INFLUENCE OF LIGHT ON THE GERMINATION OF RAGWORT (*Senecio jacobaea* L., Asteraceae) SEEDS PREVIOUSLY STORED IN THE SOIL SEED BANK OF A PASTURE

INFLUÊNCIA DA LUZ NA GERMINAÇÃO DE SEMENTES DE TASNA (Senecio jacobaea L.) PREVIAMENTE ARMAZENADAS NO BANCO DE SEMENTES DO SOLO DE UMA PASTAGEM

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ABSTRACT

*An experiment was carried out to determine the effect of light on the germination of ragwort (**Senecio jacobaea** L.) seeds found in the soil seed bank of a cultivated perennial pasture of temperate species. Previous studies used seeds drawn from seed heads, which may not represent the actual physiological conditions of seeds found in the soil. Thus, soil containing ragwort seeds was extracted in the dark (150 soil samples, 2.6cm in diameter, 0-2cm deep) from a dairy pasture and left in plastic pots within two growth cabinets kept either in the dark (scotophase) or in constant light (photophase) conditions at 20°C. Seed germination, assessed through seedling emergence, was four times larger in the light than in the dark, totalling 55.6% and 13.9%, respectively. Of particular interest was the germination in the dark, which suggests that the active form of phytochrome is stable in ragwort seeds. These results are discussed on the basis of the knowledge of phytochrome activity. It is concluded that ragwort germination is positively affected by the presence of unfiltered light and it is argued that, in field conditions, germination would not take place in the dark.*

Key words: seedling, ecology, weed, dormancy, phytochrome.

INTRODUCTION

Ragwort (*tasna* in Portuguese; *hierba de santiago* in Spanish) is a non-perennial (frequently biennial) monocarpic dicotyledonous species, native to Europe, western Asia and northernmost African regions, but widely found in the USA, Canada, Australia, New Zealand and Argentina (SCHMIDL, 1972). It is a herbaceous pasture weed of economic importance (BOURDÔT et al., 1994), particularly because of its poisonous effects on cattle, horses, and occasionally on sheep, either if eaten fresh, in hay or in silage (HARPER, 1958), much like the various species of *Senecio* that are found in southern Brazil and Uruguay (MÉNDEZ, 1993; GAVA & BARROS, 1997; KARAM et al., 2002). Additionally, its presence in the pasture is detrimental to herbage production (HARPER, 1958) and utilisation by cattle (POPAY & THOMPSON, 1981).

The species is capable of overcoming a range of adverse conditions imposed by climate, herbivores and humans. It reproduces itself both vegetatively and reproductively, regrows after physical or chemical damage (even from root segments), produces a massive amount of seeds with different morphology and dispersal mechanisms, and remains dormant in the soil seed bank for several years (WARDLE, 1987). These remarkable adaptations allow ragwort to succeed in competitive environments, prone to moderate levels of disturbance.

Because ragwort is a non-perennial species, an effective control strategy is to avoid seed production and prevent seedling establishment. CAMERON (1935) suggested that seedling establishment would be minimised if a dense, vigorous and uniform sward was developed and maintained, which has been corroborated by a number of other studies (POOLE & CAIRNS, 1940; HARPER, 1958; SCHMIDL, 1972; POPAY, 1980; RAHMAN et al., 1993; BESKOW et al., 1994; BESKOW, 1995). However, tiller population density *per se* may not provide a reliable estimate of ragwort seedling density in the pasture (ARMSTRONG et al., 2001).

To understand ragwort seedling establishment, it is important to determine the factors that influence its germination. There have been suggestions that ragwort is light dependant, but confounding factors have not allowed a reliable conclusion.

PHUNG & POPAY (1981) demonstrated that ragwort seeds have their germination affected by different pasture heights. Seeds sown on bare plots produced more seedlings than under a pasture canopy. The red/far-red light ratio was higher on the bare ground surface so it was suggested that ragwort seed germination is regulated by light quality, although the effect of temperature fluctuations was not ruled out (bare ground exposed to the sun would be heated up more than partly shaded soil).

VAN DER MEIJDEN & VAN DER WAALS-KOOI (1979) covered ragwort seeds with sand layers of variable thickness and found less germination at greater depths. Light was thus thought to be the limiting factor, as its intensity would be reduced with increasing depth, but there was no control over temperature.

FERREIRA et al. (2001) tested the effect of light on the germination of three species of Senecio native to southern Brazil and Uruguay (*S. heterotrichius* DC., *S.oxyphyllus* DC., and *S. selloi* DC.) and found a positive response.

The studies above used seeds collected from seed heads and seeds found in the soil seed bank of pastures might not have the same light requirement as those from seed heads (CRESSWELL & GRIME, 1981; FENNER, 1991; OROZCO-SEGOVIA et al., 1993).

This paper reports an experiment designed to determine the germination behaviour of ragwort seeds drawn from the soil seed bank of a dairy pasture where the presence of light was set up as the only variable factor, so that differences in seed germination could be positively attributed to the presence or absence of light.

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MATERIAL AND METHODS

The natural seed bank of an organic dairy farm (Palmerston North, New Zealand) with a history of ragwort infestation was sampled with a soil corer of 2.6cm in diameter from a depth of 0-2cm. A total of 150 samples amounting to 5.5kg of soil were taken. The soil was a Manawatu sandy loam close to the Manawatu river with the following chemical characteristics: pH 5.7; Olsen P 10mg kg^{-1}; SO_4 4.5mg kg^{-1}; K 9.3$mmol_c$ kg^{-1}; Ca 78$mmol_c$ kg^{-1}; Mg 13.8$mmol_c$ kg^{-1}; cation exchange capacity 200$mmol_c$ kg^{-1}; organic matter 7.2%.

To avoid any reaction of seeds with light, soil collection was carried out during the night, in summer when the soil was very dry (January 1994, prior to seed rain), with average moisture content of 11% (±SE 1.4). The moisture was below the permanent wilting point of -1500 hPa, which was reached at 12%, as recorded in a parallel study (BESKOW, 1995).

Samples were bulked together and transported in a bag consisting of four layers of thick brown paper to provide a light proof container. Prior measurements with a Li-Cor LI-1000 light meter showed there was no light penetrating the bag.

The soil was processed in a darkroom at Massey University under a fluorescent light covered with three layers of green cellophane filter. The bulk sample was thoroughly homogenised by hand mixing and sieved through a 2mm mesh to remove coarse material like roots, stolons, etc. Its high sand content and its dryness allowed good homogenisation and sieving.

Sixty plastic pots were filled with pure sterile sand up to 1cm from the top. Forty of them received 60g (70cm^3) of the homogenised soil, resulting in a thin layer of 4-5mm on top of the sand. All pots were covered against light and taken to growth chambers at night. Lights outside the darkroom were turned off and pots transported under the light of a 6-volt torch, which had also been covered with three layers of green cellophane filter (a safe torch).

The experiment consisted of two treatments (light and dark) within two growth chambers set up at a constant 20°C and 80% relative humidity. One of the chambers was left with its white fluorescent lights turned on during the whole time, which constituted the light treatment. This chamber had an average photosynthetically active radiation (measured with a Li-190SA quantum sensor connected to a LI-1400 datalogger) of 570µmol s^{-1} m^{-2} (±SE 6.5) and a red/far-red light ratio of 1.3 (±SE 0.03). In the dark treatment, the chamber lights were kept off all the time.

Each growth chamber contained 20 pots of the dairy farm soil, placed into metal trays to absorb water from underneath. Another 20 pots, containing sand only, were placed in the same way into the illuminated chamber. Etiolated seedlings, found in the dark chamber, were transplanted to these pots to acquire the minimum characteristics needed for identification.

Trays in both chambers were refilled periodically with water. The dark chamber was always opened only at night with the room lights turned off and the operations were illuminated with the safe torch. The dark chamber was sealed to make sure it would not be opened inadvertently.

Emerged seedlings in the light treatment were mapped and dated at weekly intervals and followed through until they could be identified with certainty. After being identified, they were cut at ground level and removed. Seedlings found in the dark chamber were transplanted to the sand pots in the lighted chamber, mapped and had their transplanting date recorded as well. Their identification and removal followed the same procedure as for the seedlings in the light treatment.

The soil layer in each pot of both treatments was stirred thoroughly on the third week of germination to expose seeds near the bottom of the layer to surface conditions. The experiment continued until seedling emergence ceased for two weeks. Top layers of all pots were stirred again and the pots were taken to a glasshouse to encourage germination of the dark treatment seeds and to determine whether further emergence in the light treatment pots would occur in the glasshouse. Seedling identification, mapping, counting and removal were carried out as in the chambers. The pots remained in the glasshouse for three weeks.

Because germination could not be assessed directly, emergence of ragwort seedlings was used to determine germination behaviour. This was obtained in the following way: $E = (E_{chamber} / E_{total})x100$; where E is the percentage of ragwort seedling emergence; $E_{chamber}$ is the number of ragwort seedlings obtained in the chamber; E_{total} is the total number of ragwort seedlings emerged, i.e. $E_{chamber}$ plus the number of ragwort seedlings that emerged in the glasshouse.

To compare the final accumulated emergences a two-sample *t*-test was performed using SAS 6.1 TTEST procedure for unequal variances. Also, the means of treatment E_{total} were tested for location to determine whether the soil had been well homogenised so that a similar number of seeds were able to produce a visible seedling under the conditions imposed for either treatment. This was achieved through the same *t*-test procedure mentioned above. Non-linear regressions of percentage seedling emergence in time (weeks) were fitted using the SAS NLIN procedure.

RESULTS

Seed germination of the dark and light treatments took place within three and five weeks, respectively (Figure 1).

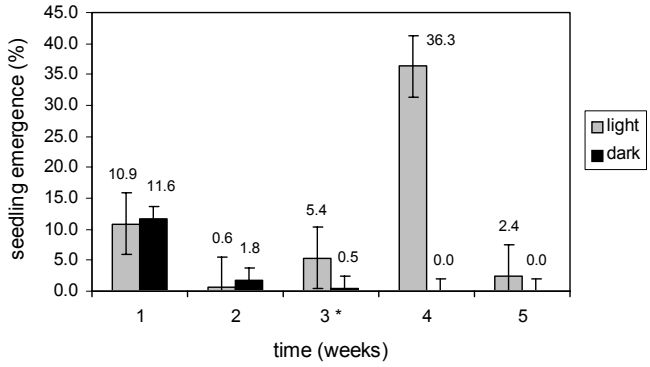

Figure 1 – Weekly emergence of ragwort (*Senecio jacobaea* L.) seedlings from soil kept constantly in light or dark conditions, at 20°C and 80% relative humidity (asterisk shows when soil was stirred). Palmerston North, 1994.

Emergence was initially very similar in both treatments, but the overall pattern was markedly different. The mean seedling emergence of the dark treatment decreased steadily in time ($Y=11.94X^{-2.84}$ for X=1 to 3; $r^2=0.88$; P<0.001), while the light treatment decreased to the second week as in the dark treatment, but picked up exponentially thereafter, reaching its peak at the end of the fourth week ($Y=0.01e^{2.05X}$ for X=2 to 4; $r^2=0.79$; P<0.01) to then decrease sharply. Additionally, stirring of the soil resulted in a marked increase in seedling

emergence in the light treatment, but no response in the dark one. Curiously, seedling emergence was reduced by 94% in both treatments by the second week and again by a similar amount (93%) by the fifth week in the light treatment (one week after disturbance). No more seedlings emerged after five weeks of exposure to light in any of the treatments.

As a result of the pattern described above, the light treatment accumulated mean seedling emergence reached 55.6%, which was four times larger (P<0.0001) than the dark treatment mean (13.9%), as shown in Figure 2.

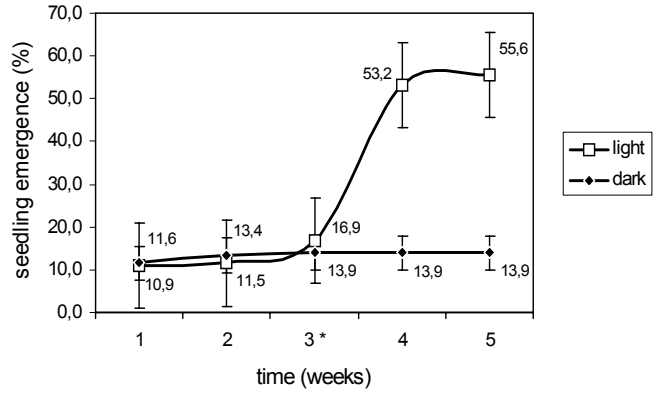

Figure 2 – Cumulative emergence of ragwort (*Senecio jacobaea* L.) seedlings from soil kept constantly in light or dark, at 20°C and 80% relative humidity (asterisk shows when soil was stirred). Palmerston North, 1994.

The calculated time taken to achieve 50% emergence was 4 and 26 days for the dark and light treatments, respectively.

The glasshouse seedling emergence coming from the light treatment accounted for 44.4% of its total emergence (E_{total}), whereas in the dark treatment, glasshouse emergence accounted for 86.2% of E_{total}.

No significant difference for E_{total} was found between light and dark treatments (9.1 ±0.96 and 8.2 ±0.63 seedlings per pot, respectively), confirming that the soil homogenisation was effective.

DISCUSSION

The significant differences between treatments for seedling emergence clearly indicate that ragwort seeds were responsive to light, a physiological mechanism strongly associated with phytochrome. To assist with the interpretation of the results, key aspects of the role of phytochrome in the germination of seeds are summarised below (BORTHWICK et al., 1954; BORTHWICK, 1972; BRADBEER, 1988; SALISBURY & ROSS, 1992):

(i) All plant organs, including seeds, contain phytochrome (P).
(ii) There are two types of P: Type 1 and Type 2. The type found in seeds is Type 2. It is more stable than Type 1 and, unlike Type 1, it does not disappear in darkness by destruction and reversion.
(iii) P (either Type 1 or 2) can exist as P_r or P_{fr} forms. P_r is the blue, inactive form of the pigment and is the form in which P is synthesized. It absorbs red light thus being transformed into P_{fr}, the olive green and active form that absorbs far-red light.
(iv) The actual physiological action of P_{fr} is still controversial, but its participation as a trigger of seed germination is almost universally accepted. There is a need for a minimum amount of P_{fr} for seed germination to be promoted. This critical amount is called φ, obtained by dividing the amount of P_{fr} by the total P (total P = P_{fr} + P_r).
(v) Both P forms are interconvertible. The ratio of red to far-red light (R:FR) determines which form is more abundantly formed. Even very low irradiances with red and far-red light are adequate to establish a photoequilibrium between P_r and P_{fr} because both absorb these wavelengths very effectively.
(vi) In seed germination, for instance, responses caused by red light are nullified by an immediate exposure to far-red light and vice versa.
(vii) The sunlight R:FR is about 1.1 to 1.2. P_r absorbs red light more effectively than P_{fr} absorbs far-red light. Consequently P_r is converted more effectively to P_{fr} than vice-versa. For this reason the sunlight acts primarily as a red source that forms more P_{fr} than P_r.
(viii) Photodormancy is broken by light only when seeds are partially or fully imbibed (seeds that require light for germination are said to be photodormant). Only then is P_r sufficiently hydrated to be converted into P_{fr}.
(ix) In seeds that survive many years in the soil, P_r is stable and only awaits the proper combination of moisture, light, and temperature to be converted into P_{fr} and induce germination.
(x) Some seeds (e.g. Grand Rapids lettuce) when imbibed, exposed to light to form P_{fr}, and then immediately dehydrated, will germinate in darkness upon remoistening for up to a year, which shows that P_{fr}, like P_r, is stable in dry seeds for long periods.

SALISBURY & ROSS (1992) argued that seed requirement for light will depend on how much P_{fr} is produced in it during ripening on the mother plant. However, based on the points outlined above, it is evident that the light requirement actually depends on how much P_{fr} is produced at any imbibed state until dehydration, be it in the mother plant or in the soil seed bank.

Maternal conditions experienced by seeds during their development can be important in determining whether they will require light to germinate (CRESSWELL & GRIME, 1981; FENNER, 1991; OROZCO-SEGOVIA et al., 1993), at least for seeds harvested from seed heads. However, the maternal factor becomes irrelevant in the present experiment because the seeds had been in the soil for at least one year, where they were subjected to very different and variable conditions of light, moisture and temperature. Maternal conditions would only be determinant in this case if they had been fully covered by the pasture canopy, by a thick soil layer or by litter immediately after shedding and remained that way all the time, but is very unlikely. Thus, maternal conditions do not seem to provide an explanation for the results obtained in this experiment.

The difference in emergence between the light and the dark treatments appears to have resulted from conditions experienced by the seeds during the soil seed bank phase. Seeds were collected from a depth of 0-2cm, so the ones closer to the soil surface would have received a higher R:FR, thus containing a higher φ (Item iv, described earlier) than those deeper in the soil. Therefore 13.9% (the percentage emergence obtained in the dark treatment) could be a percentage of seeds exposed to higher R:FR in the field during its last imbibition. Their P_{fr} would be at a φ level capable of triggering off germination, i.e. they did not need further P_r/P_{fr} photoconversion when they were collected. Their germination

would have been prevented in the field only by lack of moisture (it should be noted that this proportion of seeds might not be applicable to other pastures, as it will depend on particular vegetation cover, seed distribution in the soil profile, etc.).

As mentioned earlier, Type-2 P does not undergo dark reversion or destruction, at least for one year (SALISBURY & ROSS, 1992). Therefore, as far as P_{fr} is concerned, seeds in the dark treatment had conditions to germinate for longer than three weeks. Therefore, it can be assumed that their emergence stopped when all seeds containing a minimum φ had germinated.

The green light torch used in the dark chamber could be suspected as a possible explanation of the results. SALISBURY & ROSS (1992) stated that green safe lights have to provide low irradiance and advised that it should be tested before being used, while GRIME & JARVIS (1975) and BLOM (1978) implied that some species are more sensitive to green light than others. However, evidence suggests that our torch was a safe light source. Firstly, a large proportion of the seedlings occurred in the first count when the chamber had not even been opened. Secondly, emergence steadily decreased thereafter. If the green light had stimulated germination there should have been some reaction after the disturbance, when more photodormant seeds were brought up (as was observed in the light treatment).

Another possibility could be that the darkroom green light triggered germination. However, seeds were very dry when exposed to the darkroom green light, so the P_r/P_{fr} photoconversion could not happen (Item viii, above). BRADBEER (1988) stated that some air-dry seeds can show a response to light, but the statement was not substantiated and the author was apparently referring to white light or any light containing red wavelength rather than green light.

As disturbance did not stimulate any emergence in the dark treatment, the post-disturbance emergence in the illuminated chamber can be entirely attributed to light. Had the dark treatment seeds reacted to disturbance, other factors might have been involved (e.g. better aeration), but it was not the case.

Because seeds had the same source and were thoroughly homogenised, the 55.6% of seeds which emerged in the light treatment would consist of 13.9% (this is the dark emergence figure) which came from the field with a minimum φ, plus 41.7% (i.e. 55.6 minus 13.9%) which had their φ augmented by exposure to the red photons from the white light. This P_r/P_{fr} photoconversion took three weeks to become apparent, when more seedlings started to appear in the light treatment than in the dark treatment (prior to disturbance).

The large proportion of seedlings emerging in pots coming from the light treatment during the glasshouse phase was unexpected. As the main objective was stimulating germination in the dark treatment pots, glasshouse temperature was not monitored. However, the glasshouse light conditions were assessed and showed a R:FR of 1.5 (±SE 0.01) on a cloudy day and 1.8 (±SE 0.09) on a sunny day. These values are similar to the R:FR found in the growth chamber (1.3), thus would not seem to account for the large emergence observed in the glasshouse. Glasshouse photosynthetically active radiation varied from 106 (±SE 2.9) μmol s^{-1} m^{-2} to 1197 (±SE 42.5) μmol s^{-1} m^{-2} for cloudy and sunny days, respectively. As discussed earlier, the photoconversion of P is a low fluency process (Item v), which seems to rule out the possibility that a higher irradiance in the glasshouse would have been more favourable to germination than the irradiance in the growth chamber.

There could also have been a partial inhibition of germination caused by the constant, hence rather artificial, light conditions in the light treatment chamber contrasting with a closer to normal day/night cycle in the glasshouse. However, the most likely cause was probably the difference in temperature conditions. In the growth chambers seeds were at a constant 20°C, but in the glasshouse this would have varied greatly. The nearby AgResearch Grasslands meteorological station recorded the following variation in air temperature during the time pots were in the unheated glasshouse at Massey University: minimum 4.6°C, mean minimum 9.5°C, maximum 25.4°C, mean maximum 20.4°C. Because the glasshouse was not set to maintain any given temperature its pattern of variation was probably comparable to the station, perhaps achieving higher temperatures during the day. Thus the glasshouse range of temperature was around 10°C, which would be very different from the constant 20°C in the growth chambers.

Some studies found ragwort seeds germinate better when kept at alternating temperatures (SCHMIDL, 1972; VAN DER MEIJDEN & VAN DER WAALS-KOOI, 1979). However these studies were all conducted with seeds collected directly from seed heads and none conclusively showed that alternating temperatures were the actual trigger. Nevertheless, there is strong experimental evidence derived from other species (including seeds from soil banks) that alternating temperatures can even substitute for light as a trigger for germination of light sensitive seeds (THOMPSON et al., 1977). Further studies are required to determine the role of temperature on the germination of ragwort seeds found in the soil seed bank.

Finally, it should be noted that the results of this experiment do not suggest that a proportion of ragwort seeds (in this case 13.9%) can germinate in the field under a closed pasture canopy. The 13.9% figure only showed that the active form of phytochrome found in ragwort seeds is stable in the dark. In the pasture, seeds would only be in complete darkness if they were buried deeply, but seeds of any species remain dormant under such conditions. Seeds that are close to or on the soil surface receive either direct light (if a gap is present) or light filtered by the canopy and, as discussed earlier, filtered light inhibits germination of light sensitive seeds.

CONCLUSION

The germination of ragwort seeds drawn from the soil seed bank of a pasture was strongly and positively affected by the incidence of unfiltered light over imbibed seeds. However, 13.9% of the seeds did germinate in the dark at constant temperature. It was suggested that seeds acquired a minimum proportion of the active form of phytochrome by prior exposure to unfiltered light while imbibed. Temperature seems to play an important role in ragwort germination as well, but further studies are required to clarify this.

RESUMO

*Este trabalho relata um experimento desenvolvido para determinar o efeito da luz na germinação de sementes de tasna (**Senecio jacobaea** L.) extraídas do banco de sementes de uma pastagem perene cultivada de espécies temperadas. Estudos prévios utilizaram sementes extraídas de inflorescências, o que pode não representar as reais condições fisiológicas das sementes estocadas no solo. Assim, o solo de uma pastagem contendo sementes de tasna foi coletado no escuro (150 amostras, 2,6cm em diâmetro, 0-2cm de profundidade) e disposto em potes dentro de duas câmaras de crescimento, uma com luzes ligadas (fotofase) e outra desligadas (escotofase), ambas mantidas a 20°C. A germinação, avaliada através*

da emergência de plântulas, foi quatro vezes maior na luz do que no escuro, totalizando 55,6% e 13,9%, respectivamente. De particular interesse foi a germinação no escuro, o que indica que a forma ativa do fitocromo é estável nas sementes de tasna. A discussão destes resultados baseia-se no conhecimento sobre da atividade do fitocromo. Conclue-se que a germinação da tasna é positivamente afetada pela presença de luz direta e sugere-se que, em condições de campo, provavelmente não ocorra germinação na ausência de luz.

Palavras-chave: plântula, ecologia, invasora, dormência, fitocromo.

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