Ecophysiological responses of some maquis (Ceratonia siliqua L., Olea oleaster Hoffm. & Link, Pistacia lentiscus and Quercus coccifera L.) plant species to drought in the east Mediterranean ecosystem

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Abstract: The objective was to examine the adaptation strategies of four maquis species to drought prone environments; typical of the east Mediterranean area in degraded and healthy sites in Turkey. A comparison made between sites for Pistacia lentiscus and Quercus coccifera shows higher net daily photosynthesis in the degraded site, when compared with the healthy site; but Ceratonia siliqua and Olea oleaster exhibited no difference in their photosynthetic activity in environmentally contrasting conditions. The pattern of daily transpiration shows higher values in the degraded site in the case of P. lentiscus and Q. coccifera, while no site effect was observed for C. siliqua and O. oleaster. In the case of Q. coccifera, a behavior similar to C. siliqua was observed. A comparison made between C. siliqua and O. oleaster to observe seasonal differences in daily patterns of net photosynthesis and transpiration reveals that Q. coccifera had the highest water use efficiency (slope = 2.88; r\textsuperscript{2} = 0.61), followed by C. siliqua (slope = 2.74; r\textsuperscript{2} = 0.7), P. lentiscus (slope = 2.56; r\textsuperscript{2} = 0.92) and O. oleaster (slope = 2.40; r\textsuperscript{2} = 0.78). Olea oleaster and P. lentiscus performed as a drought tolerant species, being more resistant to aridity and thus indicative of the degradation state of the site. Ceratonia siliqua and Q. coccifera were found avoiding drought by adopting first a water-spending strategy, and then a water-saving strategy.

Key words: Drought, Maquis plants, Photosynthesis, Transpiration, Water use efficiency

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Introduction

Almost all countries around the Mediterranean basin are facing a mass habitat destruction due to several anthropogenic activities like fires, over grazing, wood cutting and uncontrolled urbanization (Ozturk et al., 2008). The basin is characterized by mild and short rainy winters but long and dry summers and poor soils. All these influence the water availability of plants (Vertovec et al., 2001; Loreto and Centritto, 2004; Centritto and Loreto, 2005). In addition to abiotic destructions the anthropogenic stresses duplicate the influence of water scarcity in the area and of course in plant behavior (Sakcali and Ozturk, 2004; Sakcali et al., 2008). Low water availability is considered as one of the main environmental factors limiting photosynthesis and, consequently, plant growth and yield worldwide. It can induce morphological and ecophysiological changes in plants affecting their growth, survival, distribution and abundance (Flexas et al., 2006). Most Mediterranean sclerophyllous plants develop numerous morphological and physiological adaptations like small, thick and microphyllous leaves, dense pubescence, deep water extraction system, high water use efficiencies in frequent drought stress during the long and dry summer period. Strong diversity in physiological adaptations to the intense insolation and high temperature environments, likely to be of adaptive value, such as the specificity factor of Rubisco; the response of relative growth rate and its components to water stress; or leaf water relations and stomatal control (Faria et al., 2008). The basin is characterized by diversity in physiological adaptations to the intense insolation and high temperature environments, likely to be of adaptive value, such as the specificity factor of Rubisco; the response of relative growth rate and its components to water stress; or leaf water relations and stomatal control (Faria et al., 1999; Galmes et al., 2005).

Lately, attempts have been made to generalize the responses of photosynthesis to water stress in higher plants (Lawlor and Comin, 2002; Chaves et al., 2002). There has been a long-standing controversy as to whether drought mainly limits photosynthesis through diffusive resistances or by metabolic impairment. Measurements based on the photosynthetic response to chloroplast CO\textsubscript{2} often confirm that the photosynthetic capacity is preserved, but photosynthesis is limited by diffusive resistances under drought conditions. These evaluations reveal that diffusion limitations on photosynthesis predominate under most water-stress situations which not only involve closure of stomata, but also
decreased mesophyll conductance to CO$_2$ (g) (Ennahlil and Earl, 2005; Pons et al., 2009).

A general failure of metabolism is reported to occur when daily maximum stomatal conductance (g) drops below 0.1 mm$^2$s$^{-1}$ H$_2$O (Flexas et al., 2004; Garatani, 1997), but very little information is available in this connection on natural vegetation of different origins. Indeed, many studies have described reductions in photochemical efficiency and low photosynthetic rates during summer drought (Damesin and Rambal, 1995; Tazoe et al., 2009). In addition, temperature during Mediterranean summer may reach potentially damaging thresholds for physiological processes (Epron, 1993), especially when drought-induced stomatal closure limits the ability of plants to avoid heat stress by transpirational cooling (Ladjal et al., 2007).

The natural vegetation of the Mediterranean basin is the proper area to understand the photosynthesis response of plants to drought due to land degradation continuing from centuries. The objectives of this study were 1) to examine as to whether future warming and extended drought events could have a different effect on the physiological performance and water use of some Mediterranean sclerophyllous species, 2) how changes occur in the photosynthetic response of selected plant species to water stress in degraded and healthy areas, 3) to find the most suitable species for reclamation of degraded areas of the Mediterranean basin and 4) to evaluate the suitable parameter for indication of the level of degradation in this area.

Materials and Methods

Two different areas were selected as study sites situated on the Aegean coast of Eastern Mediterranean basin. First site was chosen in National Park, in the northern side of Dilek Peninsula (37°41' 46" N latitude, 29°09' 44" E longitude) classified as healthy site (H). It lies very near to the coast at an altitude of 10 m, with a total rainfall of 600-700 mm yr$^{-1}$. The dominant plant cover is represented by Ceratonia siliqua, Pistacia lentiscus, Olea oleaster, Quercus coccifera, Phillyrea latifolia, Pinus brutia, Arbutus andrachne and Laurus nobilis. The second site is Karina, at the south of Dilek Peninsula (37°37' 53" N latitude, 27°07' 11" E longitude) classified as degraded site (D), with poor vegetation cover since it was burnt. This site too lies at an altitude of 10 m facing the coast, with an annual precipitation of 600-700 mm. The dominant species are P. brutia, Q. coccifera, Q. ilex, C. siliqua, O. oleaster, L. nobilis, P. lentiscus, P. terebinthus, P. latifolia, Styrax officinalis, Calicotome villosa and Arbutus species.

The selection of the species and the experimental sites was done upon considerations of diffusion and relevance on the whole environment. Measurements of CO$_2$ exchange, air temperature, PAR (photosynthetic active radiation) and transpiration were made in the field on sunny leaves of single trees of Ceratonia siliqua L., Olea oleaster Hoffm. and Link, Pistacia lentiscus L. and Quercus coccifera L. LI-COR (Lincoln, NE) LI-6000 Portable Photosynthesis System (Li-Cor, 1991) was used for photosynthetic measurements. Diurnal time course of measurements were started before sunrise and completed after sunset.

Sampled leaves were chosen in full sunlight. The attached leaves remained in their natural orientation for approximately 45-60s inside the cuvette. One single leaf per tree was selected for measurements and two replicates of diurnal patterns of the ecophysiological parameters were made on hourly basis from sunrise to sunset so as to examine the response of the species under question to different levels of daily stress, and to characterize hourly variability of environmental conditions. The same individual trees of all species were measured in May and September. Data was collected and treated using the C6000 software program available from LI-COR (Leuning and Sands, 1989).

Results and Discussion

Diurnal variations of air and leaf temperatures, relative humidity and PAR intercepted were measured in both healthy and degraded sites in May and September (Fig. 1). The daily pattern of net photosynthesis with emphasis to site varied among species (Fig. 2). A comparison made between sites for P. lentiscus and Q. coccifera shows higher net daily photosynthesis in the degraded site, when compared to the healthy site. A similar behavior was observed by Fleck et al. (1998) in Q. ilex. Such behavior can result from the reduced plant competition in degraded sites, which increases the availability of water and other nutrients (Vertovec et al., 2001). An increase in the net assimilation rate per unit of leaf area also occurs due to reduced leaf area index as observed in fire-exposed plants. Flexasa et al. (2001) examined the variations in net photosynthesis, stomatal conductance, and several other parameters in P. lentiscus. The net photosynthesis peaked in spring and autumn, when water was abundant and temperature was moderately high. It was reduced in winter paralleling reduced carboxylation efficiency. Photosynthesis was at the annual minimum in summer due to drought-induced stomatal closure. This data coincides with our observations. Q. coccifera experiences lower transpiration rates and higher net photosynthetic rates and water use efficiency than P. latifolia. Under severe summer drought conditions none of the two species was able to reach a positive carbon gain. P. latifolia was able to increase WUE by reducing transpiration losses during midday. According to Galms et al. (2007a) there is a general pattern of photosynthetic response to water stress when stomatal conductance is used as a reference parameter and as the values decrease the total photosynthetic limitation rises. The studies on the leaf gas exchange and fluorescence of P. latifolia, P. lentiscus and Q. ilex saplings under severe drought and high temperature conditions revealed that the watered plants of Q. ilex had lower photosynthetic activity and stomatal conductance than P. latifolia and P. lentiscus (Filatia et al., 1998), which indicates a different relationship between photosynthetic activity and electron transport rate in Q. ilex compared to the other two species which are better adapted to severe drought, but to compare different adaptive strategies it is better to conduct long term experiments (Tretiach, 1993; Galle et al., 2009).
The thermophilic species *C. siliqua* and *O. oleaster* show no significant difference in the photosynthesis between healthy and degraded sites (Fig. 2). This may be primarily due to their mesomorphic leaves, which appear to be unable to prevent wilting under daily water stress if conditions of high evaporation demand prevail, resulting thus in a reduction of the photosynthesis as postulated by Lo Gullo et al. (1996). The pattern of daily transpiration shows higher values in the degraded site in the case of *P. lentiscus* and *Q. coccifera*, while no site effect is observed for *C. siliqua* and *O. oleaster* (Fig. 3). A comparison was made between *C. siliqua* and *O. oleaster* to show the seasonal differences in daily patterns of net photosynthesis and transpiration. Fig. 4 shows the average across healthy and degraded sites in photosynthesis rates. This figure shows that *O. oleaster* has high rates of daily photosynthesis in May. The highest values were reached in the morning followed by an immediate depression at midday that continues in the afternoon to less consistent values. In September, the hourly values were significantly lower than those obtained in May. In contrast, data on *C. siliqua* indicates higher values in September, stressing thereby the fact that the strategy adopted by these species to withstand water stress was completely different from *O. oleaster*. In the case of *Q. coccifera*, a behavior similar to *C. siliqua* was observed, where the lowest values were obtained in May and the highest in September.

The low net CO₂ assimilation rate observed at the beginning of the growing season may be attributed to the fact that *Q. coccifera* is classified as a drought resistant species and thus it may require conditions of water stress before the stomata start to act effectively (Rambal, 1984). In *P. lentiscus*, no clear difference was observed, which leads to assume the insensitivity of this species to water stress, with regard to seasonal variation. Similar findings are reported by Ogaya and Penuelas (2003) in their studies on the photosynthetic response to experimental drought conditions in *Q. ilex* and *P. latifolia*.
Fig. 2: Daily pattern of net photosynthesis: comparison among species with emphasis to site (unit of measurement: mmol CO$_2$ m$^{-2}$ s$^{-1}$)
The effects of drought on three Mediterranean cedar species by Ladjal et al. (2007) point out that moderate drought provokes a decrease in osmotic potential at full leaf turgor and a long-lasting osmotic adjustment, net photosynthesis (A) and stomatal conductance (gs) are lower under dry conditions as compared to the wet.

Plants following water spending strategy for water stress avoidance are incapable of reducing significantly their water loss, and as a consequence are characterized by maintaining high levels of hydration when exposed to external water stress. This means that water can be extracted from soil rapidly enough to compensate for water loss by transpiration, which in turn leads to a sharp decrease in plant water potential in response to water loss. Some Mediterranean plants such as P. lentiscus and C. siliqua and O. oleaster (Lo Gullo et al., 1986; Angelopoulos et al., 1996) appear to adopt this strategy to withstand water stress. These three species are characterized by mesomorphic leaves that show wide variation in daily water potential, which might be achieved by rapid changes in turgor pressure (Ozturk et al., 1983), in response to a change in the air temperature and relative humidity, as well as in soil water availability. However, a night recovery of the plant water status is made possible in response to a decrease in the vapor pressure deficit of the air and an increase in the soil water potential. C. siliqua and O. europaeae are accepted as a paradigm for drought tolerance in the Mediterranean. Fig. 5 shows that the average values between healthy and degraded sites of transpiration rates. Figure reveals that the transpiration rates of C. siliqua and Q. coccifera were much higher in September than in May. In contrast, as the season progressed, and consequently water stress episode became more severe, O. oleaster plants appeared to be unable to prevent dehydration in spite of consistent decrease of transpiration when exposed to prolonged water stress. Stomatal closure in fact, was not sufficient to prevent water loss in September where water stress is at its maximum. As a result, O. oleaster behaved in such a way as to maintain its frequency constant even in degraded site, although at the cost of strongly reducing plant size. The investigations undertaken on olive show that this species possesses a series of physiological mechanisms to tolerate drought stress and grows under adverse climatic conditions like carob. The olive plants can lower the water content and water potentials of their tissues, establishing a particularly high potential gradient between leaves and roots, and stop canopy growth but not photosynthetic activity and transpiration (Sofo et al., 2007). At severe drought-stress levels some antioxidant enzymes involved in the scavenging of activated oxygen species increase during a period of drought. Fig. 6 gives the slope of the correlation curve between net photosynthesis and transpiration, or water use efficiency. It can be noticed that Q. coccifera has the highest water use efficiency (slope= 2.88; r² = 0.61), followed by C. siliqua (slope= 2.74; r² = 0.71), P. lentiscus (slope = 2.56; r² = 0.52) and O. oleaster (slope = 2.40; r² = 0.78). Fig. 7 shows the values of average seasonal net photosynthesis and transpiration. C. siliqua has the highest rate of net photosynthesis early in the season when water stress episodes are not as much as to affect seriously plant behavior. Late in the season, low values of net photosynthesis and transpiration were obtained, indicating thus the susceptibility of this species to severe water shortage periods. In terms of water loss, C. siliqua behaves as an efficient water spender, but late in the season, this species is no longer capable of compensating for water loss during severe summer water stress, than it does in early season when water stress intensity is mild. In conclusion, this species switched to a water saving strategy.

Early in the season, photosynthesis and transpiration rates are relatively low except for O. oleaster where the range of variation of these two parameters is higher than the other species. In that period of the year, the lowest values of photosynthesis and transpiration were observed in Q. coccifera, resulting thus in higher water use efficiency in comparison with other species under study. Late in the season, photosynthesis and transpiration decrease drastically in O. oleaster, while they increase significantly in C. siliqua. For Q. coccifera, the increase was slight in the healthy site in comparison with the degraded site. In both sites, a contrasted behavior can be identified between O. oleaster and Q. coccifera. Meanwhile the first species seems to have higher photosynthesis and transpiration late in the season; these two parameters are very low in the case of Q. coccifera. In September, when water stress reaches its maximum, Q. coccifera shows higher photosynthesis and transpiration than O. oleaster and this difference was mostly evident in degraded site as compared to the healthy one. Our results are in agreement with other reports showing different behavior of photosynthetic activity and water use efficiency on daily and seasonal basis (Tenhunen et al., 1985; Penuela et al., 2000) as well as the findings of Tretiach (1993), Penuelas et al. (2001), Assenso et al. (2007) on the response of gas exchanges to the drought in the Mediterranean on seasonal basis. All species develop different physiological responses to the drought.

In the marked seasonality of Mediterranean climate conditions, drought has strongly influenced evolution and plant life (Pereira and Chaves, 1995). Predicted water stress in the Mediterranean Basin (Houghton et al., 2001) may be associated with physiological and phenological responses in plant species (Penuelas and Filella, 2001), but different species can develop different responses to these climatic changes. It is likely that more drought- and heat-resistant species such as P. latifolia will tolerate the increase of temperature and dry conditions better than more mesic ones. These physiological responses could be followed by changes in carbon acquisition of Mediterranean forests, and in a long term, by changes in species distribution conferred by the different capacity of different species to survive under the new climatic constraints. The ecophysiological characteristics described in this study are in agreement with the different distribution of these species. They are in agreement with predictions of a possible change in dominance of species with similar adaptations to drought in a warmer drier climate such as the one predicted in the Mediterranean region by global change circulation models (Houghton et al., 2001).
Fig. 3: Daily pattern of transpiration: comparison among species with emphasis to site (unit of measurement: mmol H$_2$O m$^2$ s$^{-1}$)
Fig. 4: Daily pattern of net photosynthesis: comparison among species with emphasis to season (unit of measurement: mmol CO$_2$ m$^{-2}$ s$^{-1}$)
The consistent global climate change will definitely introduce changes in the plant growth therefore data is needed for the most important tree crops to make long term prediction in this connection. Although stress is laid on the CO₂ increase, the extent to which annual temperature and rainfall patterns will be altered is very important in determining if local species will be benefited by the increased photosynthesis and water use efficiency. Most probably a combination of higher temperature, reduced availability of water and increased use of saline irrigation waters will enhance several stressing factors that will be very difficult to overcome. Local variability in the climate can cause dramatic differences in photosynthesis among populations within short distances. These differences are likely to be translated into large differences in the annual carbon balance between local populations of the same species. It is therefore very important that conservation and sustainable use of water resources should be planned now particularly in the Mediterranean basin. The shrub species show lower shoot water potentials, transpiration rates and stomatal conductance under drought and there is a significant reduction in the overall leaf net photosynthetic rates depending on the species. The drier and warmer conditions may change the competitive relationship among species of Mediterranean scrublands. The future drier conditions may decrease the annual productivity of Mediterranean shrubs, although the magnitude of such decreases will be species-specific, and warmer conditions could alleviate the low temperature constraints on the photosynthetic performance during the colder seasons, possibly increasing the length of the growth period. The evergreen oaks have the capability of exploring larger soil volumes thus surviving the drought and assimilating some carbon using the water stored in the soil free from the competition of other plants. The closed canopy plantation seems to be less sensitive to moderate droughts, but more vulnerable to severe droughts than the systems dominated by herbaceous plants. *Q. coccifera* is found to be a drought resistant species. This has been observed on the basis of seasonal average net photosynthesis and transpiration that showed a strategy of water loss avoidance. *P. lentiscus* and *O. oleaster* are found to be water spender species since they suffer from water stress problems much earlier than do *C. siliqua* and *Q. coccifera*. *O. oleaster* is shown to be unable to prevent the negative effects of prolonged water stress. Seasonal values of water use efficiency of the species under study are presented in Table 1. According to this table, *P. lentiscus* and *Q. coccifera* exhibit similar seasonal values of water use efficiency and the highest values were observed in September, i.e. at the end of the drought period. In contrast, in the case of *C. siliqua* and *O. oleaster* the highest values were obtained in early spring. The results of the of photosynthesis and transpiration measurements demonstrated that *C. siliqua* and *Q. coccifera* are species that can be considered as suitable candidates for natural reforestation of degraded areas of the east Mediterranean Basin. Although *P. lentiscus* and *O. oleaster* proved to be sensitive to aridity, wild olive species proved to be a suitable indicator of the degree of degradation of the different areas under study. *Q. coccifera* and *C. siliqua* proved to be drought resistant species, while *O. oleaster* suffered water stress, largely. *Q. coccifera* should be planted first, because it is drought resistant and, in fact, is affected by environmental aridity.

The diurnal and seasonal trends of the measured parameters, with regard to site and seasonal variation depict that differences between species are evident and explain different responses to the environmental pressure, based on proper physiological demand. In particular, differences help to discriminate between drought avoiding or resistant species (*Q. coccifera* and *C. siliqua*) and drought tolerant or vulnerable to aridity (*O. oleaster*). This means that different species can be differently used with regard to desertification monitoring attitude. *O. oleaster* behaves as water-spender, while *Q. coccifera* behaves as a water-saver. On the basis of our data and in accordance with previous reports (Lo Gullo and Salleo, 1988; Giorio et al., 1999) *O. oleaster* can be regarded as a desiccation tolerant (drought avoider) species in accordance with the definition of Levitt (1980). *C. siliqua* shows low photosynthesis and transpiration at the beginning of the growing season and these two parameters tend to increase remarkably in September with the acceleration of the water stress period. As far as for *P. lentiscus*, the situation was less clear as compared to the other species. However, results showed that this species had relatively low photosynthesis and transpiration rate in comparison with other species, which however did not differ significantly between sites. Our results agree with well-known patterns of annual variation of gas exchange in Mediterranean evergreen shrubs. Initially, stomatal control is the major cause of photosynthetic depression during summer. The main control of photosynthesis is through stomatal limitation, triggered by variation in water availability. The stomatal control requires both hydraulic and chemical signaling to be effective. The stomatal conductance represents an optimal solution of a hierarchically structured system.

Low photosynthetic rates have been reported during winter. Some investigators suggest that winter cold stress plays a relevant role in the development and distribution of Mediterranean evergreen species (Tretiach, 1993; Karavats and Manetas, 1999). Low photosynthetic rate in dry summer period is almost due to the stomatal control in evergreen species of Mediterranean basin as reported by several investigators (Tenhunen et al., 1990; Filella et al., 1998; Penuelas et al., 1998; Galmes et al., 2007b). A marked decline in maximal rate of photosynthesis at saturating irradiance and high

| Table 1: Seasonal water use efficiency for the species under study (mmol H₂O m⁻² s⁻¹) |
|---------------------------------|--------|--------|--------|--------|
|                                | *C. siliqua* | *O. oleaster* | *P. lentiscus* | *Q. coccifera* |
| **Healthy site**               |         |         |         |        |
| May                             | 2.61    | 2.44    | 3.65    | 3.71   |
| September                       | 3.26    | 3.63    | 4.80    | 4.15   |
| Average                         | 2.93    | 3.03    | 4.22    | 3.93   |
| **Degraded site**              |         |         |         |        |
| May                             | 2.80    | 2.66    | 3.72    | 3.35   |
| September                       | 2.94    | 2.39    | 3.97    | 3.93   |
| Average                         | 2.87    | 2.52    | 3.84    | 3.64   |
Fig. 5: Daily pattern of transpiration: comparison among species with emphasis to season (unit of measurement: mmol H$_2$O m$^{-2}$ s$^{-1}$)
internal CO₂ concentration has been observed at temperatures ranging from 35 to 40°C (Tenhunen et al., 1985; 1990; Niinemets et al., 2005). Therefore, an increase in the duration and severity of summer drought as well as indirect effects of future warming, can significantly increase leaf heat stress, limiting growth and survival of plants due to severe restrictions on photosynthesis, and may affect the physiological activity of the Mediterranean plants.

Osmond et al. (1980) demonstrated that the greatest effect of water stress on plants is observed in coincidence of peak irradiance, either on daily or seasonal bases. The midday stomatal closure observed in many Mediterranean species has been reported by Vardar and Ozturk (1972), Sheikh (1976) and Tenhunen et al. (1985) as a feature of these species, which allows them to limit water loss when the atmospheric demand is at its maximum during the course of the day. The relation between photosynthesis and transpiration requires a certain degree of stomatal aperture, but not necessarily maximum aperture, which is important for the success of plants in habitats, which are partially or entirely dry. The balance between carbohydrates and nitrogen may have a triggering role in plant response under elevated CO₂. Carbon export rates by the leaves seem to be independent of total carbon assimilation, suggesting a sink limiting effect on growth and photosynthesis under elevated CO₂ (Chaves et al., 2002).

The global change is expected to produce an effect on the photosynthesis and productivity of plants, but it will vary with the regions depending on the pre-existing climatic conditions and the adaptation potential of the species (Niinemets et al. 2009). The carbon balance of a plant enduring a water-stress depends on the rate and degree of photosynthetic recovery as well as its decline during water depletion (Centritto et al. 2009; Flexas et al. 2009). There is a strong relationship between stomatal conductance and environmental factors under Mediterranean climatic conditions therefore high temperature and low rainfall will lead to high evapotranspiration losses, increasing the water stress problems, thus crops in the Mediterranean will have to grow under more hot and dry environment (Chartzoulakis & Psarras, 2005; Vitale et al. 2007; Galle et al. 2009). Seasonal gradients are important to characterize the intensity of water stress duration of different species. In particular, in view of the recently highlighted importance

Fig. 6: Photosynthesis versus transpiration comparison between species
of decreased $g$ in the regulation of photosynthesis during water stress, this parameter will attract more attention under natural conditions. The results presented here underline the response in terms of photosynthesis and transpiration variation on both daily and seasonal bases. The correlation between these two parameters, called also water use efficiency, WUE, gives an indication of the degree of adaptation of each species to the environmental condition.

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