when environmental conditions enable successful emergence. Buffer effects are also the reason why the way density dependence is modelled is so important (Chapman et al. 2000; Henle et al. 2003). Simple models often use a ceiling population size as a brute-force model of density dependence. However, if in good years the population is able to overshoot the long-term average capacity of the habitat, environmental noise will be lowered.

To summarize, it is important to consider buffer mechanisms as they can be crucial when evaluating management options using PVA. This does not necessarily mean that complex models are always a better option. With no doubt simple models with less parameters have many advantages because they can be applied to multiple species with similar functional traits. This is important in nature conservation where the time horizon and financial support is often restricted. Rather, the point is to use (plant) PVA tools that are, on one hand, simple enough to allow a multi-species and functional approach, and, on the other hand, able to implement species-specific buffer mechanisms.

#### **4.2 *Habitat capacity, density dependence and competition***

In the previous section we showed that variation in the habitat capacity may result in differing PVA results, depending on the consideration of plant buffer mechanism (e.g. such as dormancy or episodic recruitment). Habitat capacity is an important management scenario because if conservation strategies aim at the acquisition of potential habitat, PVAs may evaluate how much and which habitat should be protected. The crucial role of habitat capacity is also supported by Mills et al. (1996) who found that the incorporation of density dependence (which indirectly determines habitat capacity) caused the largest discrepancies among commercially available PVA software. Despite this clear relationship, it is noteworthy that most plant PVA studies ignore either habitat capacity or density dependence as a contributing factor.

However, what is the link between habitat capacity, density dependence and plant competition? On one hand, habitat capacity can be interpreted in terms of space (e.g. number of prairie remnants in an agricultural landscape as potential recruitment sites). On the other hand, however, habitat capacity represents the carrying capacity  $K$  for a given population. The size of  $K$  in turn is affected by density dependent processes through plant competition. Even if the amount of “available” habitat is constant, the carrying capacity of a population may vary depending on the severity of inter-specific competition (note due to usually low population densities of PVA species intra-specific competition can be largely ignored). For example, in a subpopulation where the target species is heavily suppressed by other competing plants (e.g. invasive species) the carrying capacity will be lower, whereas it would be higher under low inter-specific competition. The result is that demographic variability between subpopulations likely increases with increase in the variation of  $K$ . Without considering this relationship estimates of parameter variability may be wrong and this could eventually modify important management decisions.

### **4.3 Linking genetics with demography**

Genetic variation is important for the persistence of small plant populations. Due to inbreeding effects, low genetic variation reduces individual fitness and thus the ability to cope with environmental variability. Generally, few studies have linked genetic variation and demographic rates of plant populations (Menges 2000). Of the twelve recent studies selected for this review only one paper included genetic variation (see Menges & Dolan 1998). In their analysis of the viability of *Silene regia* populations Menges & Dolan found that more genetically variable populations had a lower probability of extinction. Based on population genetic theory, one would generally assume that smaller and more isolated populations have lower levels of genetic variation. However, a previous study on *Silene regia* conducted by Dolan (1994) did not support the latter relationship: isolation of *S. regia* populations was not significantly correlated with genetic variation in this species. It is therefore critically important to consider how genetic variation is correlated with population size and isolation.

Due to these unpredictable patterns and because too much is unknown about the effects of genetic variability on demographic rates of plant populations, Beissinger & Westphal (1998) suggested to limit the mixing of genetics and demographic parameters. This, of course, would make the process of model development much easier. However, one can not ignore the effects of genetic variation. This is particularly true for small populations and if mean time to extinction is substantially low. Thus, more effort should be given for data acquisition. Only understanding the biology of a particular species will ensure reliable PVAs.

## 5 Conclusions

Population dynamics of plants represent a difficult challenge in ecological risk assessment. On the base of the current literature, we found particular aspects of plant life history which should be obeyed in plant population viability analysis. Aspects of plant life history such as dormancy are strongly linked to buffer mechanisms. Buffer mechanisms, i.e. the capability to buffer environmental variation by controlling the time and intensity of reproduction, are important to consider because they can significantly affect population projections and possible management recommendations. In addition, we found the implementation of plant genetics and consideration of density dependence particular crucial. Both may also alter the outcome and modify management suggestions.

Due to the extensive use of PVA in managing species and the potential for misuse of models and their output (e.g. Beissinger & Westphal 1998), there is an ongoing debate about the usefulness of PVA. Some authors are concerned about the precision of predictions in view of the short time series of data available and the sensitivity of estimates of extinction risk to estimated parameters (e.g. Ellner et al. 2002). Beissinger & Westphal (1998) concluded that poor data cause difficulties in parameter estimation, which in turn lead to unreliable estimates of extinction risk. However, as pointed out by Brook et al. (2002), even if data are sparse or of low quality (commonly the case for threatened species), no alternative methods may be superior to PVA other than some vaguely defined hypothesis. This is of particular importance in conservation biology where decisions have to be made quickly, even in the face of incomplete data.

Despite a relatively large body of population viability studies and PVA program packages, we found no commercial plant PVA simulation tool. Generally, most of the currently available PVA computer programs have been developed for animal conservation purposes and reveal difficulties when applied to plants. This is particularly true for plant-specific life history traits. Of the twelve studies shown in this report the majority use either simple deterministic matrix models or user-defined, species-specific stochastic models. Unfortunately, these models are specific to one population or taxon and may not extent to other species. The reason for this lack of commercially available software may be due to the fact that, until now, plant PVAs (compared to animal PVAs) are relatively scarce. Moreover, risk assessment in plants is subject to a wide array of methodological issues which might have inhibited modeling approaches on a multi-species level. However, there is no doubt that ecological risk assessment needs user-friendly, scenario-based modeling tools for population viability in plants.

In Canada, for example, the species-at-risk program lists 62 vascular plant species which have been designated as endangered and may go extinct if current population trends continue. With the aid of a plant PVA computer tool population viability analysis of these species may help cost-effective decision-making in nature conservation. This is particular important for plant species which are endemic to Canada, e.g. the Barrens Willow, a dwarf woody shrub of the northwest coast of the Great Northern Peninsula of Newfoundland. Even if empirical data are scarce, population viability analysis presents a useful tool in species management, as it allows us to identify, through e.g. sensitivity analysis, which ecological processes

matter and which further data should be collected. Based on this review, we suggest that, particularly for plants, care should be taken in terms of the absolute values derived from PVA (e.g. mean time to extinction). It is the relative assessment of different management or environmental scenarios which is important in plant species risk assessment.

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