

Simcha Lev-Yadun

# Defensive (anti-herbivory) Coloration in Land Plants

Anti-Herbivory Plant Coloration and  
Morphology

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and Morphology

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Simcha Lev-Yadun  
Department of Biology & Environment  
Faculty of Natural Sciences  
University of Haifa – Oranim  
Tivon, Israel

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*This book is dedicated to my school biology teachers, the late Hanna Kedari and Levi Ovdia, my many university teachers and mentors, colleagues and students, and especially to my family.*

# Foreword

This book is unashamedly a provocation. Simcha has long believed that a significant proportion of the coloration, patterning, and even structure of plants can be explained by selection pressures associated with influencing the sensory and cognitive systems of herbivores to reduce the damage they impose on plants. That is, Simcha believes that just as camouflage, mimicry, and aposematism are widespread among animals, so they will be in plants. Simcha has been publishing on this for 15 years, but this book represents by far the fullest exposition of his arguments.

Bluntly, I think Simcha's ideas remain (as he admits himself) only a little proven but logically plausible. There is no doubt that herbivores certainly impose selection pressures on plants and that there should be potential for the appearance of plants to be selected because of the effect that this has on the sensory and cognitive systems of herbivores. Further, some defenses open to animals against would-be attackers are not available to plants. Animals can often flee when detecting a predator, can gang together to mob the predator and drive it away, or can adapt their behavior to avoid places where they have seen predators. None of these options are open to plants; if a plant is detected and recognized by a herbivore, then there is very little the plant can do to stop the herbivore from attacking. Thus you might argue that plants might have particular need of the type of sensory defenses that Simcha champions (to hide from herbivores or otherwise dissuade them from attacking).

Alternatively, it may be that herbivores simply do not apply sufficiently strong selection pressures compared to an animal's predators. When a rabbit is captured by a fox, all its chances of further contributing to its fitness are at an end, but a plant attacked by caterpillars can still flower and set seed. It might also be that exploitation of herbivore vision is restricted by the demands of exposing large areas of chlorophyll to sunlight and/or by the lack of mobility to influence the lighting regime and microhabitat that together form the viewing environment. I don't think we can address the importance of herbivore senses in shaping plant traits with argument; we need careful experiment. One way or another, it would be a disservice to science if Simcha's provocative book is ignored; we should strive for an understanding of how important sensory and cognitive manipulation of herbivores has been in shaping plant traits – at the moment we simply don't know. Simcha's book argues

powerfully that searching for an answer to this question should be a valuable exercise, and he points us to some very interesting case studies that would benefit from experimental manipulation now.

The good news is that the extensive experimental effort that we have seen expended on the investigation of attraction of pollinators should transfer readily to repulsion of herbivores, as should much of the methodology associated with sensory aspects of animal predator-prey interactions. More good news is that these experiments generally require relatively low-tech and inexpensive approaches; we really could make a lot of progress with short-term, small-scale projects like those that typify the research projects often carried out by final-year undergraduates.

There has been one conspicuous exception to the general neglect of how the senses of herbivores might have influenced plant traits. As Simcha covers in Chaps. 45, 46, 47, 48, 49, 50 and 51, there has been substantial interest in the last 15 years or so on the involvement of herbivores as a selective force in the coloration of autumn leaves. This was originally triggered by a set of papers arguing that at least some autumn leaf coloration might be a signal of individual plant “quality” selected because of its effect on autumn-flying aphids. This interest soon made clear that there was a question to answer: why is there so much variation in autumn leaf coloration between species, between years, between individuals, and even within individual plants. It became clear that we really could not explain this, and the aphid idea was a novel, plausible, and testable hypothesis. This triggered a great deal of activity testing not just that hypothesis but generating a plethora of alternative hypotheses for mechanisms influencing leaf coloration. The upshot of this endeavor is that we are beginning to have a much better idea of what the key mechanisms are that underlie variation in autumn leaf coloration. As it transpires, there is still (in my view) no strong evidence that autumn-flying aphids are an important component of this, but we are much further forward than we were in understanding what the important components are. The fact that some of these have nothing to do with the senses of any herbivores in no way detracts from the vital role that the original hypothesis had in stimulating activity. On a broader scale, even if Simcha is ultimately proved wrong, if this book is the trigger for causing us to investigate the impact that herbivore sensory systems have on which plants they exploit, then that will be an important stride forward not just for pure but also applied plant science.

The seminal work in animal camouflage was that of Hugh Cott around the time of the Second World War. Cott’s insights were sharpened both by his military experience and by his considerable talent as an artist. It is probably no coincidence that Simcha’s background features photography and military experience very strongly. Cott and Simcha were and are extraordinary careful and thoughtful observers of the natural world. Science needs a small number of such people that are fecund generators of original ideas, but it also needs rigorous and imaginative developers and testers of these ideas. We had to wait almost 50 years before there was a thriving community of scientists developing and testing Cott’s ideas; it would be a great shame if the same fate befell Simcha’s. Both Simcha and I would be happy if this book falls rapidly out of date. I urge all those interested in plant-herbivore interactions and all those interested in sensory ecology to read this fascinating, thoughtful,



and stimulating book and then join Simcha in understanding an unjustly neglected and important aspect of the natural world.

School of Biology  
University of St Andrews,  
Fife, Scotland

Graeme D. Ruxton

# Preface

This book about various types of visual defense (coloration, morphology, movement) of plants against herbivores is not just a list of facts and hypotheses, with a reference source, but mainly an ideological one, a manifesto. The book aims to establish visual anti-herbivory defense as an integral organ of botany or plant science as it is commonly called today by people with insufficient knowledge of botany. It is intended to be the modern and updated botanical parallel to Cott's (1940) book *Adaptive Coloration in Animals*, in order to intrigue and stimulate students of botany/plant science and plant/animal interactions for a very long time. This book is tailored to a readership of biologists and naturalists of all kinds and levels and more specifically for botanists, ecologists, evolutionists, and those interested in plant/animal interactions. It is written from the point of view of a naturalist, ecologist, and evolutionary biologist that I hold, considering natural selection as the main although not the only drive for evolution. According to this perspective, factors such as chance, founder effects, genetic drift, and various stochastic processes that may and do influence characters found in specific genotypes are not comparable in their power and influence to the common outcomes of natural selection, especially manifested when very many species belonging to different plant families, with very different and separate evolutionary histories, arrive at the same adaptation (convergent evolution), something that characterizes many of the visual patterns and proposed adaptations described and discussed in this book. I think that when the same apparent adaptive solution is found in many species with independent evolutionary histories, this can point more strongly to both the evolution and function of a character than many meticulous experiments conducted on a specific species or genotype and under specific experimental conditions. Many of the visual defensive mechanisms I propose, describe, or discuss are aimed at operating before the plants are damaged, i.e., to be their first line of defense. In this respect, I think that the name of the book by Ruxton et al. (2004) *Avoiding Attack* is an excellent phrase for the assembly of the best types of defensive tactics. While anti-herbivory is the theme of this book, I do remember, study, and teach physiological and developmental aspects of some of the discussed patterns of coloration and morphology, and I am fully aware of the simultaneous and diverse functions of many plant characters. The complexity of

many of the discussed and proposed adaptations and the many and even contrasting selection directions of the various selective agents involved in the evolution of these characters makes things difficult to understand, model, and test in the field or in the laboratory.

Since the mid-nineteenth century, in parallel with the emergence of Darwinism and certainly after its meteoric establishment in the year 1859, the evolution of defensive coloration and morphology in animals has been and will probably continue to be the bread and butter of many zoologists, including in recent decades some molecular ones, and in an absurd way, an unknown or in the best cases considered an anecdotal issue for botanists till the beginning of the twenty-first century. I am trying clearly, sharply, and frankly to put an end to this absurdity. To make the absurdity even greater, many animal species acquire both their defensive coloration and their associated defensive chemistry directly from plants or indirectly from prey herbivores that got them directly from plants, to establish their chemically based visual aposematism. However, the plants that serve as the source for these defensive and signaling molecules were almost never, except for some of the pioneering works of Miriam Rothschild and a few others, considered to be aposematic.

After the introduction chapters that outline several essential theoretical issues related to coloration, visibility in general, and attack and defense, the main part of the book begins with camouflage and related defenses, followed by aposematism (warning coloration), and proceeds with the still only partly understood spectacular phenomenon of autumn leaf coloration of temperate and boreal trees and shrubs. The book ends with a review of defensive visual animal and animal action mimicry by plants. Defensive olfactory issues, especially of an aposematic nature, are described and discussed only briefly, and they are mentioned when it illuminates or complements visual issues.

I have had a special, complicated, and variable career background that attracted me to and allows me to explore nature and visual (as well as other) defenses as a naturalist. I grew as a nature boy in the pre-urban central coastal plain of Israel when it was still dominated by partly natural noncultivated grazing lands and by agricultural areas. As a child who used to walk barefoot in the summer, I had many opportunities to encounter and suffer from thorns, spines, and prickles in the environs of my home, some ending with extracting spines or thorns from my foot with metal pliers usually used to extract nails from wood, followed by burning iodine application and sometimes by an anti-tetanus injection. In my youth, I did not consider the defensive signaling of the defended plants and suffered again and again because of this, but I got a first-class understanding of their defensive functions. I also had a 15-year-long career as a military and civil photographer, something that sharpened my sensitivity and awareness of visual issues. As a military photographer, I lost my whole left leg and suffered several additional wounds in the 1973 war, but this did not block my military or any other career. My pre-1973 and later diverse military experiences gave me a special point of view about risks, damage, and recovery and a realistic view of defense and attack, a view that cannot result from working only in the ivory tower of the academy. My great interest in military history, which began at age 14 and resulted in some 1000 books that I have bought and read on this

subject, further helped me in my studies of biological defense and attack mechanisms. My university studies were long and diverse [B.Sc. in biology (1980), M.Sc. in botany-ecology (1986), and M.A. in archaeology (1991) – including 3 years of full complementary studies for a B.A.; I received my Ph.D. in developmental botany (1992) and did a postdoc in molecular genetics and cell biology (1992–1994)]. During my M.Sc. studies, I decided that since the academic system pressed young people to focus on a single narrow issue, I would do the opposite and train myself to deal with multidisciplinary issues. Throughout my studies, the official program was only a minor part of what I did. I read much more than I had to officially and conducted research outside my official theses in both related and unrelated subjects (i.e., reproductive plant biology, ethnobotany, plant architecture, etc.). After my postdoc, 21 years after losing my leg in war, I declined a civilian tenure-track scientist position, passed an officer course, and served for several tense, hectic, and educational years as a captain and a major in the IDF (Intelligence). This gave me an even broader and deeper understanding of defense and attack. Originally, when I began to study biology at Tel Aviv University, I wished to be a zoologist, but there were several factors that operating together caused me to change my major interest from zoology to botany only several months after I began my studies. However, my love of zoology since my early youth serves me very well and is fulfilled when I study plant/animal interactions. I think that this combination of diverse education and my various other experiences not mentioned here allows me to deal better with multidisciplinary issues in general and with visual plant defenses in particular.

Interestingly, my career background is similar in salient points to that of the American artist Abbott H. Thayer with his critical contributions for understanding countershading and animal and military camouflage; the British naval painter and marine officer Norman Wilkinson, with his critical contribution of inventing military naval dazzle painting; and the British officer Hugh B. Cott, the great contributor to the area of defensive animal coloration, who was also a wildlife artist and a photographer.

My theoretical interest in the biological significance of plant coloration not related to photosynthesis or reproduction began when I was still an M.Sc. student in botany. I started to read papers and gather data on nonreproductive and non-photosynthetic plant coloration in the year 1982, although with no specific theoretical framework or clear direction. I just thought that there is no basic ecological and evolutionary hypothesis concerning nonreproductive and nonphysiological plant coloration paralleling the many areas of research into defensive coloration in zoology and that this issue should be studied and shaped into an organized scientific botanical discipline. My long and vast experience as a professional photographer and my excellent visual memory helped me to notice and document various pigmentation patterns that either went unnoticed or were not considered important by many others. As with many other scientific ideas, I decided that one day I would try to understand what is going on with non-photosynthetic and nonreproductive plant colors. During my massive fieldwork in the 1980s and 1990s, it became obvious to me that in addition to several coloration mutants that I found in various wild plant populations and species, there is a huge array of types and patterns of vegetative

**Fig. 1** A typical zebra like leaf of *Silybum marianum*. My determination to understand the evolution of this unique leaf coloration initiated my targeted field and theoretical work on defensive plant coloration. After considering it just to mimic tunneling damage mimicry for defense from herbivory, it took a year and a half to understand the potential aposematic function of this type of coloration. Additional defensive types by this coloration emerged later.



coloration in plants that was not described in floras and plant identification field handbooks and that were not considered to be functional or important by almost any botanist or zoologist.

Concerning defensive plant coloration, I made my significant and target-oriented move only in the early winter of 1994/1995. Then, I decided that I must understand why some local wild plant species look like green zebras (Fig. 1). In February 1996, I understood following my fieldwork that like many dangerous animals, such plants visually advertise their defensive qualities, and I began a very broad study of defensive plant coloration, knowing that visually oriented animals were the selective agent for such types, because they attacked differently defended and non-defended genotypes.

Even when animal coloration is considered, there are many only partly solved and totally unsolved questions (e.g., Kemp et al. 2015), let alone in plants. The classic works of Bates (1862), Müller (1879), Poulton (1890), Thayer (1918), Cott (1940), and Kettlewell (1973) and their hypotheses are still studied and examined today, some after more than 150 years. The situation concerning defensive plant coloration will probably not be different 100 years from now. I am fully aware of the meager amount of direct experimentation concerning defensive plant coloration and that many of the proposed hypotheses (including those proposed by me) need both rigorous experimentation (see Ruxton 2014) and, even more important and naturally, a much more complicated proof by documentation of their various functions in the wild. However, I am not afraid of failure in the shape of hypotheses turning

out to be wrong or if they only partly explain reality. I do not claim to always be right; I just do my best to understand, intrigue, and stimulate. Many of the defensive mechanisms I proposed should currently be considered only as working hypotheses, something that will allow progress, and they should not be considered as the ultimate possible level of understanding. I know scientists who say that they have all the answers concerning the issues they study, but I freely admit, although with great frustration, that I don't even have all the good or essential questions. Since my goal in writing this book is not only technical but also educational, I will in some chapters describe my personal road to formulating a hypothesis, because this may help young scientists not to give up interesting questions and to expect that wonderful moments of discovery may arrive by surprise. At this initial stage of the study of defensive plant coloration, I am certain that many additional types and aspects of defensive plant coloration remained unrecognized, notwithstanding experimentally explored and refined. I am currently studying several such issues, but they are not sufficiently ripe to be presented. Moreover, I am certain that these are not the only yet undescribed types of visual defensive plant systems. Consistent with Grubb's (1992) view that defense systems are not simple and with Diamond's (2005) view that single-factor explanations can fail when complex environmental issues are being discussed, I consider that the evolution of various types of plant coloration reflects adaptations both to physiological pressures and to relations with other organisms but not only defensive ones. Such synergistic gains may cause the evolution of plant color traits to be quicker and more frequent. Another important issue is that practically nothing has been done concerning defensive plant coloration with the aid of modern molecular techniques, including studying the epigenetic components that are probably involved in some of the visual defenses. The time is ripe to do it, and the first ones to do so may gain highly valuable results and reputation.

My frequent contributions to defensive plant coloration are also partly related to geography. I did most of my fieldwork in the Near East, a region with a very long history of strong mammalian herbivory impact on the vegetation during the Pleistocene or possibly already in the Miocene, which increased dramatically after the establishment of herding as an important lifestyle in the Near East several millennia ago. This has resulted in both the evolution and the spread of many plant taxa with various types of anti-herbivory mechanisms. Hundreds of thorny and spiny species, as well as many poisonous ones, are very common in the landscape. Fieldwork in an ecosystem that has a millennia-long history of large-scale grazing, such as the land of Israel, clearly and "sharply" indicates the ecological benefit of being spiny. A continuous blanket of thorny, spiny, and prickly trees, shrubs, and thistles covers large tracts of the land, and other parts of the landscape are just rich with up to dozens of such plant species per km<sup>2</sup> that comprise a significant part of the vegetation. This dominance clearly indicates the adaptive value of being thorny or spiny when grazing pressure is high. It does not just slow the rate of feeding but gives a considerable advantage to such plants. For instance, spiny plants, such as *Echinops* sp. (Asteraceae), which usually grow as individuals or in small groups, sometimes become the most common perennial plant over many acres in grazing lands, and the thorny low shrub *Sarcopoterium spinosum* may cover large tracts of

land in a continuous blanket (Ronel et al. 2007). A wealth of various nonreproductive (and non-documented) color patterns exists in our regional flora, and they deserve to be explained. Fieldwork in Canada, the eastern USA, Estonia, Finland, Germany, Hungary, northern Italy, Norway, Russia, Sweden, Switzerland, and the UK clearly indicated to me that the level of mammalian herbivory there is very much lower than in the Near East, as reflected by the low levels of grazing and browsing damage to the vegetation and therefore by only a few thorny, spiny, or prickly plants at both the flora and landscape levels.

Tivon, Israel

Simcha Lev-Yadun

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**Part I**  
**General Background**

# Chapter 1

## Introduction

Defensive plant coloration (camouflage, aposematism, various types of mimicry, undermining herbivorous insect camouflage, masquerade, dazzle effects, trickery coloration, exploiting animals' perceptual biases, various types of signaling) and related visual aspects has received very limited attention till the year 2000 (e.g., Hinton 1973; Wiens 1978; Rothschild 1986; Smith 1986; Givnish 1990) compared to defensive animal coloration (e.g., Bates 1862; Müller 1879; Wallace 1889; Poulton 1890; Thayer 1918; Cott 1940; Kettlewell 1973; Edmunds 1974; Majerus 1998), but gained much more attention in the twenty-first century (e.g., Archetti 2000, 2009a, b; Lev-Yadun 2001, 2006a, 2009a, 2014a, b, c; Lev-Yadun et al. 2004a; Ruxton et al. 2004; Lee 2007; Lev-Yadun and Gould 2007, 2009; Archetti et al. 2009a; Fadzly et al. 2009; Klooster et al. 2009; Lev-Yadun and Holopainen 2009; Schaefer and Ruxton 2009, 2011; Burns 2010; Cooney et al. 2012; Lev-Yadun and Ne'eman 2012, 2013; Farmer 2014; Hughes and Lev-Yadun 2015). The surprisingly small number of papers in botany related to defensive coloration or defensive mimicry as compared to zoology is clearly reflected in the annotated bibliography by Komárek (1998) with thousands of related publications on animals and only hardly a handful about plants.

The most important comment about leaf colors and their potential defensive functions published before the year 2000 was a short paragraph by Harper (1977), who wrote in his seminal book on plant demography “botanists have been reluctant to accept precisions of adaptations that are commonplace to zoologists and often seem reluctant to see the animal as a powerful selective force in plant evolution except in the curiously acceptable realm of adaptation to pollination! It may be that much of the fantastic variation in leaf form, variegation, dissection and marking that is known in the plant kingdom is accounted for by the selective advantage to the plant of associating unpalatability with a visual symbol” (page 416). This, however, should be changed, and this book on defensive plant coloration is a continuation of the recent efforts to bridge this gap, reviewed in Ruxton et al. (2004), Lev-Yadun (2006a, 2009a, 2014a), Lev-Yadun and Gould (2007, 2009), Archetti et al. (2009a), Schaefer and Ruxton (2009, 2011) and Farmer (2014).



Almost every color imaginable has been observed in foliage of some plant taxa due to variations in concentrations and combinations of vacuolar pigments (e.g. anthocyanins and betalains), photosynthetic pigments (chlorophylls and carotenoids), cuticular waxes, and iridescent structures (e.g., iridosomes) (Lee 2007; Glover and Whitney 2010). Organs or tissues with colors other than green, may in many cases, but certainly not always, have an extra cost. The cost to the plant of producing colored organs has three aspects. First, it requires allocation of resources for the synthesis, application, degradation, and regulation of the expression patterns of the pigments. Second, any color of a non-woody aerial plant's organ, other than green, may in many cases, but certainly not all, since anthocyanins, betalains and carotenoids defend photosynthesis, be linked to lower photosynthesis (see Chalker-Scott 1999; Matile 2000; Hoch et al. 2001, 2003; Lee and Gould 2002; Gould et al. 2002a, 2002b; Close and Beadle 2003; Gould 2004; Ougham et al. 2005; Manetas 2006; Hatier and Gould 2008; Jain and Gould 2015). Third, conspicuousness may potentially attract herbivores. In general, the benefits in fitness from defensive coloration should be higher than its fitness costs for such characters to evolve.

Plant pigments and coloration caused by air spaces or other physical effects serve many physiological and communicative functions, such as photosynthesis, protection from UV, scavenging of oxygen radicals, pollination, seed dispersal, thermoregulation and defense from herbivores and pathogens (e.g., Gould et al. 2002a; Close and Beadle 2003; Lee 2007). Gould et al. (2002b), Lev-Yadun et al. (2002, 2004a), Gould (2004), Lev-Yadun (2006a, 2009a), Schaefer and Wilkinson (2004), Lev-Yadun and Gould (2007, 2009), and Archetti et al. (2009a), have already argued that the non-photosynthetic plant pigments have the potential to serve more than one function concurrently, including physiological ones. I stress that I fully agree with Endler (1981) who commented concerning animal coloration “we must be careful not to assume that because we have found one apparent function to a color pattern, it necessarily means that we have a complete explanation”. Thus, various hypotheses concerning the function of coloration of leaves and other plant parts need not contrast with or exclude any other functional explanation of specific types of plant coloration, and traits such as coloration, that might have more than one type of benefit, may be selected for by several and even very different agents. Consistent with Grubb's (1992) view that defense systems are not simple, I usually consider that defensive plant coloration may defend by more than one method (including by signaling), reflect an adaptation to physiological pressures, and also serve non-defensive relations with other organisms.

Since some of the proposed defensive functions of leaf, flower and fruit coloration and shape (morphology) involve mimicry, I briefly describe the two major types (out of a longer list that includes various subtypes, see Wickler 1968; Pasteur 1982; Starrett 1993) of plant defensive mimicry. An innovative and elegant attempt to overcome the problematic, complicated and not fully satisfying definitions of mimicry by defining them as “adaptive resemblance” (Starrett 1993) did not manage to convince many and was not cited sufficiently to be used instead of the imperfect term mimicry.

Müllerian mimicry is a phenomenon in which two or more species with effective defenses share a similar appearance or signaling, and by this sharing reduce the cost of associative learning and evolution of refraining from attack by their enemies, a refraining that may sometimes have a genetic basis (Ruxton et al. 2004). Batesian mimicry is a phenomenon in which members of a palatable species or a group of such species, gain protection from predation by resembling an unpalatable or defended species (Bates 1862; Müller 1879; Wallace 1889; Cott 1940; Wickler 1968; Ruxton et al. 2004). There are, however, intermediate types (quasi-Batesian mimics) between these two extremes when defended and signaling species differ in their strength of defense or signaling (e.g., Rowland et al. 2010). Most of our knowledge about defensive mimicry has emerged from animal studies, and while even the better-studied animal mimicry systems such as butterfly aposematism and its Müllerian and Batesian mimicry, are still not fully understood (e.g., Forbes 2009), the operation of defensive mimicry in plants and its ecology and evolution is dramatically much less understood (e.g., Hinton 1973; Wiens 1978; Lev-Yadun and Inbar 2002; Lev-Yadun 2009a, b, c, 2014a; Schaefer and Ruxton 2009, 2011; Lev-Yadun and Ne'eman 2012; Farmer 2014).

In plants there is an additional recognized type of Müllerian and Batesian mimicry. Accordingly, flowers that attract pollinators with rewards are called Müllerian mimics and those without rewards are called Batesian (e.g., Dafni 1984; Roy and Widmer 1999; Schaefer and Ruxton 2011). Being non-defensive, they will not be discussed here. Only defensive Müllerian and Batesian plant mimicry will be discussed in this book. Moreover, I think that borrowing the terms Müllerian and Batesian mimicry for rewarding and rewardless flowers is inappropriate and has a logic discrepancy because defensive Müllerian and Batesian mimicry is aimed to repel animals and in pollination they are aimed to attract. I suggest that concerning pollination, rewarding flowers that mimic other rewarding flowers are named Darwinian mimics because Darwin contributed critically to the understanding of pollination, and that for obvious reasons non-rewarding mimics are named Wallacian mimics.

The evolution of mimicry requires a model or models, a mimic, and a predator or predators (an operator). The model should be another species or a group of species, or their actions (e.g., release of chemicals or physical damage to other organisms) (Wickler 1968). Organisms may also mimic a biological or non-biological substrate on which they grow as a camouflage against enemies or to hide from potential prey (Cott 1940; Wickler 1968; Edmunds 1974; Ruxton et al. 2004; Caro 2005; Stevens and Merilaita 2011). Masquerade (close resemblance of inedible and often inanimate objects that will be discussed in more detail later) (Endler 1981; Allen and Cooper 1985; Skelhorn et al. 2010a, b; Lev-Yadun 2014b; Skelhorn 2015) is a related visual but not a crypsis-based defense, or at least, it is non-cryptic at close range. This character may sometimes initially evolve not for defense but for physiological reasons, e.g., the common light plant coloration that reflects excess light in sandy coastal or desert environments, resulting (probably as a secondary gain) in actual substrate mimicry that may potentially also reduce herbivory by camouflage or by just not being green (Wiens 1978; Lev-Yadun 2006b, 2014b, 2015a; Reeves

2011). Such multifunctional situations make it difficult to evaluate the relative role of the mimicry in various morphologies and types of coloration, but may explain the advantages during early stages of the evolution of such cases (Schaefer and Ruxton 2009).

Another significant theoretical problem that was highlighted recently is the difficulty in distinguishing between cases in which plants exploit perceptual biases of animals that may by convergent evolution arrive at a morphology that just looks like mimicry but is not a true mimicry (Schaefer and Ruxton 2009). For the convenience of discussion, and because of the very small number of experiments directly testing defensive plant mimicry, and because of our current very limited ability to distinguish between the situations of exploitation of perceptual biases of herbivores by plants and true mimicry by plants, I will usually refer only to mimicry. However, the exploitation of perceptual biases should be taken into consideration when “mimicry” is discussed or tested. I am sad to state that it is still not practical to do so in most cases and hope that this frustrating situation will change in the coming decades.

## Chapter 2

# Plants Are Not Sitting Ducks Waiting for Herbivores to Eat Them

Human patients with severe brain damage due to trauma or ischemia may never regain recognizable mental functions and they never speak because of absence of function in the cerebral cortex. Such patients were described in a classic medical paper as in a “persistent vegetative state” (Bryan and Plum 1972), and are referred to as “plants” or “vegetables” by laymen depending on language and culture. This attitude towards plants was recently manifested by Laundré (2014) in an essay about the hunting hardships of large carnivores. Laundré (2014) posited that “meeting daily energetic needs by large carnivores is not as easy as just going out and gathering plants that are waiting around to be found and eaten”. I clearly and sharply posit that except for rewarding flowers towards legitimate pollinators (Faegri and van der Pijl 1979), ripe animal-dispersed fruits towards seed dispersers (van der Pijl 1982), or various food rewards to mutualistic ants (Jolivet 1998), plants do not wait around to be found and eaten. They do everything evolution has allowed them to do in order not to be eaten.

This common approach towards plants is a great underestimation of the huge and variable arsenal of defensive plant strategies. Moreover, many if not all land plants may employ several simultaneous constitutive and induced defensive strategies. Even plant parts that eventually wait to be found and eaten such as animal-dispersed ripe fleshy fruits that are intended to be eaten eventually by seed dispersers, defend themselves when they are unripe by means of chemistry, timing, camouflage, aposematism, and mechanical defenses (Herrera 2002; Schaefer et al. 2008; Lev-Yadun et al. 2009a; Lev-Yadun 2013a). Moreover, they, in the case of spiny *Opuntia* fruits may be still defended even when they are ripe. Plants employ bodyguards such as ants (Jolivet 1998), and call, using volatiles, to predators and parasitoids of their attacking invertebrate herbivores (Kessler and Baldwin 2001; Karban 2015). From time to time, they overwhelm and satiate herbivores by their sudden appearance in huge numbers in cases of mast fruiting or synchronous flowering (Janzen 1976; Kelly and Sork 2002), cause false satiation by various molecules (Lev-Yadun and Mirsky 2007), intimidate herbivores visually and chemically (Lev-Yadun 2009a), and possibly even by movement (Lev-Yadun 2013b). Plants also use camouflage

(e.g., Wiens 1978; Givnish 1990; Fadzly et al. 2009; Kloster et al. 2009; Burns 2010; Lev-Yadun and Ne'eman 2013; Niu et al. 2014), and pathogenic bacteria that they insert into the tissues of herbivores (Halpern et al. 2007a, b, 2011), they undermine the camouflage of herbivorous insects (Lev-Yadun et al. 2004a), and use strong wind-induced leaf movements to get rid of herbivores (Yamazaki 2011; Warren 2015), all these in order to defend themselves from herbivory. Plants have many types of mechanical defenses (Lucas et al. 2000) including even anisotropic arrangement of structural defenses that can lead invertebrate herbivores away from the plants (Vermeij 2015). Plants can even chemically identify (Karban 2015) and remember herbivore attacks for a long time (Gagliano et al. 2014; Karban 2015) and receive volatile cues from kin individuals that result in reduced herbivory damage compared to plants that receive such cues from non kin (Karban et al. 2013). This list is only a short partial summary of the many ways plants defend themselves from herbivores or manipulate them, and manipulate various herbivores' predaceous or parasitic enemies to the benefit of the plants.

Considering plants as defenseless and motionless victims of herbivores, because they are not fast and agile like large mammalian herbivores or carnivores, is a huge underestimation of plant defensive abilities, as many plants outsmart and even exploit many invertebrate and vertebrate herbivores and carnivores for pollination and for seed dispersal, and even carnivores and parasitoids, as was mentioned above, for defense. For instance, when thorny branches and spiny leaves move in the wind, they are actually "patrolling", and will hit anything positioned in their way and inflict wounds on large herbivores that enter their territory. Similarly, when such branches and leaves are bent by a large animal, they often return quickly and forcefully to their original position, stabbing their herbivores. I was painfully wounded by such plant spring actions numerous times during field work and fully appreciate their nasty reaction.

## Chapter 3

# The Many Defensive Mechanisms of Plants

Defensive plant coloration, morphology and movement, i.e., visual defenses, although variable as will be described and discussed in this book, are only a small part of the complicated and sophisticated anti-herbivory defense system employed by plants. In order to give the reader the right perspective, and to add to the previous chapter, below I describe the basics of their defensive system against other organisms. I stress that there is not a single species that has all these defenses together, but that this is the arsenal that evolution has allowed plants to possess. Since a full discussion of the defense system of plants will need a monograph larger than this book, I will present the data almost in the shape of an abstract.

Defenses are aimed towards enemies, and the biotic enemies of land plants include herbivores (vertebrates including mammals, reptiles and birds, and invertebrates), fungi, bacteria, viruses, parasitic plants and competitors (Harper 1977; Crawley 1983; Futuyma and Agrawal 2009; Gong and Zhang 2014; Karban 2015). Evidence from fossils indicates that herbivory on land plants began not later than the Early Devonian, some 400 million years ago (Labandeira 1998), and since earlier land plant fossils are not common and not well-preserved, it probably started at least dozens of millions years earlier.

Plants have ways to sense in many cases who attacked them and thus employ specific induced defenses through cues such as chitin (fungi, insects), volatiles, and probably by other cues and signals (Crawley 1983; Karban and Baldwin 1997; Karban and Agrawal 2002; Kant et al. 2015; Karban 2015). In spite of the large arsenal of anti-herbivory defenses that plants possess, herbivory in terrestrial ecosystems may consume up to about 75 % of the net primary production, however, the range of plant consumption is enormous, and can be as low as less than 0.1 % (Cebrian and Lartigue 2004), with a median of 18 % (Cyr and Pace 1993). I do not wish to elaborate on the question: why is the world green? The debates about this that began with Hairston et al. (1960) and developed into two contrasting views: top-down by predators, or bottom-up by plant defenses and low nutritional level (see review in Schmitz 2008). From my general experience and my involvement in several hot scientific debates, I think that both hypotheses are valid, one under