



## Allelopathic Mechanisms in Fire-Prone Ecosystems

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ARTICLE INFO	ABSTRACT
<p><i>Review Article</i></p> <p>Received : 06/03/2021 Accepted : 31/03/2021</p> <p><b>Keywords:</b> Allelopathy Fire Prone Ecosystems Succession Fire Ecology Allelochemicals</p>	<p>Understanding the fire-prone arid-zone pine species and maquis vegetation's response to fire is very important to reveal the ecology and evolution of these species. During the succession of vegetation, there are complex relationships between allelopathic metabolites and fires. Many plant communities such as pines, maquis, savannas and woodlands are known to play a critical role in the development of succession. However, studies revealing the relationship between succession processes and allelopathic mechanisms in fire-prone ecosystems are quite limited. Most evergreen maquis vegetations are one of the most studied fire ecosystems. In maquis vegetation, fire causes the formation of plant communities that continue with allelochemicals produced by plants, as well as shaping the climate of the region. The event of a living species inhibiting another species by secreting toxic compounds is expressed as allelopathy. These toxic compounds are generally referred to as allelochemicals. Many maquis species that grow in fire-prone ecosystems excrete their allelochemicals, preventing the development of herbaceous species around them and invade their habitats. These chemicals, which accumulate in the soil during the dry season, affect the succession processes in vegetation in the event of a fire and determine which species will follow each other. Considering these relationships, it can be said that allelopathic plants have the potential to change plant diversity in vegetation by changing their functional plant characteristics. The purpose of this review is to determine the relationship between allelochemicals and fire of plant species in fire-prone ecosystems, and to reveal how this affects the succession processes.</p>

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## Yangına Eğilimli Ekosistemlerde Allelopatik Mekanizmalar

MAKALE BİLGİSİ	ÖZ
<p><i>Derleme Makale</i></p> <p>Geliş : 06/03/2021 Kabul : 31/03/2021</p> <p><b>Anahtar Kelimeler:</b> Allelopat Yangına Eğilimli Ekosistemler Süksesyon Yangın Ekolojisi Allelokimyasallar</p>	<p>Yangına eğilimli kurak bölge çam türleri ve maki vejetasyonlarını oluşturan bitkilerin yangına karşı geliştirdikleri tepkileri anlamak, bu türlerin ekolojisini ve evrimini ortaya çıkarmak adına oldukça önemlidir. Vejetasyonun süksesyon sürecinde, allelopatik metabolitler ile yangınlar arasında karmaşık ilişkiler bulunduğu ve yangının; maki, savanalar ve ormanlık alanlar gibi birçok bitki topluluğunun süksesyon gelişiminde kritik bir rol oynadığı bilinmektedir. Ancak yangına eğilimli ekosistemlerdeki süksesyon süreçleri ve allelopatik mekanizmalar arasındaki ilişkiyi ortaya koyan çalışmalar oldukça sınırlıdır. Geneli herdem yeşil maki vejetasyonları en çok çalışılan yangın ekosistemlerinden birisidir. Maki vejetasyonlarında yangın; bitkiler tarafından üretilen allelokimyasallarla birlikte en iyi şekilde yetişen ve devamlılık gösteren bitki topluluklarının oluşmasına neden olarak o bölgenin iklimasının oluşmasını sağlar. Bir canlı türünün toksik bileşikler salgılayarak, başka bir canlı türünü engellemesi olayı allelopati olarak ifade edilmektedir. Bu toksik bileşikler genel olarak allelokimyasal olarak nitelendirilir. Yangına eğilimli ekosistemlerde yetişen birçok maki türü sahip oldukları allelokimyasalları dışarı salgılayarak çevrelerinde bulunan otsu türlerin gelişimini engellemekte ve habitatlarını işgal etmektedirler. Kurak mevsimde toprakta biriken bu kimyasallar da herhangi bir yangın anında vejetasyondaki süksesyon süreçlerini etkileyerek, hangi türlerin birbirini izleyeceği konusunda belirleyici olmaktadır. Bu ilişkiler göz önüne alındığında, allelopatik bitkilerin, fonksiyonel bitki karakterlerini değiştirerek vejetasyondaki bitki çeşitliliğini değiştirme potansiyeline sahip olduğu söylenebilir. Bu derlemenin amacı, yangına karşı eğilimli olan ekosistemlerde bulunan bitki türlerinin sahip olduğu allelokimyasallar ve yangın arasındaki ilişkinin belirlenmesi ve bu durumun süksesyon süreçlerine nasıl bir etkisi olduğunun ortaya çıkarılmasıdır.</p>

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## Introduction

Fire has an important role in structuring ecological systems and plant communities from savannas to meadows, boreal forests to shrubs and forest areas (Tyler, 1995; Küçük ve Bilgili, 2006; Aktepe, 2021). The common phenomenon for many of these fire-prone plant communities is the realization of plant germination by performing different adaptations in order to survive after the fire and renew itself (Tyler, 1995; Keeley et al. 2011; Pausas, 2015). In his work, Axelrod (1958) suggested that fire has been an effective force in the progress of chaparral/maquis communities for at least the last two million years. In addition to being the most important cause of secondary succession in these communities (Hanes, 1977), fire is also responsible for the continuity of chaparral communities (Keeley and Keeley 1988). Mature chaparral/maquis communities, defined as large bushes, consist of species that can survive for many years and show little regeneration in the lower vegetation. While significant seed progress is observed in the first year after fire, decades must pass before new species emerge (Tyler, 1995). Although there have been many studies on the succession processes in the chaparral/maquis communities, there is little empirical research on the relative importance of the factors affecting these processes (Tyler, 1995). Fire is one of the important factors that affect these processes. Fire causes rapid progress in chaparral/maquis communities directly and indirectly after combustion. This development can take place in two ways. First, the soil and the seed bank are heated directly, seed germination takes place, allelochemicals are blown away by changing soil structure and nutrient levels. Second, by eliminating the above-ground vegetation, it reduces the allelochemical effects and temporarily drop off competition. In areas where small mammals usually feed on shrubs, it temporarily reduces the activity of herbivores.

The direct burning of fire and its indirect effects (competition and decrease in herbivores) caused an increase in seedling production in chaparral/maquis communities (Tyler 1995). Studies on allelopathy have increased rapidly since 1970 and have become an interesting subject in many research areas. Allelopathic interaction is one of the important factors contributing to species distribution and abundance in plant communities (Cheng & Cheng, 2015; Abou El-Enin & Abdel-Ghffa 2017). Allelopathy is the phenomenon where a living species secretes toxic compounds and prevents the development of another species. These toxic compounds are generally referred to as allelochemistry. For example, algae secrete substances that have important effects on the structure and functions of aquatic communities. Likewise, some substances secreted by the leaves and roots of advanced plants may have detrimental and harmful effects on other living things. Blacknut trees (*Juglans nigra*) secrete an allelochemical substance, juglone, in order to prevent the development and germination of the plant species around (Willis, 1985). These allelopathic metabolites are washed away from the rash in the rainy environment. In arid climates, on the other hand, its effects are more common as it tends to accumulate.

Recent studies have revealed that there are complex relationships between allelopathic metabolites and fires in

the process of sequential change (succession) in plant communities in arid regions (such as desert and maquis vegetation). These allelopathic metabolites are washed away from the rash in the rainy environment. In arid climates, on the other hand, its effects are more common as it tends to accumulate. Whittaker and Feeny (1971), Rice (1974), Harborne (1982), Gopal and Goel (1993), and Seigler (1996) discussed in detail the role of biochemical secretions in the development and structuring of communities (Odum and Barrett 2005).

However, there is no comprehensive study concerning the relationship between allelopathy and fire. In literature on allelopathy generally deals with the effects of allelopathy on germination and seedling (Aguilar-Franco et al., 2019), plant performance (Zhang et al., 2021) and invasive plant species (Uddin and Robinson, 2017). Although there are not also many studies in the Turkish literature on allelopathy, it mainly deals with the effects of allelopathy on plant production (Yarnia et al., 2011; Gürsoy et al., 2013) invasive plant species (Arıkan and Elibüyük, 2015; Kitiş et al., 2016; Özen et al., 2017; Karakuş et al., 2019), seed germination and seedling development (Gülsoy et al., 2008; Akın et al., 2017; Bingöl and Battal, 2017; Özbay, 2018; Yorulmaz and Yergin, 2020). However, studies on allelopathy require the examination of the interaction between the associated plant species and fire, as this ecological phenomenon is caused by the effect of allelochemicals. In this context, the contribution of the study to the existing fire ecology and botanical sciences is to find out the effects of allelopathy on succession processes and fire plant species.

The purpose of this review is to determine the relationship between allelochemicals and fire of plant species in ecosystems that are prone to fire, and to reveal how this affects the succession processes. For this purpose, the study focuses on the relationship between fire, succession and allelopathy. The study reveals how allelopathic effects play a role in the change of system dynamics, especially in fire-prone ecosystems. In this context, the study presents a different perspective to fire ecology in the field of environmental studies by evaluating the chemical properties of plants.

## Allelopathy

Allelopathy can be defined as the effect of one species on another species by releasing allelochemicals in the plant's body to the environment (Rice, 1974). It has been determined that allelochemicals obtained by extracting plant leaves and roots are effective on many of the physiological mechanisms of other plants (Rice, 1974; Putman and Tang, 1986). When these effects are taken into consideration, it is seen those plants with allelochemicals have the potential to change the number of species and individuals in that community by affecting the functional plant characteristics of the plants that show the distribution in their vegetation (Hunter and Menges 2002). Interaction between plants typically refers to either competition for resources (e.g., food, light, water) or chemically regulated (e.g., allelopathy) interaction (Fernandez et al., 2016). Overall, resource competition is an important driver for the diversity and

dynamics of the plant community (Tilman, 1982; Schluter, 2000). However, recent studies show that allelopathy has a significant role in the formation of plant communities that include different vegetations (Fernandez et al., 2016). When describing allelopathy in Mollish (1937), it was used to denote all effects caused by biochemical compounds that are directly or indirectly transferred from one plant to another. In the studies conducted so far, the effect of allelochemicals on plants as well as on algae, fungi and various microorganisms have been studied. The current definition of allelopathy was extended to the literature by the International Allelopathy Society in 1996 to address processes involving secondary substances produced by fungi, microorganisms, plants and viruses that affect agricultural and biological processes (Cheng and Cheng 2015).

### Allelopathic Metabolites

Allelopathy is a biological event in which a living thing releases compounds that prevent another creature from reproducing, developing and surviving. These secreted compounds are known as allelochemicals and they can have a positive or negative effect on the living things (Cheng and Cheng 2015). Substances that do not have nutritional properties and are secreted as plant secondary metabolites are called allelochemicals. Allelochemicals belong to different chemical families and are examined in 14 categories according to their chemical similarity (Rice, 1974) (Table1).

Especially compounds such as salicylic acid, gibberellic acid and ethylene, that act as regulators in plant growth, are described as allelochemicals. Recent studies have made it possible to insulate and describe very small proportions of allelochemicals and reveal the structural analysis of these molecules (Cheng and Cheng 2015). The fact that most of the allelochemicals also cause insect resistance is a proof that many plants perform plant defense by using allelochemicals. It is demonstrated that allelopathic effects directly affect metabolic processes, resulting in secondary expressions (Einhellig, 1995a; Einhellig, 1995b). While evaluating the effects of plants with high allelopathic properties, the effects of allelochemicals responsible for allelopathy should also be revealed.

Studies have allowed the classification of different allelopathic compounds (Gallet and Pellissier, 1997; Wink et al., 1998; Inderjit and Keating, 1999b). Cell division, membrane permeability, germination, plant conduction tissues, mineral uptake, movement of stomata, respiration,

amino acid synthesis, photosynthesis and nitrogen fixation are among the best examples that can be given to the areas affected by allelochemicals (Wink et al., 1998, Kruse et al., 2000). It has a wide spectrum of activity of many allelochemicals. Phenolic compounds such as alkaloids, lignin and terpenes are among the most important allelochemicals. Many of the alkaloids have been found to be toxic to plants, microorganisms, mammals and many insect species (Wink et al., 1998). In addition, they are known as multi-functional defense agents due to their wide range of actions. This situation reveals that determining how the allelochemical substances secreted by the plant affect the diversity of other plant species requires an ecosystem approach (Gallet and Pellissier, 1997). Terpenoids and alkaloids together with phenolic compounds form plant secondary metabolites. The most important phenolic compounds are known as flavonoid, lignin, terpene and tannin. Recent studies have revealed that among these compounds, terpenes, in particular, are effective in the formation of fire and plant flammability (Kruse et al., 2000; Pausas et al., 2016; Küçük and Aktepe 2017). Terpenes are synthesized by plants with more than 15,000 known varieties (Langenheim, 1994). It is known that many plant species found in fire-prone vegetations produce and secrete high amounts of volatile terpenes. In addition, terpenes have an important role in the survival and participation of plants in defense mechanisms against pathogens, herbivores and environmental factors (Gouinguene & Turlings, 2002; Peñaflor and Bento, 2013). In addition, they regulate the competition between rival plants (Gniazdowska and Bogatek, 2005). However, very few studies have shown that the secondary metabolites with carbon structure and the competition of plants with each other are dependent on environmental factors. In Mediterranean type ecosystems where fire occurs frequently, competition among plants is the most important environmental factor (Sardans et al., 2004; Küçük et al., 2005; Sağlam et al., 2008). As the plant begins to compete for soil, nutrients and other resources necessary for its growth, the rate of photosynthesis, its development, and the amount of nitrogen are reduced (Wang et al., 2005). Fluctuations in these factors change the amount of terpenes secreted by the plant (Staudt et al., 1993). Terpenes are moderately abundant in many plants (Banthorpe et al., 1972), but in high-rise plant species they are stored in special structures in only 50 families (Gildemeister and Hoffmann, 1955-1960). Although terpenes are thought to have a very large range of action, they can be quite specific in dosage in different plant communities and organisms (Kruse et al., 2000).

Table 1. Allelochemicals belong to different chemical families

Allelochemicals			
1	purines and nucleosides	8	simple unsaturated lactones;
2	flavonoids;	9	tannins;
3	long chain fatty acids and polyacetylenes;	10	terpenoids and steroids;
4	benzoquinone, anthraquinone and complex quinones;	11	amino acids and peptides;
5	alkaloids and cyanohydrins;	12	simple phenols, benzoic acid and derivatives;
6	cinnamic acid and derivatives;	13	sulfur and glucosinolates;
			aliphatic aldehydes and ketones;
7	coumarin;	14	water soluble organic acids,
			straight chain alcohols,

Source: (Rice, 1974)

## Exploring the Relationship Between Fire and Succession

Fires are quite common in chaparral/scrub vegetation. The plant species found in these vegetations have developed different adaptations that allow them to regenerate and survive after a fire (Keeley et al., 2011; Pausas, 2015). These adaptations developed by plants against fire appeared in the form of (1) fire dependency or (2) fire tolerance. The species that are dependent on fire are those that can sprout again after a fire. These species consume very little energy for the above-ground reproductive organs and use their energy to develop the subsurface storage organs. Thus, when the above-ground organs die after the fire, new shoots and new individuals emerge from the underground organs rapidly. Fire-tolerant species are those that die when they reach mature age. Unlike the fire-dependent species, these species produce abundant and resistant seeds. These seeds, which do not burn easily during fire, have the ability to germinate immediately after the fire (Keeley et al., 2011). The most studied fire ecosystems are chaparral/maquis vegetation, most of which consist of maquis that can remain green in all seasons. In these ecosystems, the fire interacts with allelochemicals generated by plants, creating a site-specific climax cycle. Periodically occurring and external disruptive factors such as fire, especially in temperate ecosystems, significantly affect the recession process (Hanes, 1977).

In regions with Mediterranean climates, where spring and winter are generally rainy and summers are dry and long, fires occur most frequently in the dry season and little or no plant development occurs before the next rainy season begins (McPherson and Muller, 1969; Küçük ve Sağlam, 2004). In this case, new growth begins from the underground parts of some maquis and the seeds of many maquis' species germinate rapidly and in large quantities. Herbaceous plant species germinate in large numbers following the onset of the rainy season after fire (Horton and Kraebel, 1955; McPherson and Muller, 1969). The interesting thing about this is those mature chaparrals usually have few or no herbaceous species. After a fire, herbaceous plant species are most prominent in the first growing season. These species consist of annual grasses, biennials, tuber-forming perennials, and short-lived semis. In the second growing season after the fire occurs, weeds and herbaceous species appear. After the second growing season, a rapid decrease begins in the number and vitality of herbaceous plant species (McPherson and Muller, 1969). More than 200 herbaceous species have been reported in fire-stricken areas, the majority of which are annuals. Some of these herbaceous species disappear after the first year and are called "pyrophyte endemic" (Hanes 1977; Keeley et al., 1985). Based on the study by Sampson (1944), McPherson and Muller found that the weed population decreased by about 25% in the fifth growing season compared to the first year. Few herbaceous plant species have been observed to germinate seeds seven to nine years after the fire. On the other hand, the half-dwellers reach their maximum numbers in the third and fourth seasons after the fire and then gradually their numbers begin to decrease. Finally, about 12 years after the

fire, very few herbaceous plant species or semi-shrubs remained (Rice and Kozlowski 1974).

## Understanding the Allelopathic Effect in the Ecosystem: Interactions between Fire and Allelopathy

Woody plants in fire-prone vegetations have evolved different adaptations for survival and reproduction in response to sudden but acute forest fires. Adult plant species develop different mechanisms to escape genetic death (death without reproduction). Woody species often survive surface fires if they have thick, insulating bark and are tall enough to prevent scorching damage to twigs and buds. If the seeds of the plant fruit exposed to the crown fire are released in the form of a serotiny shell and seed bank, they will colonize again in the soil formed after the fire. These strategies demonstrated by the plant are the fire adaptations that the individual performs in order to regenerate and survive. These adaptations shown by plants are directly related to variables such as fire frequency, fire intensity and fire period. These variables are dependent on some environmental factors such as precipitation, temperature and, lightning strike and biotic factors such as the plant itself (Mutch, 1970; Platt et al., 1988; Rebertus et al., 1989). In other words, the responses of plants and the way they create debris are highly effective in regulating fire variables in a society. For instance, the fall of leaves and dead branches causes frequent but less severe fires, while the retention of dead branches and leaves in the plant causes less frequent but more intense crown fires. Likewise, a dense bush layer increases crown fires, while dense debris cover increases surface fires (Williamson et al., 1992). The studies of C. H. Muller on chemical inhibitors produced by shrub species growing in chaparral vegetation in California can be given as classic examples of allelopathy. In these studies, both chemical properties and physiological effects of these inhibitors on other species were revealed. Furthermore, these inhibitors have been found to significantly control the species composition and dynamics of the chaparral/scrub community (Muller et al., 1964; Muller, 1966; Muller et al., 1968, Muller, 1969).

Some aromatic scented shrub species avoid the improvement of herbaceous plant species in their immediate surroundings with the volatile terpenes they release. *Salvia leucophylla* and *Artemisia californica*, which are among the aromatic species, thrive in an area covered with herbaceous annual plants, prevent the improvement of these annual plants and occupy their habitats with the biochemical inhibitors they secrete. Volatile toxins (especially cineole and camphor) are generated in the leaves of these shrubs and accumulate in the soil during the arid season. The seeds of other plant species that have come to a few meters wide margin around the bush after it has rained cannot germinate or are prevented from growing. Some other types of shrubs produce other types of water-soluble antibiotics (eg phenols and alkaloids). These antibiotics also prevent the growth of other plant species in the immediate vicinity of the bush. Thus, the resources in the environment such as water, nutrients and light can only be used by the bush type itself (Odum and Barrett 2005). However, fires are a natural part of chaparral/scrub ecosystems. These fires, which occur periodically, on the one hand remove the

shrub species that are the source of toxins from the area, on the other hand, they degrade and decompose the toxins accumulated in the soil.

Different herbaceous plant species with colorful flowers germinate and develop in the first rainy season following the fire, when the aromatic shrubs and toxins are eliminated. However, these herbaceous plants can only sustain their existence in this way for a few years. Because in the years following the fire, the seeds of the aromatic bushes germinate and develop again in the same area and start to emit toxins again. For this reason, herbaceous plants cannot grow in this area until another fire occurs. These interactions between fires and antibiotics continue with repetitive cyclical changes in the chaparral/scrub composition adapted to these factors. Allelopathic effects determine which species will follow each other during the succession process in a plant community. In addition, the allelopathic effect also affects the species composition in stable plant communities. Chemical interaction between species can both decrease and increase species diversity. The extracted chemicals cause a decrease in species diversity with their inhibitory (allelopathic) effects in some communities, while in some communities they increase species diversity by acting as a chemical supporter (especially in the creation of some new ecological niches) (Odum and Barrett 2005).

## Conclusion and Discussion

Evidence from C. H. Muller and colleagues revealed that the allelopathic effects of many shrubs found in California chaparral communities are mainly responsible for the fire cycle. The chemical inhibition exerted by mature shrubs has been found to be sufficient to prevent the seeds of most plants from germinating. The evidence clearly shows that fires release the allelopathic effects of shrubs by clearing out sources of toxins, removing some of the toxins found in soil and debris. Thus, the regeneration of a new plant arises from seeds that have been dormant in the soil since the previous fire and are no longer blocked by toxins. As the bushes stand out again after the fire, so does the competitive intervention that emphasizes the increased addition of toxins and any inhibition caused by the toxins.

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