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Effect of temperature and moisture on the dormancy and activation pattern of *Oxalis latifolia* bulbs

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Abstract

The effect of temperature and moisture on the activation of two forms of *Oxalis latifolia* Kunth bulbs —common and Cornwall— was studied. Gaining knowledge about the conditions needed for their activation may contribute to the control of this weed. Bulbs were kept in a refrigerator at +4°C for 13, 20, 27, 41, 48 and 55 days. At each sampling date, three sets of 30 bulbs of both forms were transferred from 4°C to 21°C; 15 were kept under dry conditions and 15 under wet conditions. For both forms, and under both wet and dry conditions, activation occurred over a prolonged period of time. Dry bulbs were activated earlier than the wet bulbs, and the common form was activated earlier than the Cornwall form. Two different patterns of activation behavior were observed: dry bulbs of the common form usually followed a logarithmic activation pattern, while those subjected to the wet treatment were activated in a linear fashion. Bulbs of the Cornwall form were activated exponentially in the majority of cases. The mean time required for activation after cold storage was constant in the common form, while in the Cornwall form, activation was faster the longer the period of cold storage the bulbs had been previously subject to.

Additional key words: biology of weeds, cold, Cornwall form, fishtail oxalis, humidity, warmth.

Resumen

Efecto de la temperatura y de la humedad sobre la dormancia y el patrón de activación de bulbos de *Oxalis latifolia*

Con objeto de buscar información para un mejor control de *Oxalis latifolia* Kunth, se ha estudiado el efecto que presentan la temperatura y la humedad sobre la activación de sus bulbos, tanto en la forma común como en la forma Cornwall de la misma. Los bulbos de la mala hierba se mantuvieron en un refrigerador a +4°C durante 13, 20, 27, 41, 48 y 55 días. Se sacaron tres grupos de 30 bulbos de cada forma en cada fecha de muestreo y se colocaron a 21°C; 15 de ellos se mantuvieron en condiciones de sequía —no se regaron— y otros 15 en condiciones de humedad —añadiendo el agua necesaria—. Los resultados muestran que la activación ocurre durante un período prolongado de tiempo en ambas formas, tanto en seco como en húmedo. También se observó que los bulbos secos se activaron antes que los húmedos y los de la forma común antes que los Cornwall. Se observaron dos patrones de activación: los bulbos secos de la forma común generalmente presentaron una activación que sigue un patrón logarítmico, mientras que sus bulbos humedecidos mostraron una tendencia linear; los bulbos Cornwall se activaron con una tendencia exponencial en la mayoría de los casos. El tiempo medio requerido para la activación después del almacenamiento en frío fue constante en la forma común, sin embargo la activación de Cornwall fue más rápida cuanto más tiempo permanecieron almacenados en frío.

Palabras clave adicionales: biología de malas hierbas, forma Cornwall, frío, humedad, templado, trebolillo de huerta.

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Introduction[1]

Oxalis latifolia Kunth, commonly known as fishtail oxalis, is a noxious weed of several crops in northern Spain. Its control is extremely difficult as it produces hundreds of small underground bulbs that are easily dispersed by any soil movement, such as plough and tillage. In conventional maize production, the first *O. latifolia* individuals appear just before, during, and even after emergence of the crop (Royo, 2004). The emerging bulbs compete with the crop seedlings (Church and Henson, 1969) making the application of effective herbicides (glyphosate and oxadiazon) complicated or nearly impossible (De Liñán, 1999). Early defoliation has been suggested as an alternative control strategy against *O. latifolia* (Parker, 1966; Chawdhry and Sagar, 1974a) since it weakens the bulbs. Given that emergence follows activation (protrusion of roots at the base of the bulbs) (Royo, 2004), understanding the mechanisms and the factors that induce activation of the bulbs after their dormant period would be extremely useful in order to develop better control tactics for this weed.

In tropical climates, *O. latifolia* loses its above ground organs during the dry season (Chawdhry, 1974). These then reappear with the onset of the rainy season (Chawdhry, 1974; Royo, 2004). In temperate and Mediterranean climates, however, the above ground organs disappear during the cold and wet autumn conditions, and reappear in late spring, when temperatures increase (Jackson, 1960; Holm *et al.,* 1997; Royo, 2004). Given these contrasting responses, further consideration is needed on the main climatic factors that influence the activation of bulbs. For example, in temperate and Mediterranean climates, rainfall is high during the spring, and therefore, bulb activation actually occurs under moist conditions. This suggests that moisture may be a less important activation factor than temperature (Royo, 2004).

There is a narrow temperature window for storage of *Oxalis* bulbs: subzero temperatures kill all the bulbs (Chawdhry and Sagar, 1974b; Jehlik, 1995; Holm *et al*., 1997; Royo and López, 2004) while temperatures between 2-5°C keep them in a dormant state (Chawdhry and Sagar, 1974b). A similar temperature interval is used for storage of other bulb species, such as *Nerine bowdenii* (Groen and Kok, 1997). Jackson (1960) and Holm *et al*. (1997) indicated that activation takes place when soil temperatures reach 15°C. In the distribution range of this weed, mean monthly winter temperatures usually do not drop below 0°C, nor are spring temperatures very high (around 18°C) when the first leaves appear above the soil surface. Using all this information we designed an experiment to test the effect that different lengths of cold storage (4°C), followed by dry and wet storage at warmer temperatures (21°C), would have on the activation of the bulbs. Periodical observations of protruding roots were used as the criterion to evaluate activation.

The two forms of *O. latifolia* that have been described (Young, 1958) are known as the common and the Cornwall forms (López and Royo, 2002). The common form is generally found in slightly to moderately disturbed ecosystems while Cornwall form is usually found in more disturbed ones (López and Royo, 2003).

Field observations show that in northern Spain (A. Royo, unpublished observation) and in the central Ebro Valley (C. Zaragoza, personal communication), the Cornwall form normally emerges earlier in the season than the common form. This leads us to believe that there may be differences in the timing and activation mechanisms between both forms.

This study seeks to determine the activation pattern of both the common and Cornwall forms of *O. latifolia* under dry and wet storage conditions, as well as the roles that temperature and moisture play in the activation of *O. latifolia* bulbs.

Material and Methods

Both forms of *O. latifolia* were collected on November 2002 from a farmland, 7 km East from San Sebastian (northern Spain). Even though both forms may coexist in the same crop, the common form bulbs were collected mainly from a maize field where they were more abundant, while the Cornwall bulbs were obtained from a nearby orchard. Once they were washed with tap water and dried with blotting paper, 540 dormant bulbs of each form were selected in terms of uniformity (0.150-0.250 g), and subsequently stored in a refrigerator at 4°C. After 13, 20, 27, 41, 48 and 55 days of cold storage, three 15-bulb replicates of each form were transferred to 21°C. Each replicate of 15 bulbs was

[1] Abbreviations used: DC_{50} (days required to activate 50% of the bulbs), MD (common dry), MW (common wet), ND_i (average number of days at 21°C required to activate one bulb), RD (Cornwall dry), RW (Cornwall wet).

placed in a soilless culture, i.e., a plastic bowl with filter paper on the bottom, and the bowls were stored in dark laboratory conditions. In three of the bowls, the filter paper was moistened by adding approximately 20 mL of tap water (conductivity 350-450 µS cm^{-1}, pH 7.35-7.6) every three days, while the filter paper in the other three bowls remained dry. This resulted in 12 treatments (6 distinct cold periods, followed by either wet or dry treatments under growth-inducing temperatures) with three replications for each *O. latifolia* form.

Observations of the number of activated bulbs (bulbs with protruding roots of 1 mm in length) were carried out weekly for a total of 15 weeks. After this period, bulbs that did not show any activity were cut open to verify their viability. Bulbs containing live tissues were deemed viable and those rotten or with dry scales were not.

Linear, logarithmic, polynomial, potential and exponential models were fitted to the cumulative activation (in percentage) over time to determine which pattern fitted best. The fit of the models was evaluated using the percentage variation explained by the models (R^2). Two variables were analyzed in order to identify differences between storage treatments: (1) the number of days required to activate 50% of the bulbs (DC_{50}), and (2) the average number of days at 21°C required to activate one bulb (ND_i). As there were some dead bulbs, the percentage of activation was calculated using only the viable bulbs. The percentage of dormant bulbs was calculated based on the number of bulbs that did not produce roots at any time during the trial but were considered alive at dissection. For both variables, DC_{50} and ND_i, a regression analysis was conducted with time (number of days) as the independent variable. In the case of the first variable, DC_{50}, analysis was followed by Wilcoxon comparison (Field, 2000) to compare bulbs stored under dry and moist conditions, and to compare bulbs of the two forms. Since the percentages of activated and dormant bulbs are inversely proportional after the dead ones have been deducted, only the activated bulbs were analyzed. The second variable, the delay in activation, was transformed before the analysis. The number of days it took a bulb to produce roots was considered as an individual bulb count. For example, if after transfer to 21°C, it took a bulb seven days to produce roots, its value was 7, and if it took three weeks, its value was 21. The averages of these values were square root ($\sqrt{x}$) transformed to maintain normality and subjected to regression analysis, using form, humidity treatment, and duration of cold storage as factors. In addition, a three way ANOVA was applied to investigate interactions between these factors.

The regressions suggested a different pattern of activation for the common and the Cornwall forms, and the ANOVA showed a significant interaction between bulb forms and the duration of cold storage. Therefore, the data set was split and a separate two way ANOVA was applied to the common and Cornwall form, using the duration of cold storage and dry/wet incubation as factors.

Results

Out of the 540 bulbs, 28 common (5.2%) and 33 Cornwall (6.1%) bulbs were rotten or completely dead when tested for viability. This mortality could have been due to occasional frosts in the field before collecting the bulbs.

No activation of bulbs occurred at 4°C, so this temperature effectively maintained dormancy in storage during the two months that the experiment lasted. Bulbs became activated 2-3 weeks after they had been transferred to a higher temperature (21°C). The presence of moisture after transferral to higher temperatures seemed to delay bulb activation. After 15 weeks of exposure to 21°C, there were still 35 common (6.5%) and 55 Cornwall (10.2%) dormant bulbs.

Bulbs kept under wet conditions were able to develop elongated roots and shoots, while those kept under dry conditions showed a less prominent growth: apart from tiny roots, small shoots developed but no elongation occurred.

Polynomial models provided the best description of the activation patterns observed. These models explained a minimum of 89% of the variation in all treatments (Table 1). Other models provided an almost equal fit with high R^2 values. Eleven models had R^2 values higher than 0.90 and nine had values between 0.80 and 0.90. The lowest R^2 value was 0.5999. Three distinctive activation patterns —associated with the different storage treatments— could be distinguished: 1) common dry bulbs, for which the activation followed a logarithmic, linear or sigmoid pattern; 2) common wet bulbs, for which the activation followed a linear pattern; and 3) Cornwall wet and dry bulbs, for which the activation followed an exponential pattern (Table 1, Fig. 1).

With regards to the DC_{50}, under dry conditions, there was no relationship between the duration of the cold storage and the activation of the common form bulbs

Table 1. Activation pattern in common dry (MD), common wet (MW), Cornwall dry (RD), and Cornwall wet (RW) bulbs. In bold, activation tendency and its R^2 value

Days at 4°C	MD		MW		RD		RW	
	Pattern	R^2	Pattern	R^2	Pattern	R^2	Pattern	R^2
13	Polyn	0.9587	Polyn	0.9648	Polyn	0.9916	Polyn	0.8954
	Log	**0.9338**	**Lin**	**0.9596**	**Expo**	**0.9045**	**Expo**	**0.8691**
20	Polyn	0.9677	Polyn	0.9268	Polyn	0.9791	Polyn	0.9738
	Log	**0.9341**	**Pot**	**0.9053**	**Expo**	**0.8574**	**Expo**	**0.5999**
27	Polyn	0.9324	Polyn	0.9397	Polyn	0.9898	Polyn	0.9803
	Lin	**0.9307**	**Lin**	**0.9348**	**Expo**	**0.8483**	**Expo**	**0.6365**
41	Polyn	0.9428	Polyn	0.9805	Polyn	0.9923	Polyn	0.9944
	Sig	**0.8743**	**Lin**	**0.9087**	**Pot**	**0.9342**	**Expo**	**0.8149**
48	Polyn	0.9584	Polyn	0.9907	Polyn	0.9621	Polyn	0.9943
	Lin	**0.9314**	**Lin**	**0.8817**	**Expo**	**0.9312**	**Expo**	**0.7433**
55	Polyn	0.9436	Polyn	0.9875	Polyn	0.9607	Polyn	0.9753
	Log	**0.8897**	**Expo**	**0.7761**	**Expo**	**0.8510**	**Expo**	**0.8565**

Expo. exponential: Ln, linear; Log, logarithmic; Polyn, polynomial; Pot, potential; Sig, sigmoid.

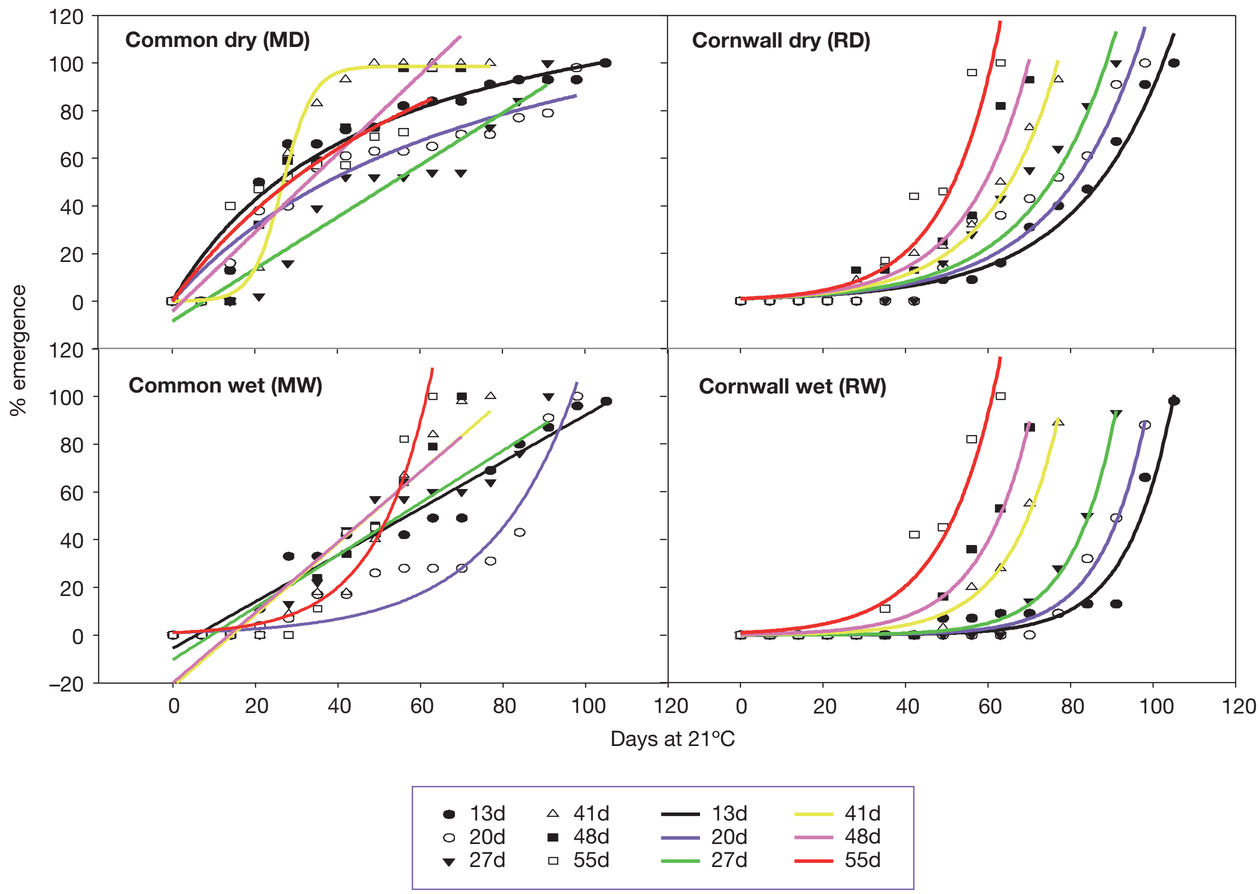

Figure 1. Emergence pattern curves for common dry (above left), common wet (below left), Cornwall dry (above right) and Cornwall wet (below right). 13d, 20d, 27d, 41d, 48d, and 55d: symbols and lines for 13, 20, 27, 41, 48 and 55 day-storage at 4°C, respectively.

Table 2. Mean number of days for 50% of activation; MD, common dry; MW, common wet; RD, Cornwall dry; RW, Cornwall wet. Regression results are also provided, as well as their R^2 values

Days stored at 4°C	MD	MW	RD	RW
13	20.9	70.4	85.2	95.9
20	32.4	85.1	75.3	91.2
27	40.9	67.9	67.2	84.0
41	26.2	51.6	62.9	68.7
48	25.7	50.4	58.1	61.7
55	25.6	51.2	49.6	49.9
Regression	n.s.	*	**	**
R^2	0.0256	0.7256	0.9554	0.9924

n.s.: non-significant. * Significant at $P < 0.05$. ** Significant at $P < 0.01$.

(Table 2). However, a relationship did appear under moist conditions for this form. On the contrary, there was a strong and negative relationship between the Cornwall form bulbs and the duration of cold storage, regardless of the moisture condition (R^2 was 0.9554 and 0.9924 for dry and wet, respectively). In the Cornwall form, the percentage of activated bulbs increased with the length of the period of cold storage (Table 2).

Fifty percent activation was reached earlier in the common bulbs than in the Cornwall bulbs (Table 3, Fig. 2). Also, 50% activation was reached earlier in dry bulbs than in wet ones, irrespective of the form of the bulb (Table 3, Fig. 2).

Results for the mean number of days required for activation (ND_i) were similar to those of DC_{50}. The common form showed a significant regression with cold storage, together with very low R^2 values (Table 3). On the other hand, the Cornwall form had a significant regression and higher R^2 values (0.380 and 0.729 respectively). Differences between dry and wet bulbs and between forms also remained significant, with the dry and common forms being activated earlier than moist and Cornwall ones (Table 3).

Discussion

None of the bulbs developed roots when stored continuously at 4°C, even if the duration of cold storage was short. This leads us to believe that an increase in temperature following the cold storage is essential for activation. *Oxalis latifolia* is included in the group of evergreen tropical geophytes that are forced into dormancy (Borochov *et al.,* 1997). This classification is in accordance with the tropical origin of the species, its lack of tolerance to subzero temperatures (Chawdhry and Sagar, 1974b; Jehlik, 1995; Holm *et al*., 1997; Royo and López, 2004), and its seasonal growth cycle (Chawdhry, 1974; Royo, 2004). Chawdhry (1974) explains that, in tropical climates, *O. latifolia* loses its foliage during severe droughts, while in temperate and Mediterranean climates leaves are lost during the autumn (Jackson, 1960; Royo, 2004). Anderson *et al.* (2001), when referring to *Euphorbia esula*, said that

Table 3. Comparison with the number of days for 50% (DC_{50}) of activation between dry and wet and forms (Wilcoxon). Linear regression of ND_i (mean number of days for activation) for each treatment group; MD, common dry; MW, common wet; RD, Cornwall dry; RW, Cornwall wet. Significances between activation condition, dry/moisten and comparison between forms (ANOVA)

DC_{50} (ANOVA)	Common	Cornwall	Dry	Wet
Comparison	Dry/wet	Dry/wet	Common/Cornwall	Common/Cornwall
Significance	**	*	**	*
Probability	0.0014	0.0237	0.0015	0.0220
ND_i (regression)	**MD**	**MW**	**RD**	**RW**
Significance	*	**	**	**
R^2	0.022	0.054	0.380	0.729
Coefficient	—	—	–6.7112	–9.2893
ND_i (ANOVA)	**Dry/wet in common**	**Dry/wet in Cornwall**	**Common/Cornwall**	
Significance	**[a]	** [a]	** [b]	

n.s.: non-significant. * Significant at $P < 0.05$. ** Significant at $P < 0.01$. [a] Two way ANOVA. [b] One way ANOVA.

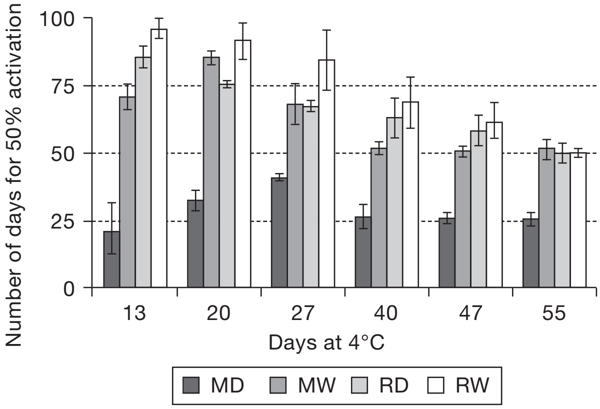

Figure 2. Mean number of days required to activate 50% of the bulbs of each form and incubation condition. Results are shown by the length of storage at 4°C. MD: common dry. MW: common wet. RD: Cornwall dry. RW: Cornwal wet.

this weed appears to develop endodormancy but eventually shifts to a state of ecodormancy for overwintering. Being tropical in origin, *O. latifolia* is accustomed to constant temperatures throughout the year. Therefore, it is presumable that an environmental signal such as the decrease of temperature in autumn may induce dormancy. On the other hand, some bulbs remained dormant at the end of the experiment. Thus, contrary to *E. esula*, in temperate and Mediterranean climates, *O. latifolia* may have developed an ecodormancy that could turn into endodormancy for overwintering.

In this study, constant moisture, a common feature of spring in temperate and Mediterranean climates, delayed activation. This could be because humidity may have decreased the temperature of the bulbs. In northern Spain, the delay in activation caused by soil moisture results in an almost simultaneous emergence of maize and the common form of *Oxalis* (Royo, 2004). In the common form bulbs, moisture also provoked a change in the activation pattern from logarithmic to linear. A logarithmic pattern means that the highest amount of activation occurred early on, while a linear pattern refers to a constant amount of activation throughout the entire storage period. Nevertheless, there was no significant relationship between activation and the duration of cold storage (regression analysis) for the common form bulbs, which means that low temperatures keep the bulbs from activating and that, regardless of the duration of cold storage, it will always take the bulbs approximately the same amount of time to activate their roots once they are under optimal conditions. On the other hand, in the Cornwall form bulbs, moisture did not change the activation pattern, but there is a negative relationship between activation and the duration of cold storage. That is, the longer the period of cold storage, the faster the activation of the bulbs. This also happens in other bulbs species like *Lilium* (Abreu *et al*., 2003; Langens-Gerrits *et al*., 2003). The ANOVA analysis yields similar results in that the interaction between the duration of cold storage and the bulb form was significant.

It was surprising to find that, under laboratory conditions, the common form bulbs were activated before the Cornwall form bulbs, because just the opposite happens in nature. However, after 55 days of cold storage followed by constant moisture conditions, the DC_{50} was equal in both *O. latifolia* forms. This trend could be the reason for the field observations, but trials with longer periods of cold storage are needed to ensure this supposition.

If temperature is the main external factor needed for activation, then deeply buried bulbs should be activated later in time. Thus, a 25-35 cm burial would delay both activation (Esler, 1962; Popay *et al.,* 1996; Royo-Esnal and López, 2007) and emergence (Royo, 2004). Also, if the crop could be sown earlier, the competition with *O. latifolia* would be minimized. Alternatively, black plastic mulches, which raise the soil temperature and therefore induce an earlier activation of the bulbs, could be used for the control of the weed (Ingle *et al*., 1995) since they provide an opportunity to apply a herbicide treatment before sowing the crop.

Summarizing, temperature seems to be the most important external factor that is needed for the activation of *Oxalis* bulbs, while the main effect of moisture is a delay in the activation. Under low temperature laboratory conditions, the common form bulbs remain dormant and activation takes place 2-4 weeks after they have been placed under warmer conditions. Activation of the common form bulbs follows a logarithmic pattern when they are subject to dry storage conditions and a linear pattern under moist storage ones. On the other hand, the Cornwall form bulbs present a faster activation the longer the period of cold storage, and their activation follows an exponential pattern.

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