African Journal of Biotechnology Vol. 11(31), pp. 7855-7863, 17 April, 2012
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB12.382
ISSN 1684–5315 © 2012 Academic Journals

Full Length Research Paper

Light-sensitive features of seed germination in the invasive species *Ageratina adenophora* (syn. *Eupatorium adenophorum*) in China

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Accepted 30 March, 2012

Ageratina adenophora **(Crofton weed) is a noxious invasive plant in several countries and its germination features favor its invasiveness. The aim of this study was to characterize the light-sensitive seed germination of this weed. Two to five-fold higher germination was observed under light conditions than under dark conditions. Dormancy-breaking methods of low temperature pre-treatment, pre-soaking with KNO_3 solution, polyethylene glycol, and salicylic acid did not influence germination under either light or dark conditions. Very low light (39 μmol·m^{-2}·s^{-1}, 25% light transmittance) tripled seed germination from 22.3 to 66.7%, when compared to no light. Germination under violet, blue and green glass papers was significantly lower than that under yellow, orange, and red ones. Significant correlations between red-light intensity, red/far-red ratio and germination indicated that these 2 types of light may be responsible for the germination differences. Experiments under narrow band filters also proved this; red light at 630 nm could induce germination, while far-red light 740 nm could prevent germination. Thus, red/far-red light was effective in the photoblastic germination of Crofton weed, while other treatments could not replace light during germination. This photoblastic germination could favor the fast colonization of this weed when the seeds in deep soil approach the surface.**

Key words: Crofton weed, plant invasiveness, light quality, light quantity, red/far-red ratio, biological control.

INTRODUCTION

At present, there are approximately 170 species (41 families) of invasive terrestrial plants in China (Sang et al., 2010) and similarly, many invasive species have been reported in Africa (Olckers, 2004). *Ageratina adenophora* (Spreng.) R. M. King & H. Rob. (syn. *Eupatorium adenophorum* Spreng), commonly called Crofton weed, is a representative of the Asteraceae family (49 invasive species) and is a noxious weed found in many countries, including the United States of America, New Zealand, Australia and many African and Asian countries (Cronk and Fuller, 1995; Dong et al., 2011). Crofton weed is a perennial herb, with a woody rootstock and many stems reaching up to 1.5 m in height (Wang et al., 1994). Originally from Mexico, it first appeared in China in the Yunnan Province in 1935 (possibly from Burma), and its dispersal continued northwards and eastwards at an average speed of 20 km·year^{-1} (Sang et al., 2010). In this paper, we discussed the effect of light on seed germination and its possible role in the invasiveness of Crofton weed.

Crofton weed is highly effective in invading heavily disturbed areas along streams, roadsides, large tracts of pasture and horticultural land in both South Asia and Africa (Wang et al., 1994; Dong et al., 2011; Buccellato et al., 2012). The successful invasion of this species has been attributed to a number of mechanisms, including plasticity in photosynthesis and nitrogen utilization (Wang and Feng, 2005), a lack of natural predators (Raj Mohan and Ramaswamy, 2007), allelopathy for other native plants (Yu et al., 2004), large amounts of seed production and variable methods of dispersal (Wang et al, 1994; Yang et al., 2007). Like other seed traits, germination (the first step in colonizing a new habitat), can also evolve in response to the selective pressures of different habitats,

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thereby producing genetic differentiation (Li and Feng, 2009). Light can affect the germination process of Crofton weed; however, there is wide variation in the results of published studies (Lu et al., 2006; Wang et al., 2006; Xu et al., 2011; Niu et al., 2011). Liu et al. (1985) found that stable light, together with a hot and moist environment, is necessary for successful germination of Crofton weed seeds. Lu et al. (2006) also found that the major invasion of Crofton weed should be limited to parts of Southwest China, while germination failure is likely in other regions. Wang et al. (2006) found that the peak germination rate of Crofton weed was below 28% of full sunlight, and additional light could decrease the germination rate. Moreover, Niu et al. (2011) found that low light (<6%) improved germination and seedling survival, and Lu et al. (2006) reported that germination increased to over 90% under light, while germination in the dark was 17%.

Plasticity in the germination of seeds in variable elevations and different soil-depths may also favor invasiveness of Crofton weed in variable environments (Li and Feng, 2009; Shen et al., 2011). These data suggest that environmental factors, together with light, may influence the germination of this weed, although large differences exist in the results of the studies conducted to date. On the basis of the data from the literature, it is difficult to define the amount and type of light required to break photodormancy. In addition, it is not clear from the studies undertaken so far if other traditional dormancy-breaking methods can replace light and initiate germination. Hence, a systematic study is required to investigate these areas.

In this study, we aimed to define the light-sensitive features of seed germination of Crofton weed and to answer the following questions: (1) Is the germination of Crofton weed light sensitive? (2) Can traditional dormancy-breaking methods [low temperature, polyethylene glycol (PEG) treatment, salicylic acid treatment and KNO_3 treatment] stimulate germination equally as well as light? (3) Does radiation intensity affect the germination of this weed? (4) What effect do radiation wavelengths (color) have on germination? (5) Can red/far-red light inhibit germination?

MATERIALS AND METHODS

Seed origin

All seeds were harvested in March 2010 close to the World Horticulture Exposition Garden in Kunming, China (102.76°N, 25.08°E). Fully matured seeds were naturally dried in the laboratory, and even-sized good seeds were selected for this experiment. The weight of the seeds was 48 mg/1000 seeds. The seeds were stored in the laboratory for less than 1 month prior to the germination experiment.

Combined experiments of traditional dormancy-breaking methods and light

The traditional dormancy-breaking methods used included low-temperature (LT) treatment, salicylic acid (SA) treatment, PEG treatment and KNO_3 treatment. Prior to germination in growth chambers, the following treatments were conducted. For LT treatment, the seeds were placed in a refrigerator (5°C) for 7 days. For SA treatment, the seeds were pre-soaked in 3 concentrations of SA (0.01, 0.05 and 0.1 mmol·L^{-1}) and 1 control of distilled water for 20 to 21 h. For PEG treatment, the seeds were pre-soaked in 3 concentrations of PEG (5, 10 and 15%) for 20 to 21 h and the control of distilled water. For KNO_3 treatment, the seeds were pre-soaked in 10, 25 and 50 mmol·L^{-1} of KNO_3 solution for 22 to 23 h, and the control seeds were pre-soaked in distilled water for the same duration.

For each treatment, 40 seeds were evenly placed on wet filter papers (2 layers) in Petri dishes (diameter, 9 cm) and then cultivated in growth chambers (Dongtuo, ZPW-400, Harbin, China) under the following conditions: 25°C for 16 h·day^{-1} in complete light by using 24 fluorescent lamps (ca. 11640 lux, 158 μmol·m^{-2}·s^{-1}), and 15°C for 8 h·day^{-1} in complete darkness. For each treatment, at least 3 replicates were performed.

Light quality experiment

To test the effect of different colors of light on germination, 6 colors of glass paper (the color of the filters perceived by the eye: red, green, orange, yellow, blue and violet) (Hongtu film and TV appliances Inc., Beijing, China) were used to cover the Petri dishes during germination in growth chambers. The control was not covered with glass paper (white). The light transmittance of the glass papers was measured using an AvaSpec dual-channel fiber-optic spectrometer (Avaspec-2048-2, Aventes, Netherlands) (Table 3). For each treatment, 30 seeds were evenly placed on wet filter papers (2 layers) in Petri dishes (diameter, 9 cm), and one layer of glass paper was wrapped over the dish and kept in place until the germinated seeds were counted (7 days). For each treatment, at least 3 replicates were conducted.

Light quantity experiment

To expose the seeds to variable amounts of incident light, variable layers of medical gauze were used to cover the Petri dishes. Five light intensities were used: 100% (11640 lux, 158 μmol·m^{-2}·s^{-1}), 75% (8730 lux, 118 μmol·m^{-2}·s^{-1}), 50% (5820 lux, 71 μmol·m^{-2}·s^{-1}), 25% (2910 lux, 39 μmol·m^{-2}·s^{-1}), and <0.5% (30 lux, 0.4 μmol·m^{-2}·s^{-1}). An illuminometer (TES-1330A, Tes Electrical Electronic Corp., Taiwan) was used to measure light transmittance. A full dark treatment was performed in a growth chamber without a lamp (light transmittance, 0%, 0 lux). For each treatment, 40 seeds were evenly placed on wet filter papers (2 layers) in Petri dishes (diameter, 9 cm), and at least 3 replicates were performed for each treatment.

Red/far-red induction experiment

The red/far-red light experiment was performed in growth chambers with narrow band glass filters (Changchun Fuchun Photoelectrical Inc., Changchun, China). A halogen bulb (20 W, 220 V) fitted in front of a polished aluminum reflector was used as a source for both red and far-red light. The Avaspec spectrometer was used to measure the central wavelength and half-band width of the red and far-red light. Central wavelengths for red light and far-red light were 630 and 740 nm, respectively and the half-band widths were 30 and 20 nm, respectively. The distance from the light source to the seed dishes was 90 cm. Three test inductions and a dark control were used in this experiment. The first test was red light for 9 h (red9hour) and red light for 9 h plus far-red for 0.25 h (red9hour/far-

red0.25hour). The second test was red light for 36 h (red36hour) and red light for 36 h plus far-red for 4 h (red36hour/far-red4hour). The third test was red light for 66 h (red66hour) and red light for 66 h plus far-red for 8 h (red66hour/far-red8hour). For each treatment, 40 seeds were evenly placed on wet filter papers (2 layers) in a Petri dish (diameter, 9 cm), and at least 3 replicates were performed for each treatment.

Germination recording and data analysis

Cotyledon expansion was used as a criterion for seed germination. No new germination within 3 days was recorded as the end of seed germination. Germination percentage was calculated as the percentage of germinated seeds to the total number of seeds tested. Furthermore, germination differences between light and dark conditions under variable treatments of temperature, PEG, SA, and KNO_3 were analyzed using analysis of variance (ANOVA). The effects of light color, light quantity and red/far-red light on germination were tested using ANOVA, followed by multiple comparisons with the Duncan's test. All statistical analyses were performed using SPSS15.0.

RESULTS

Effects of traditional dormancy-breaking methods and light on seed germination

Germination of both plants that underwent LT and the control plants was significantly higher under light conditions than under dark conditions (Tables 1 and 2). However, the LT treatment did not diminish the difference between light and dark (46.3%) compared with the control (34%) (Tables 1 and 2). In all 3 concentrations of KNO_3, germination percentages under light conditions were significantly higher than those under dark conditions ($p < 0.05$). Similarly, germination in the control (distilled water) showed the same result (Tables 1 and 2), and statistical analysis showed no significant influence of the KNO_3 treatment on seed germination under both dark and light conditions (Table 2).

The various PEG pre-treatments did not affect seed germination under both light and dark conditions (Tables 1 and 2). Statistical analysis showed significant differences between light and dark treatments in all PEG treatments ($p < 0.05$); however, the PEG concentrations did not significantly influence seed germination ($p > 0.05$). Similar to the KNO_3 treatments, germination in all SA treatments under light conditions was significantly higher than that under dark conditions (Table 1). However, the SA treatment did not have any significant influence on seed germination, both in dark and light conditions ($p > 0.05$) (Table 2).

Effect of light quantity on seed germination

Light intensity was shown to strongly affect seed germination (Figure 1). Compared to no light, very low light (30 lux, <0.5% light transmittance) increased seed germination 1.5 times, from 22.3 to 35.7%, and 25% light transmittance (2910 lux) tripled the germination rate (66.7%) ($p < 0.05$). With further increases in light intensity from 50 to 100%, little increase in germination was observed (Figure 1). Regression analysis showed that germination percentage increased exponentially with light transmittance ($r^2 = 0.960$, $p < 0.05$) and light intensity ($r^2 = 0.958$, $p < 0.05$) (Figure 1).

Effects of light wavelength/color on seed germination

Radiation under different glass papers was markedly different (Table 3). In comparison with the white control, red glass paper transmitted most of the red light from 621 to 750 nm (>97%). Orange glass paper transmitted a slightly lower percentage of red lights but a 2-fold higher percentage of orange light than red glass paper from 591 to 620 nm (73%). High transmittance for blue glass paper was observed for blue (77%) and violet (60%) light from 380 to 490 nm. The transmitting wavelength for violet glass paper was similar to that of blue glass paper, but much lower than the percentage transmitted (ca. 44% for blue light and 59% for violet light). Green glass paper transmitted the least light, and peak transmittance (41%) was observed from 491 to 570 nm in green light. Yellow glass paper transmitted almost all the light in the range of yellow, orange, red, and green from 491 to 750 nm (Table 3). No significant differences were observed among the glass papers in the far-red (750 to 1100 nm) and ultraviolet (200 to 379 nm) wavelengths (Table 3).

Light wavelength markedly affected the seed germination of Crofton weed (Figure 2). Coverage by violet, blue and green glass papers induced similar seed germination, ranging from 59 to 64% ($p > 0.05$). These germination rates were significantly lower than those under yellow, orange and red glass papers ($p < 0.05$), which ranged from 80 to 83%. White light incidence produced interme-diate seed germination (72%), which did not significantly differ from either of the above-mentioned groups ($p > 0.05$). Regression analysis showed that germination was significantly correlated with red (621 to 750 nm) light intensity ($p < 0.01$) and orange (591 to 621 nm) light intensity ($p < 0.05$), while all other light intensities were not correlated with germination (Table 3). The most robust correlation ($r^2 = 0.91$) was observed between red/far-red ratio and germination (Figure 2).

Effects of red and far-red light on seed germination

Exposure to red light in excess of 36 h induced seed germination, while far-red light inhibited germination (Figure 3). Very short exposures of light did not induce seed germination, example, 9 h of red light exposure (Figure 3). With an increase in red light exposure from 36 to 66 h, germination increased from 27 to 41%, while a

Table 1. Different traditional dormancy treatments and their influence on the light-dependent germination of *Ageratina adenophora*.

Treatment	Light or dark	Germination (%)	Standard deviation
Temperature treatment			
5°C	Light	73.8[b]	8.1
	Dark	27.5[a]	7.5
Room Temperature	Light	62.3[b]	1.2
	Dark	28.3[a]	8
KNO_3 treatment (mmol L^{-1})			
0	Light	74.6[b]	4.0
	Dark	19.2[a]	2.9
10	Light	75.4[b]	2.6
	Dark	20.8[a]	1.4
25	Light	77.9[b]	1.9
	Dark	22.5[a]	10.9
50	Light	81.7[b]	1.4
	Dark	19.2[a]	2.9
PEG treatment (%) / Osmotic pressure (MPa)			
.0%/0 MPa	Light	68.8[a]	3.8
	Dark	28.3[b]	1.4
5%/-0.05 MPa	Light	74.2[a]	2.6
	Dark	30.0[b]	4.3
10%/-0.15 MPa	Light	75.8[a]	6.3
	Dark	30.8[b]	8.0
15%/-0.30MPa	Light	69.6[a]	7.5
	Dark	28..3[b]	2.0
SA treatment(mmol/L)			
0.00	Light	72.5[b]	7.0
	Dark	15.0[a]	2.5
0.01	Light	75.4[b]	5.6
	Dark	20.8[a]	10.4
0.05	Light	70.8[b]	5.6
	Dark	15.8[a]	3.8
0.1	Light	72.5[b]	5.7
	Dark	18.3[a]	12.8

In the same treatment, different letter indicates significant differences, while the same letter indicates no significant differences between light and dark.

far-red light exposure of 4 to 8 h following red light exposure terminated germination; no significant difference was observed in the dark control ($p > 0.05$) (Figure 3). The observed increase in germination was linearly correlated with red-light exposure time ($y = 0.3621x - 1.6225$, $r^2 = 0.9759$). The observed decrease in germination after exposure to far-red light was linearly correlated with far-red light exposure time ($y = 3.0432x - 1.3623$, $r^2 = 0.9161$). By using the slope gradient as rate of germination changes owing to red or far-red light

Table 2. Analysis of variance of the impact of traditional treatments and light treatment on seed germination in *Ageratina adenophora.*

Source	df	F	Significance
Temperature and light treatment			
Temperature	1	0.109	0.750
Light	1	30.584	**0.001**
Temperature * light	1	2.460	0.155
KNO_3 and light treatment			
KNO_3	3	0.839	0.492
light	1	937.959	**0.000**
KNO_3*light	3	0.990	0.423
Polyethylene glycol (PEG) and light treatment			
PEG	3	0.267	0.848
Light	1	111.161	**0.000**
PEG*Light	3	0.259	0.854
Salicylic acid (SA) and Light treatment			
SA treatment	3	0.517	0.676
Light	1	334.871	**0.000**
SA * Light	3	0.061	0.979

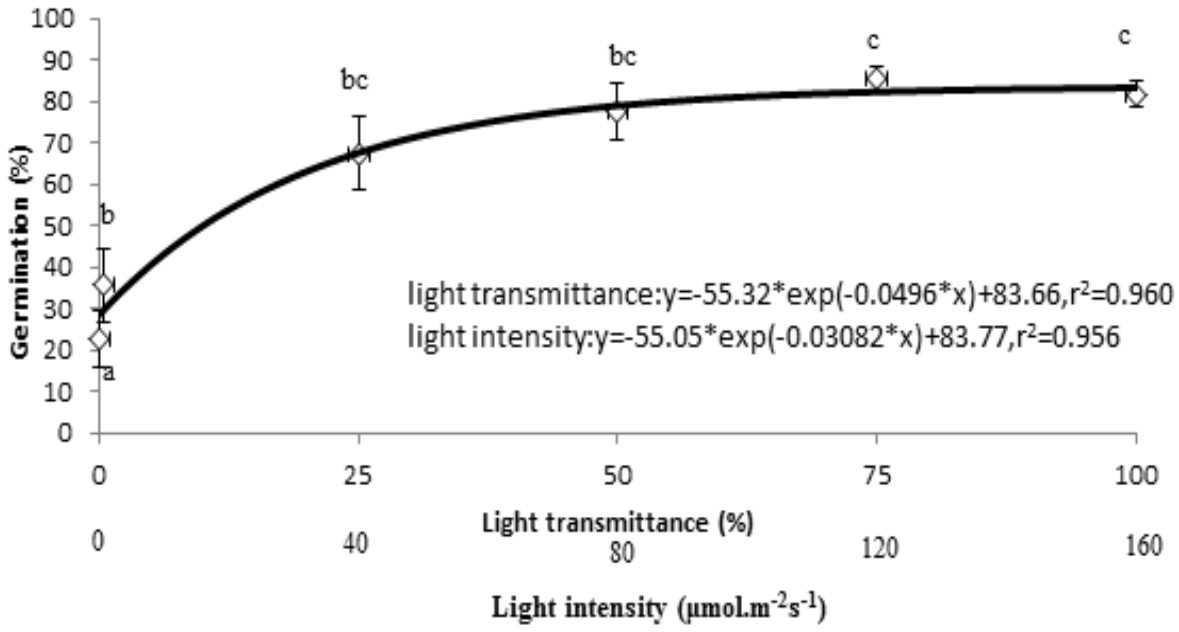

Figure 1. Relationship between seed germination and incident light intensity in *Ageratina adenophora*. Different letters indicate significant differences between different light intensity ($p<0.05$), while the same letter indicates no significant differences was found ($p>0.05$). The vertical bars showed the standard deviation of the raw data.

incidence, we observed that far-red light induced a decrease in the germination rate by 3.432%·h^{-1}, which is almost 10-fold higher than the increased germination rate observed under red light (0.3621%·h^{-1}).

DISCUSSION

Owing to the destructive nature of Crofton weed on the local ecosystem in China and other parts of the world,

Table 3. Differences in light intensity at variable wavelengths under different glass papers and their correlations with the germination rate in *A. adenophora*.

Intensity at nm range (μWatt cm^{-2} s^{-1} nm^{-1})	Color of glass paper							Regression with germination rate (y,%)		
	Violet	Blue	Green	Yellow	Orange	Red	White	Equations	R^2	p-level
Ultraviolet 200 - 379 nm	0.98(0.24)^{ab}	2.45(0.78)^{ab}	0.18(0.05)^{a}	1.05(0.26)^{ab}	1.35(0.43)^{ab}	0.65(0.15)^{ab}	5.19(1.32)^{c}	y=0.1638x + 71.612	0.0007	>0.05
Violet 380 - 450 nm	16.8(4.4)^{bc}	23.2(6.25)^{c}	0.26(0.08)^{a}	1.82(0.46)^{ab}	6.25(2.46)^{ab}	1.23(0.30)^{ab}	38.3 (10.3)^{d}	y=-0.1877x+74.244	0.0699	>0.05
Blue 451 - 490 nm	22.9(6.4)^{b}	29.5(6.47)^{bc}	1.63(0.45)^{a}	6.82(1.74)^{a}	0.97(0.40)^{a}	0.22(0.06)^{a}	38.5(5.99)^{c}	y=-0.2427x+75.374	0.141	>0.05
Green 491 - 470 nm	5.7(1.65)^{ab}	19.5(7.12)^{c}	16.1(4.4)^{bc}	32.06(6.12)^{d}	1.75(0.80)^{a}	0.19(0.05)^{a}	33.85(4.16)^{d}	y=-0.0098x+72.041	0.0002	>0.05
Yellow 571 - 590 nm	0.19(0.06)^{a}	10.11(5.13)^{ab}	5.85(1.69)^{ab}	32.85(5.98)^{c}	16.63(7.39)^{b}	1.47(0.43)^{a}	32.88(4.28)^{c}	y=0.3623x+66.715	0.2432	>0.05
Orange 591 - 620 nm	0.16(0.05)^{a}	8.37(4.37)^{a}	2.87(0.84)^{a}	40.68(8.68)^{c}	27.46(9.09)^{bc}	14.02(4.03)^{ab}	37.79(7.15)^{c}	y=0.4684x+63.099	0.5835	<0.05
Red 621 - 750 nm	11.88(4.11)^{a}	19.81(7.86)^{ab}	8.32(2.49)^{a}	47.09(11.43)^{b}	37.49(9.51)^{ab}	43.64(11.60)^{b}	44.85(12.69)^{b}	y=0.556x+54.964	0.8268	<0.01
Far-red 750 - 1100 nm	18.52(6.79)^{a}	15.05(5.03)^{a}	19.71(6.01)^{a}	21.92(6.17)^{a}	16.11(5.00) a	21.03(6.54)^{a}	23.73(8.91)^{a}	y=0.799x+56.359	0.0603	>0.05

In the same column, different letter indicates significant differences were observed in different wavelength (p<0.05), while the same letter indicates no significant differences were observed (p>0.05).Data in the parenthesis are the standard deviation of the data.

the dark to 90% in full light, while Li and Feng (2009) found that germination traits may differ at different elevations. Niu et al. (2011) found that disturbance, such as footprints of cows and horses, together with 6% sunlight could greatly influence germination and seedling survival. In a comparison of 10 species, laboratory tests demonstrated that light can significantly increase the germination of invasive species (4 invasive species, including Crofton weed), in comparison with that of non-invasive species (6 species) (Xu et al., 2011). Thus, germination of Crofton weed requires light incidence in addition to other environmental factors, such as temperature and moisture (Liu et al., 1985). These previous studies have advanced our understanding of this invasive weed and are the basis of this study.

Nevertheless, previous studies have not fully answered the questions regarding the amount and type of light necessary for breaking seed dormancy. Our findings in this investigation could answer these questions. The germination of Crofton weed is light-sensitive, and all traditional dormancy-breaking methods tested (low temperature, SA treatment, PEG treatment, and KNO_3 treatment) cannot replace light (Tables 1 and 2). Exponential increase in seed germination with light transmittance (~100%) and intensity (~160 $\mu mol \cdot m^{-2} \cdot y^{-1}$) were observed ($r^2$ > 0.95) (Figure 1). Red light and red/far-red ratio were responsible for differences in germination under different glass papers (Figure 2). Further experiments on red and far-red light demonstrated that red light could break the dormancy of Crofton weed seeds, while far-red light could terminate the germination process (Figure 3). Thus, the light-sensitive germination of Crofton weed is a typical phytochrome-related germination (Wu et al., 2004), and the reactive lights are red light and far-red light. All phytochromes have 2 mutually photoconvertible forms: Pfr (considered the active form), with maximum absorption at 730 nm and Pr, with maximum absorption at 660 nm. Seed germination requires Pfr function during a certain lapse (called the escape time). When Pfr is stable enough to remain longer than the escape time, just 1 light pulse is sufficient for germination, whereas if Pfr is reduced to ineffective levels before the end of the escape time, more than 1 pulse or a longer exposure to light is necessary for germination (Yang et al., 2003). In the case of Crofton weed, a 66-h exposure to red light can double seed germination from 20 to 40% (Figure 3), while relatively short exposures to far-red light (4 to 8 h) can reverse Pfr back to Pr and maintain seed dormancy (Figure 3).

The significance of this light-sensitive germination may be related to the seed bank in soil and the invasiveness of Crofton weed in disturbed soils. There is a large seed bank in soil (2,202 $seeds \cdot m^{-2}$), which serves as a source of regeneration for new plants in the event of disturbance (Shen and Liu, 2004). Seeds at the soil surface can remain viable for up to 5 months, while 40% of the seeds at depths of 5 and 10 cm are viable after 2 years and 20% of the seeds could still germinate after 3 years (Shen et al., 2011). Thus, a potential advantage of these photoblastic seeds is that they will not germinate when deeply buried in the soil (Lu et al., 2006) and can germinate following surface-soil disturbance, surviving much better than the seedlings from new seeds (Shen

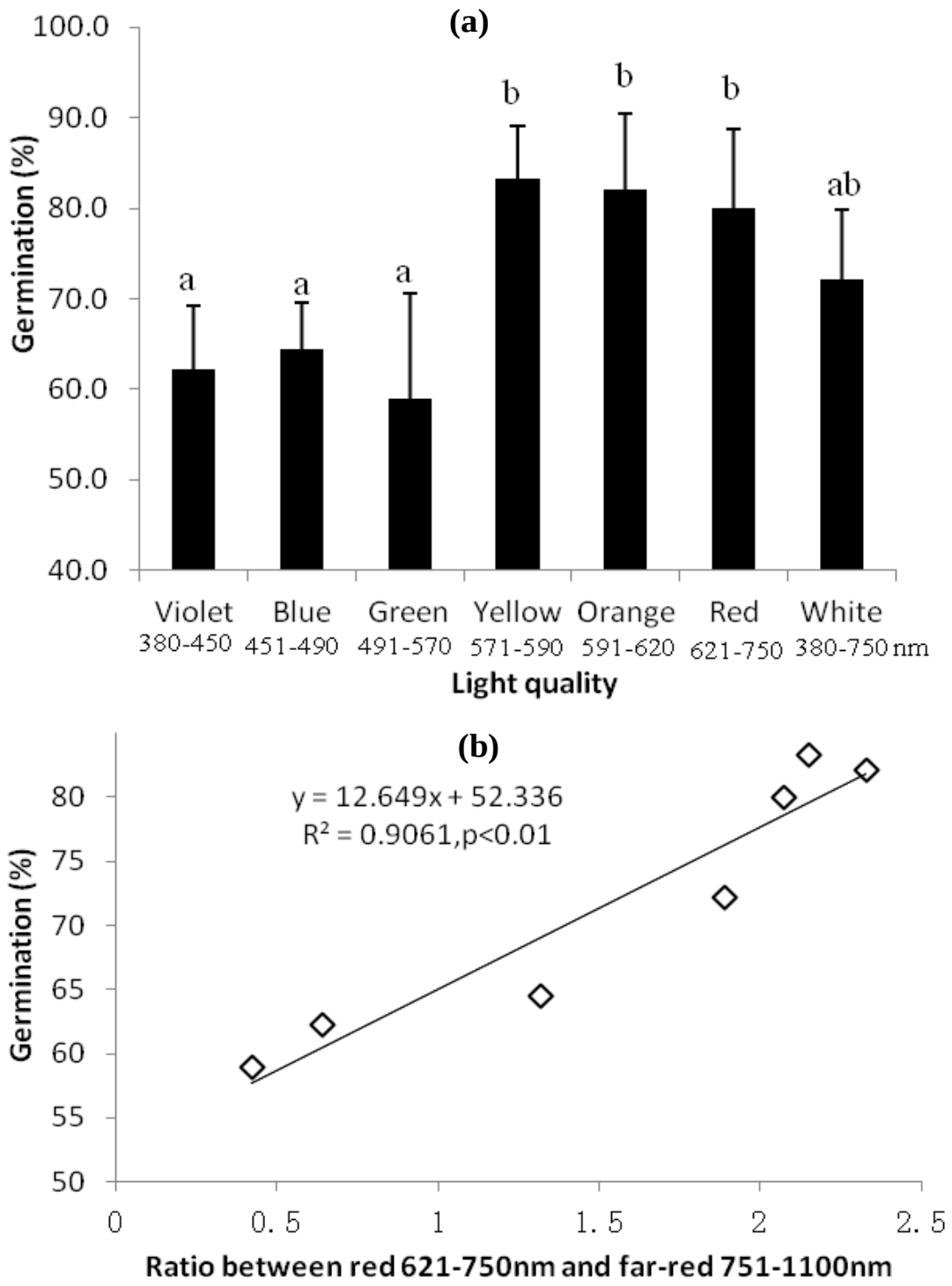

Figure 2. (a) Seed germination under different glass papers (upper) and (b) its correlation with the ratio between red and far-red light intensity (down) in *Ageratina adenophora*. In the upper figure, different letters indicate significant differences between different light ($p<0.05$), while the same letter indicates no significant differences was found ($p>0.05$). The vertical bars show the standard deviation of the raw data.

et al., 2011). High-intensity environmental disturbances (road and building con-struction, agricultural reclamation, and forest harvest) are still common in Southwest China (invasive area of this weed) because of high economic growth and high population density. Light-sensitive germination could be partially responsible for the

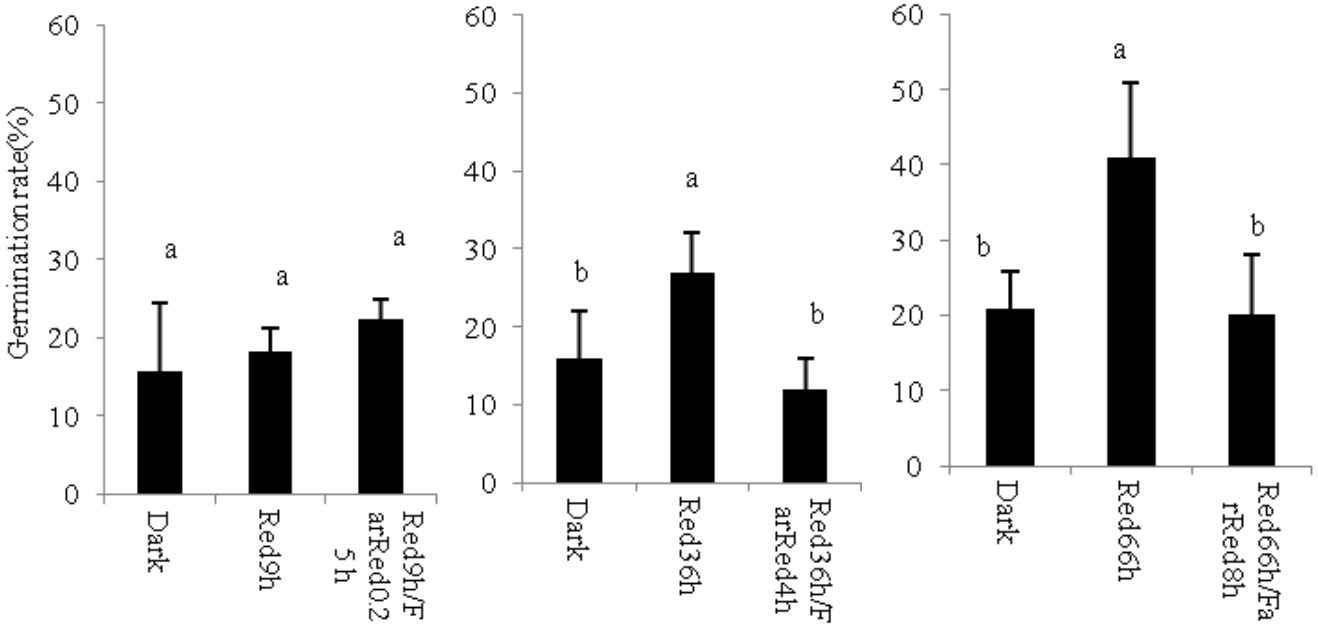

Figure 3. The influence of red light and far-red light exposure on the seed germination of *Ageratina adenophora*. Different letters indicate significant differences between different light ($p<0.05$), while the same letter indicates no significant differences was found ($p>0.05$). The vertical bars showed the standard deviation of the raw data.

rampant spread of Crofton weeds in these disturbed environments. Thus, a decrease in the disturbance of surface soil may be a method for controlling this weed.

As a common attribute of many seeds, other types of dormancy (physiological dormancy, thermodormancy and morphological dormancy, etc.) may be combined with photodormancy, and combined experiments of traditional dormancy-breaking methods and light may be used to discriminate different types of dormancy (Benech-Arnold et al., 2000). For example, fluctuating temperature treatments can stimulate or terminate light requirements, but this differs among species (Yang et al., 2003; Chen et al., 2008). PEG treatments can strengthen the effect of gibberellins (GA) on seed germination (Brocklehurst et al., 1982), and the effect of GA is generally accompanied by physiological dormancy and photodormancy (Yamaguchi and Kamiya, 2002). Nitrate may function somewhere in the membrane to break morphological dormancy (Benech-Arnold et al., 2000), and interactions between nitrate (KNO_3) and light have been detected in some species, such as *Sisymbrium officinale* (Hilhorst and Karssen, 1988) and *Arabidopsis thaliana* (Derkx and Karssen, 1994). SA pre-soaking treatment (0.01 $mmol \cdot L^{-1}$) can stimulate seed germination in *Iva xanthifolia* in the dark, similar to that under light (Xu et al., 2011).

In this study, no traditional methods (LT, SA, KNO_3, and PEG) interacted with the light-sensitive germination of this weed (Tables 1 and 2). Our findings suggest that the seed dormancy of Crofton weed requires light for its germination, and no other types of dormancy exist. By strict definition, seed dormancy is a condition of plant seeds that prevents germination under ideal conditions of temperature, moisture, and light. Thus, the lack of light (buried too deep for successful germination and growth) may just not be an ideal condition for Crofton weed. Usually, dormancy causes seeds to germinate at staggered rates, even when under naturally ideal conditions, to help ensure survival. For example, *A. adenophora* seeds will all germinate simultaneously when the germination conditions of light, temperature and moisture are met.

In conclusion, seeds of Crofton weed are dependent on light for germination. Very low light intensity (30 lux, <0.5% transmittance) resulted in germination rates that were 1.5 times higher than that in seeds exposed to darkness alone. Red light can break dormancy and induce germination, while far-red light was shown to terminate germination. This light-sensitive feature of seed germination may facilitate the fast germination of this weed from soil seed banks in disturbed soils of infrastructure construction, land reclamation and over-grazing pastures in China, and may finally favor its colonization in newly invaded habitats.

ACKNOWLEDGEMENTS

This study was financially supported by the national Natural Science Foundation of China (31100457, 31170575), and Basic Research Fund for National Universities from Ministry of Education of China (DL12DA03).

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