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A Review on Resistance to Biotic Stress in Leaf-Colored Plant

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Abstract

As sessile organisms, plants have to be subjected to insect attack. Over the long course of evolution, plants have produced many mechanisms to resist this biotic stress such as pigment accumulation. Pigment levels determined depth and distribution of leaf color, thereby indirectly or directly affecting the behavior of insect attack. Therefore, understanding the mechanism of mutual recognition between leaf color and insect will provide important theoretical insight for the cultivation and improvement of new cultivars. This paper outlines leaf-color formation and the effect of pigment on the behavior of insect attack, and explores the challenge of research in the interaction between leaf color and insect, as soon as the potential direction for future development. This will give a broad background for improvements of colored plants with resistance to insect attack.

Keywords

Leaf Coloration, Pathogen Infection, Pigment

1. Introduction

Insect attack has been considered to be one critical challenge to threaten plant survival, which strongly inhibits the growth of plant, reduces plant productivity, and even results in plant death. Consequently, in the long course of evolution, plants have to develop some helpful mechanisms to recognize and resist insect attack [1] [2] [3]. A previous study reported that accumulation of pigments play a key role in mechanisms of plant self-protection when attacked by insect [4]. This indicates that species and levels of pigments are key contributors to the aspect of insect resistance. These pigments can convey important information about the physiological status of a plant to other organisms and indirectly change the behavior of the insect attack by affecting formation of leaf color [5] [6] [7]. Thus, the intensity and distribution of leaf color become a key signal of their defensive commitment to the potential insect [8], but the mechanism remains largely unknown. Less work is focused on the relationship between host selection of insect and leaf color.

Change of leaf color is primarily determined by the progressive loss of chlorophyll coinciding with the partial retention of carotenoids and anthocyanins [9]. Genomes of these plants with leaf-color variance contain large various kinds of genes conferring resistance to insect [8]. Therefore, defense of the colored plant against insect attack comes in different forms, from accumulation of insect-deterring total pigments to regulation of color-related genes, and then to recognition of insect optesthesia to host plant. Often these processes are happening simultaneously. In the last few decades, leaf-color mutation was regarded as a bad phenotype and no more studies were conducted, but some wise breeders have devoted themselves to tapping leaf-color variance to develop new insect-resist cultivars since leaf color changing the insect behavior was discovered.

In consequence, from the perspective of biological control and prevention, leaf color is an important characteristic of plant, which affects host selection of insect, changes in biological status of plant, and plant adaption to insect. In this article, we summarize our knowledge of plant coloration as well as the close relationship and future direction between pathogen and plant color, which will give a better insight into the color-related pathogen of plant.

2. Why Are Colorful Colors Presenting on the Leaves of Plants

When leaf is exposed to visible light, the light will be absorbed partially by cells with the various pigment existed in chloroplast, vacuole and chromoplast. After that, the remaining light is reflected by the sponge tissue, and then passes back through the whole cell with pigment layer over and over again [10]. Leaf color will be observed when the unabsorbed light is perceived by ocular organs of organism.

Therefore, the formation of leaf-color is closely related to the levels of pigment accumulation in cells [11] [12]. Pigment level can intensively change spread of incident light on epithelial cells [13]. Except green color is known well was determined by chlorophyll [14] [15], presentation of bright-color such as purple, blue, red color usually is involved in accumulation of anthocyanins and carotenoid [16]. These pigments can solely or jointly affect the formation of leaf color. Of course, this also is implicated in environment factors (such as light intensity, cold stress, nutrient element, etc.), pigment distribution, as soon as plant physiological status itself. Mutation of gene encoding pigments or plastids may be a fundamental and primary factor resulting in color variance. Loss or mutation of gene plays a critical role in leaf-color variance. For example, mutation of the *BGL11*(*t*) gene whose a 9 bp segment deletion in the coding region leads to leaf yellowing [17]; function loss of the *BoPR* gene results in disorder of anthocyanin metabolism [18]; *PDS* silencing causes photobleaching on the leaves of plant. In addition, environment factor, such as cold, light, etc., also is a mainspring leading to the happening of leaf-color variance. Recent study found that cold and light induce anthocyanin synthesis by regulating the key gene or transcriptional factor, suggesting that change in leaf color enhanced the plant adaption to environment.

3. How Do Pigments Influence on Behavior of Insect Attack?

It is well known that recognition of almost insects to color is depended on wavelength of light [19], and pigments can change the length of optical wave [20], thereby regulating selection of insect behavior to host plant. A study from Aman (2014) [21] supported the statement, who reported that absorption of pigments to light significantly change in wavelength of light (**Figure 1**), and the difference in spectral absorbance of pigments results in the difference of plant to insect resistance. Besides, different photoperiods and wavelengths of light also exert a combined and important influence on the life-history traits of insect: total larval period is longest under short-day and red-light conditions. Females keep at long-day photoperiod and under white light showed better reproductive performance than those placed under other photoperiods and wavelengths [22]. In addition, wavelengths of light affected by leaf coloration also change vision of insect. Some data suggest that short-wavelength radiation can enhance plant defense and activate defense pathways in plants by changing the biosynthesis of secondary metabolites to resist insects [23], but this often is affected by their chemical structures, cellular localizations and biochemical synthesis pathways of pigments [10].

4. What Is Leaf Color Resisting to Insect Attack

As is well-known, number of green-leafed plants possess a high percentage in kingdom of colorful plant. Long-term evolution leads to the characteristic of chlorophyll with unabsorbing green light [24]. This also is the reason to result in formation of green color. The green color is often considered to be an attractive color to insect visitors [25]. Jahan *et al.* [26] believed that the wavelength of light

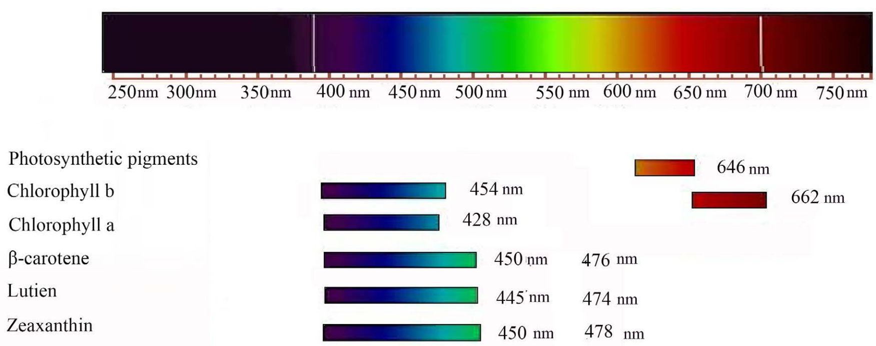

Figure 1. Absorption spectra of mass pigments (β-carotene, chlorophyll a, chlorophyll b, lutein and zeaxanthin) the number presented the wavelength of light (described by Åman *et al.* (2014) [21]).

reflected by green leaves possessed the higher attraction rate of whitefly (**Table 1**). Furthermore, attraction of green color to insect also is associated with various proteins related to green light signal from visual system of insects. In body of some insects such as *Drosophila melanogaster*, expression of proteins with sensitivity to green light is higher than others, and further study found that these proteins are belonged to the acceptor of green light signal, whose the levels and distribution play a key role in green color recognition of insects [27]. Furthermore, green-sensitive opsin, different from protein green light signal, in eyes of insect also can mightily affect behavior of an insect [28]. Functional diversification of opsins and photoreceptor evolution illuminated by genomics lead to a well development of visual systems [29].

Saturation and brightness of green color had an effect on insect attraction [30]. Chlorophyll a and b concentrations can be significantly higher in non-infested leaves compared with the infested ones, suggesting bright color may be more resistant to insect [31]. Some plants, characterized by a lower carotenoids/chlorophylls a + b quotient, are always less invaded by the investigated aphid [32]. In general, in these insect-sensitive green plants, there is a decrease in expression of gene such as *CHL2* at transcript level when subjected to insect attack [33].

In contrast, some dark color, such as red coloration, which usually is considered to be related to metabolism of anthocyanin or carotenoid as a warning signal can be against attack of insect herbivory, because the color is less easily perceived by aggressive insect photoreceptors, suggesting red-colored leaf can undermine insect camouflage [34]. Generation of red color in color-leafed plants often is due to redirection of the flavonoid pathway from delphinidin to pelargonidin [35]. The phenylpropanoid pathway as a signal which leads to the biosynthesis of anthocyanins as well as other phenolic compounds is well known as antifeedant properties [36], because insect can avoid consuming red leaves by the method of perceiving this signal [37]. The decreased reflectance in the green

Table 1. Attraction rates of whiteflies to various LED lights within the visible wavelength range (described by Jahan *et al.* (2014) [26]).

Group	TYLCV	Attraction rate (%) to various LED lights (means ± SE)						
		Violet	Indigo	Blue	Green	Yellow	Orange	Red
		400 - 420	430 - 440	450 - 460	520 - 530	570 - 580	590 - 610	610 - 630
Bt-Q	NV	1.0 ± 0.5c	0.0 ± 0.0c	0.0 ± 0.0c	47.3 ± 2.9a	1.6 ± 0.3c	15.0 ± 3.0b	1.6 ± 1.2c
	V	0.0 ± 0.0c	0.0 ± 0.0c	1.3 ± 0.7c	78.3 ± 2.9a	1.0 ± 0.6c	15.3 ± 1.5b	0.0 ± 0.0c
Bt-B	NV	0.3 ± 0.3c	0.3 ± 0.3c	0.0 ± 0.0c	62.0 ± 2.0a	1.7 ± 0.3c	17.0 ± 2.6b	0.3 ± 0.3c
	V	0.0 ± 0.0c	0.0 ± 0.0c	0.0 ± 0.0c	82.3 ± 1.8a	2.0 ± 0.6c	13.3 ± 1.9b	0.0 ± 0.0c

Whiteflies infested in tomato plants were exposed to seven LED light sources for 6 h in an insect rearing room; non-viruliferous (NV) and viruliferous (V) groups of *Bemisia tabaci* Q-biotype (Bt-Q) and B-biotype (Bt-B), and NV group of *Trialeurodes vaporariorum* (Tv). Different letters (a, b and c) in each row indicate values are significantly different at $P \leq 0.05$ * indicated wavelength (nm) of each light.

spectral band and the concomitant leveling of reflectance throughout the 400 nm - 570 nm spectral range may either make red leaves less discernible to some insect herbivores or make insect herbivores more discernible to predators [38]. Meanwhile, these warning signals increase the fitness both of plants and of herbivores [39] [40]. This hypotheses have been confirmed by previous studies, which reported that synthesis pathway of leaf anthocyanins that absorbs visible light can resist to attack of insect by increased accumulation of produce of warning substance as potent insect deterrents [41] [42].

Formation of bright red, yellow and orange colors is well known regarding carotenoid synthesis. Carotene, lutein as well as zeaxanthine is primary members of carotenoids [43]. Photosynthetic organisms utilize carotenoids for photoprotection as well as light harvesting [44], while this makes it possible to absorb visible light of wavelengths. The wavelength of light absorbed is determined by the number and properties of double bonds in these carotenoids. That is why a high level of carotenoids usually presents these colors such as brilliant red, orange and yellow [45]. Thereinto, yellow color caused by accumulation of carotenoid is a bright color to attract insect [46]. The control of lutein incorporation with combination of cuticular melanin in the morphological color regulates the adaptation of insect such as *Nymphalid pupa* [47]. Disruption of plant carotenoid biosynthesis through virus-induced gene silencing results in low oviposition behavior of the insect herbivore [48]. However, sensitivity of yellow color to insects sometimes also is an aposematic (warning) signal, which primarily are due to its high conspicuousness and also depends on physiology of the receivers [49]. In addition, recent study shows that the combined effect of anthocyanin and chlorophyll is important for resistance of color-leafed plants to insect such as whitefly, which may be due to anthocyanin preventing cell killing and lipid peroxidation, keeping PSII activity, reducing photoinhibition and photobleaching of chlorophyll and holding back degradation of chloroplast or keeping synthesis of chlorophyll and leading to improvement of immune system, Thereby increase resistance to whitefly [50].

Understanding the mechanism of host-plant resistance will aid in the identification of genes that confers resistance and in the development of resistant varieties through classical breeding or biotechnology, and plant development can be explained ultimately at the level of molecular due to decision of gene to phenotype [51] [52]. Regulation of genes related to metabolism of pigments to resist insect attack has been studied for some years. Transgenic strain displays enhanced expression of genes related to biosynthetic pathway leading to increased accumulation of pigments, which increases the resistance to insect or changes selection of insect [53], Therefore, breeders enhanced resistance to insect in plants by over-expression of some genes such *Rosea1* involved in accumulation of pigments including anthocyanins [54]. In summary, attack of insect to color-leafed plant may be affected by regulation of pigment to light as well as characteristics of pigments themselves, in turn reflecting in repression of colored leaf to insect behavior.

5. Recognition and Response of Insect Itself to Leaf Coloration

Success in this interaction between insect and plant is affected by plant ability to defend itself from devastation by insect feeding [55]. As mentioned above, and also confirmed by Cooney *et al.* [56]: some species of insects show high sensitivity to red leaf providing a reliable and effective visual signal of chemical defense (**Figure 2**). This is related to not only characteristic of plant itself but also diverse opsins existed in eyes of the insects. Further study discoveries that the opsin proteins are typical molecules that enable vision by combination of chromophore related to a vitamin-derived to form light-sensitive photopigments. The primary drivers of evolutionary diversification in opsins are thought to be visual tasks related to spectral sensitivity and color vision, while genes mutation encoding visual proteins can change the sensitivity to different light such as the ultraviolet, blue, as well as long-wavelength [57]. Interspecific variation in leaf coloration of plant is usually associated with diversity of insect herbivores [58]. Therefore, the changed sensitivity of insects to ray of light may be an important factor affecting selection of insect attack to color-leafed plant. In addition, under stress of long-termed natural selection, insects also develop polymorphism in color selection to adapt to multi-colored plants [59]. These insects by themselves can synthesis pigments such as carotenoid as well as protein related to recognition of green color, resulting in change of insect itself from green to red to avoid natural enemy, which enhances their survival ability in natural environment [60] [61].

Generally, the identical plant can attract one type of insect but may resist to another type of insect. A plant may be attacked by some species of insects, and then a kind of insects also can result in damage of many species of plants. This is the result of selection or adaption between insect and plant. For example, beetles are the dominant insects during *Eucalyptus globulus* and 99% trees can be

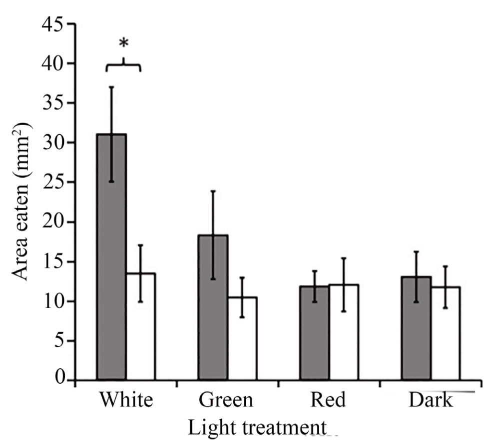

Figure 2. Area of red (open bars) and green-margined (closed bars) *Pseudowintera colorata* leaves eaten by *Ctenopseustis obliquana* larvae under white, green or red light, or in darkness (described by Cooney *et al.* (2012) [56]). Means (± SE), n = 33. Statistically significant differences between groups: *, P < 0.05.

affected by the insects [62], while some generalist wood-eating species may inflate the apparent species richness of leaf-feeding beetles and the proportion of specialist species varies significantly among tree species [63]. The complicated relationship that the recognition and adaption between plant and insect is of the essence to maintain ecological balance.

6. Effect of Other Factor Involved in Pigment Metabolism on Insect Behavior

Leaf coloration provides abundant information about defense of host plant to insect herbivores, while there is a limitation in the relationship between the color and chemical defense of leaves of plants in natural populations due to the absence of data. How dose defensive system of plant impact herbivore abundance, preference and performance? This seems to be an interesting issue for some researchers who specialized in plant protection and plant breeding.

Flavonoids as insect growth inhibitors are regarded as critical factors due to governing toxicity to insects found and studied in past years [64], which also is important in recognition and acceptance of host plant to adult insects [65]. Plant flavonoid synthesis pathway usually includes synthesis of anthocyanins, flavonoids, proanthocyanidins and so on, and their special structures depend on physiological characteristics of plant (**Figure 3**) [66]. Generally, leaf vivid coloration can be affected when accumulation of anthocyanins involved in flavonoid metabolism is carried out. One example is that as produce of flavonoids metabolism, delphinidin, cyanidin as well as pelargonidin has strong antioxidant activity [67]. Gringorten *et al.* [68] also believe that flavonoids resulting in less damage of insect to plant is due to its toxicity to insect cells in vitro. Insects can sequester these compounds into their body cuticle for protection against pathogens and predators or into their wings to attract mates. Thus insects might benefit from plants with higher levels of flavonoids, making insect pests more difficult to control using of biological control agents such as viral pathogens [69]. That suggests fitness of insect to plant with high phenolic substances. Although the self-protection of insect is existed widely, flavonoids remains to be thought to provide the protection of plants by inhibiting the formation of reactive oxygen via a range of different mechanisms [70]. A strong reduction in mean larval weight and growth inhibition intensively confirms this view in treatment of flavonoids Therefore, researchers regard flavonoids as potential substance for developing novel biopesticides in the future [71].

In addition, a range of concentration in some other phenolics such as rutin also play a key role in the interaction between insect and plant. The rutin interacts as a non-competitive inhibitor with arginine kinase (AK), a key enzyme in the cellular energy metabolism of insects, which may be one reason for its insecticidal activity. The interaction is conducted mainly by a hydrophobic force forming an inter-molecular complex with arginine kinase, which is responsible for the molting process in insects [72]. Pinocembrin as another ramification of

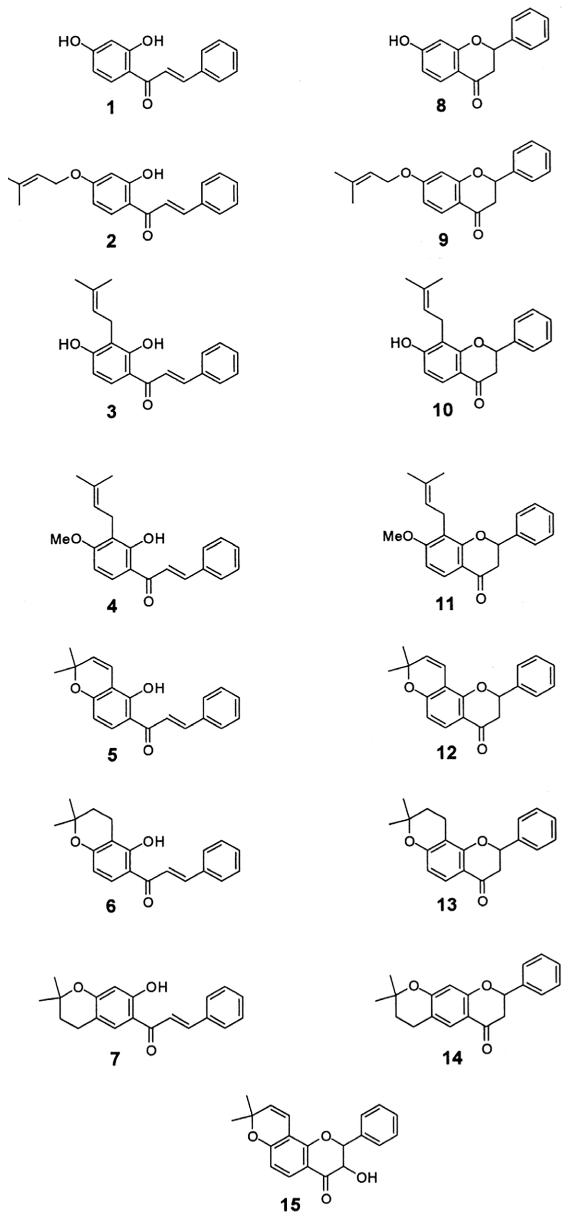

Figure 3. Structure of flavonoids (described by Simmonds *et al.* (1990)) 1 = 2', 4'-dihydroxychalconc; 2 = 4'-O-prenylchalconc; 3 = 3'-prenyl-challconc; 4 = derricin; 5 = lonchocarpin; 6 = 6-cinnamoyl-5-hydroxy-2, 2-dimethylchroman; 7 = 6-cinnamlyl-7-hydroxy-2-dimethylchroman; 8 = 7-hydroxyflavanone; 9 = 7-*O*-methyl-8-prenyl-flavononc; 10 = 8-prenyl-flavononc; 11 = 7-*O*-methyl-8-prenyl-flavanone; 12 = isolonchocarpin; 13 = dihydroisolonchocarpin; 14 = 6', 6'-dimethyl-2*H*-pyrano (2', 3', 7, 6)-flavanone; 15 = 3-hydroxyisolonchocarpin.

anthocyanin at 1 - 50 lg/cm^2 negatively affects larval weight and survival, thus showing intensively toxic effect to insect. In contrast, leaf consumption and larval weight were not significantly affected by quercetin at 0.1, 1, 5 and 50 lg/cm^2, and mortality rates only slightly increased [73], while leaves of *S. phylicifolia* containing high levels of flavonoids (173 mg/g dry weight, DW) and low levels of chlorogenic acid derivatives (0.97 mg/g DW) is closely associated with insect attack [74]. When insect herbivore such as caterpillars were reared on foliage from tree genotypes containing high amounts of phenolic glycosides, developmental time was prolonged, pupal weight declined and the number of eggs produced by females was reduced [75]. Thus, there is the closely between concentration of flavone pigment and insect attack, which depends on whether success in attack of insect to color-leaf plants.

Environmental pH as a significant factor plays an important role in regulation of plant color. Leaf coloration can be affected when color-leafed plants are grown under the environment with different pH value, which often is closely associated with stability of pigments in cells [54] [76]. Anthocyanins are unstable at pH > 4.5 and at this relatively higher pH these pigments change from red to blue, which causes change of leaf coloration with together the level of anthocyanin in cells [77], while the direct physiological effect of low pH is the key factor limiting the distribution of acid-sensitive species of insect, suggesting that selection of insect to host plant is affected by pH value [78]. Lapidot *et al.* [79] believed that compared with red color phenotypes green color suffered greater herbivore damage, as judged by the number of leaves attacked and the area lost to herbivory, because formation of red color intensively depends on lower pH but high pH in green or yellow color (**Figure 4**). Besides, the fluctuation of pH also can affect pH dependence of hydrogen activating enzyme systems in insects, which also indirectly affects attraction of plant to insect [80]. Tsai *et al.* [81] also believed that stability of pigment such as red pigment also is associated closely with pH resulting in change of light absorption, while some acids produced by plants are regarded as a defense substance change response to the insect injury (**Figure 5**).

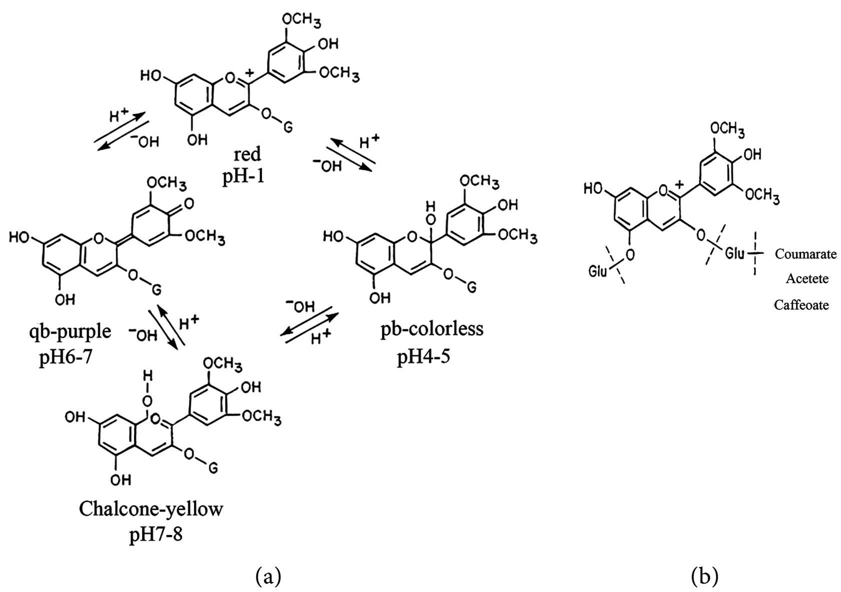

Figure 4. Anthocyanin structure at transformation by pH as well as structure of major anthocyanins (described by Lapidot *et al.* (1999) [79]) (a) Anthocyanin structure at changed pH; (b) Structure of major anthocyanin in red wine grapes.

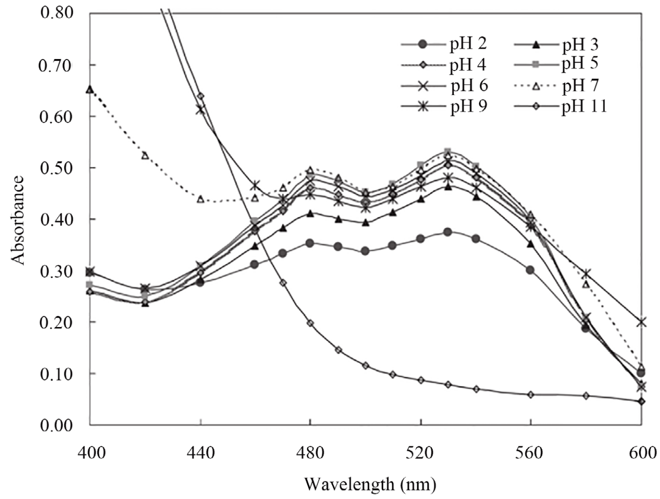

Figure 5. Absorbance spectrum of red Djulis grain pigments extracted with water and adjusted buffer pH at 2 - 11 (described by Tsai *et al.* (2010) [81]).

7. Concluding Remarks

Attraction of leaf coloration in plants to insects is the result of the joint actions of many factors. To date, a certain understanding of the mechanisms underlying leaf coloration development has been achieved, with in-depth studies on the relationship among the pigment levels and components, wavelength of light, product of secondary metabolism and key genes. In addition, a basic understanding of the types of pigments and their resistance to insects in different color-leafed plants has been reached, and then the regulatory mechanism has been explored. Along with the deepening development of rapid and effective scientific approaches such as omics technology in field of biology as well as the rapid advance of high throughput sequencing technology, new opportunities and challenges are brought for research on the development and regulation of leaf coloration to insects in kingdom of color-leafed plants. And some difficult questions could be solved by drawing on research results on the interaction between leaf coloration and insect. For example, the complete regulatory mechanisms of insects affected by leaf coloration as well as the interaction among the regulatory factors related to the mechanisms can be used for the development of new leaf coloration, prevention of pests and directed breeding of new cultivars. However, the huge amounts of data produced in the research of the development and regulation of leaf coloration to insect in color-leafed plants also pose a challenge for our analysis, and most studies in the aspect only are limited in level of the investigation related to phenotype of leaf coloration and amount of insects to determine regulation of leaf coloration to insect. Study on interaction between leaf coloration and insect seems to be developed further in recent years. In order to make great progress in the research of the development and regulation of leaf coloration in color-leafed plants, we must be skilled in bioinformatics and molecular biology as well as need the infiltration and emergence of multiple subjects.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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