

Photoperiod buffers responses to salt and temperature during germination of two coastal salt marsh colonizers Juncus acutus and Juncus maritimus

F. Mesleard, N. Yavercovski, Thierry Dutoit

▶ **To cite this version:**

F. Mesleard, N. Yavercovski, Thierry Dutoit. Photoperiod buffers responses to salt and temperature during germination of two coastal salt marsh colonizers Juncus acutus and Juncus maritimus. Plant Biosystems, 2015, 150 (6), pp.1156-1164. ⟨10.1080/11263504.2015.1007898⟩. ⟨hal-01444656⟩

HAL Id: hal-01444656

https://hal.science/hal-01444656v1

Submitted on 2 Mar 2026

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License

Photoperiod buffers responses to salt and temperature during germination of two coastal salt marsh colonizers *Juncus acutus* and *Juncus maritimus*

F. MESLEARD[1,2], N. YAVERCOVSKI[1], & T. DUTOIT[2]

[1]*Centre de Recherche de la Tour du Valat, Le Sambuc, Arles, France and* [2]*Institut Méditerranéen de Biodiversité et d'Ecologie Marine et Continentale, Université d'Avignon et des Pays du Vaucluse, UMR CNRS 7263/IRD 337 Site Agroparc, BP 1207, 84911 Avignon Cedex 9, France*

Abstract

Juncus acutus and *J. maritimus* are two colonizers of coastal marsh rangeland with worldwide distribution. We tested the effect of salt, temperature, and photoperiod on the germination capacity of seeds of the two *Juncus* from the Rhône delta (south of France). We measured the first day of germination, the mean time, speed, and rate of germination on seeds subjected to five salinity levels, three Dark–Light temperatures and two D-L photoperiods (12–12 and 10–14). The 10–14 D-L photoperiod, although it corresponds to one of the two main germination periods of *J. acutus* and *J. maritimus* in the northern Mediterranean, has never been previously used to study their germination capacity. Analyses showed significant effects of salinity and temperature on the germination parameters tested, and for these two factors we found results comparable to those of previous studies. Salinity slowed down and reduced the germination process while spring temperatures had a positive effect. A surprising result was obtained by changing the D-L photoperiod from 12–12 to 10–14 which then largely buffered the negative effect of salt and high temperatures on germination. This capacity of *J. acutus* and *J. maritimus* to withstand salty conditions during the germination phase due to the spring photoperiod could be decisive in the ability of both species to colonize saline environments.

Keywords: *Halophyte, photoperiod, recruitment, salinity, temperature*

Introduction

Juncus acutus L. and *J. maritimus* Lamk. are two perennial species of salt marsh ecosystems with worldwide distribution. Their expansion, related to grazing and water management, has been already reported for numerous regions (Mesléard et al. 1991; Parson & Cuthbertson 2001; Greenwood & Macfarlane 2006). In Mediterranean coastal zones, following the types defined by Davis and Thompson (2000), *J. acutus* and *J. maritimus* are common colonizers of type 2. They are widespread in the region and show strong colonizing aptitude at short distances (Jones & Richards 1954; Greenwood & Macfarlane 2006). Both species tolerate relative salty conditions but show different distribution patterns according to their relative salt and flooding tolerance. *J. maritimus* is more tolerant of salt and flooding (Boscaiu et al. 2011).

Seed germination is generally considered as a stress-sensitive phase (Partridge & Wilson 1987). Therefore, the salinity concentration during the germination period is seen as one of the main factors affecting sexual recruitment in salt marshes (Rozema 1975; Ungar 1991; Noe & Zedler 2000; Rubio-Casal et al. 2003). Although the most determinant abiotic factors affecting germination vary among species, for numerous species the range of tolerance is often greater for salinity than for other abiotic factors such as temperature or photoperiod (Ekstam et al. 1999; Noe & Zedler 2000).

Various studies dealing with the germination needs of *J. acutus* and *J. maritimus* (Greenwood & Macfarlane 2006; Martínez-Sánchez et al. 2006; Boscaiu et al. 2007, 2011; Vicente et al. 2007) showed that the germination capacity of the two species strongly declined according to the increase in

Correspondence: F. Mesleard, Centre de Recherche de la Tour du Valat, Le Sambuc, Arles, France. Tel: +33 4 90 97 29 52. Fax: +33 4 90 97 20 19. Email: mesleard@tourduvalat.org

salinity. For temperature, the variation in the results between authors makes the impact of this factor unclear. Greenwood and Macfarlane (2006) observed highest germination speed and rate of *J. acutus* at the lowest Dark-Light temperatures tested (10°–25°) while Vicente et al. (2007) showed an increase of these two parameters up to D-L temperatures of 20–30°C.

For both species, the studies previously cited were conducted at a 12–12 photoperiod with the exception of Martínez-Sánchez et al. (2006), who studied the germination both with 24 h dark and 12–12 photoperiod.

Photoperiod is known to play a key role in the germination process, favoring germination during the time of the year where the environmental conditions are most favorable to the seedlings' development (Khan & Ungar 1997). Although *J. acutus* and *J. maritimus* are considered capable of germinating at all times of the year (Cunningham et al. 2011), in the northern Mediterranean they mostly germinate in spring (personal observations), one of the two annual rainy periods, generally characterized by relatively high soil moisture and mild temperatures. The presence of soil moisture is known to generally increase the germination speed and rate of species as in Mediterranean-type wetlands (Noe & Zedler 2000). In the Camargue (Mesléard et al. 1991), and elsewhere throughout the Mediterranean (Sánchez et al. 1998; Gómez Mercado et al. 2012; Zörb et al. 2013), the two species are recorded with soil salinity above 300 mM NaCl, whereas, according to the literature, their germination is severely limited. However, the presence of individuals at a given salinity does not demonstrate that the species can germinate at this salinity and individuals may have germinated during milder conditions. The dissimilarity of the tolerance to salt between ecotypes must not be neglected; responses are likely to vary under the selection pressure of the local environment (Jefferies & Gottlieb 1982; Mauchamp & Mesléard 2001). The works of Greenwood and Macfarlane (2006) concern New South Wales in Australia, those of Boscaiu et al. (2011) concern the national park of La Albufera near Valencia in Spain, and those of Martínez-Sánchez et al. (2006) concern Arenales y Salinas de San Pedro del Pinatar, near Murcia, also in Spain. The germinative capacity in response to salt, temperature, and photoperiod of *J. acutus* and *J. maritimus* may vary between seeds from Spain, Australia, or Rhône delta wetlands. Nevertheless, on the one hand, the presence of *J. acutus* and *J. maritimus* at high salinities and, on the other hand, germinations largely occurring in spring, suggest that the spring photoperiod, in interaction or not with temperature, could enable germination under saltier conditions than expected according to the literature. In order to test this hypothesis on seeds of *J. acutus* and *J. maritimus* from the Rhône delta and to assess its potential generalization, we addressed the following questions:

(1) Do seeds of *J. acutus* and *J. maritimus* collected in the Rhône delta show the same type of response to salt as those presented in the literature for other regions?

We hypothesized that with 12–12 D-L photoperiod, the germination rate of the two species decreases with the increase in salt concentration, in accordance with the patterns already shown in the literature.

(2) Does the increase of temperature increase the germination capacity of the two species?

We hypothesized that with 12–12 photoperiod, the alternation of D-L temperature corresponding to the end of spring (compromise between humidity and heat) is the most favorable to germination, whatever the salinity tested.

(3) Does changing the photoperiod from 12–12 to 10–14 D-L increase the germination capacity of the two species?

We hypothesized that a photoperiod matching the end of the spring period (10–14 D-L) is more favorable to germination than a 12–12 photoperiod, whatever the salinity and the temperature tested.

Methods

Plant material

J. acutus and *J. maritimus* are both perennial, rhizomatous wetland plants. *J. acutus* is a tussock forming species which develops in various habitats throughout the world. Its colonizing capacity is essentially ensured by sexual reproduction (Jones & Richards 1954). It is a strong competitor in the upper marsh area without standing water (Auld & Medd 1987). *J. maritimus* shows a more temperate and Mediterranean distribution pattern (Boscaiu et al. 2011) and is found in western and central Europe, in southern Africa and north-western America. Its vegetative capacity related to its creeping rhizomes and its strong competitive ability (Greenwood & Macfarlane 2006) makes it capable of developing large monospecific stands (Pino et al. 2009). We collected the seeds in summer on three marshes with silty clay soil of fluvio-lacustrine origin at the Tour du Valat estate (43°5′N, 4°7′E, Otero & Bailey 2003). Seeds were mixed and kept dry in the shade until the experiment the following spring. The

climate of Camargue is of Mediterranean type with cold winters. The average rainfall is about 600 mm, concentrated in autumn and early spring. Strong winds associated with high temperatures lead to a summer evaporation/precipitation summer deficit of 700 mm (Loubet 2012). Mean annual temperature is 14.9°C with minimum, maximum and mean temperatures in January being 0.8, 13.3, and 7.05°C, respectively, and minimum, maximum, and mean temperatures in July being 15.7, 31.9, and 25.6°C, respectively.

Environmental variables tested

We estimated the average temperatures and photoperiods on the basis of the local data collected from 1995 to 2010 in Camargue on the Tour du Valat estate. We then discriminated three alternating D-L temperatures (10°/20°, 15°/25°, 20°/30°) and two photoperiods (12–12, 14–10), which roughly correspond for five of them to mid-spring, end of spring, beginning of summer, end of summer, and beginning of autumn (Table I).

The salt concentration of 400 mM NaCl corresponds to the maximum salinity where the two species are locally recorded. Then we chose the five following concentrations: 0, 100, 200, 300, and 400 mM NaCl, enabling us to compare our results with previous studies (Greenwood & Macfarlane 2006; Martínez-Sánchez et al. 2006; Boscaiu et al. 2007, 2011; Vicente et al. 2007).

Germination tests

We compared the germination rate between saturated soil (distilled water table constantly maintained at the surface) and constantly flooded soil (5 cm above the soil surface for the two species). For each of the two hydrological regimes, we exposed seven Petri dishes containing 20 seeds incubated at 10–14 D-L photoperiod at 15–25°C for 15 days. We found a respective rate of 98% and 100% for *J. acutus* and *J. matimus* with a constant flooding regime against 90% and 82% with the saturated regime (a). Although the Mann–Whitney test (Statistica 8.0, 2007 StatSoft, Tulsa, OK, USA) only showed a significant difference for *J. maritimus* ($U = 2.05$, $p = 0.04$), we selected the constant flooding regime for the experiments.

We stuck seeds on double-face plastic films, themselves stuck on tissues (Diatex) permeable from 0.2 to 20 µ particles. The whole assembly was arranged in plastic jars containing 2 cm of sand and flooded (5 cm).

The jars were placed in a growth chamber (Hotcold-GL: 12K lux). We exposed jars to combinations of salt (0, 100, 200, 300, and 400 mM NaCl), D-L temperature (10°–20°, 15°–25°, and 20°–30°), D-L and photoperiod (12–12 and 10–14), with seven jars (20 seeds per jar) for each treatment.

Germination parameters

We considered four parameters:

- the first day of germination,
- the mean time of germination (Brenchley & Probert 1998) $= (\Sigma n_i \times d_i)/N$, where n is the number of germinated seeds at day i, d is the incubation period (days), and N is the total number of germinations at day i,
- the speed of germination (Chiapusio et al. 1997): $v = (\Sigma(N_n - N_{n-1}) \times 1/n) \times 100$, where N is the proportion of germination obtained after n days,
- the germination rate.

We considered the germination effective with the emergence of the radical (Come 1970). The dishes were randomized every week throughout the monitoring period. The water level was topped up with distilled water when necessary.

Statistical analysis

We tested the role of salinity, temperature, and photoperiod and their interactions on the four parameters using factorial ANOVAs. When interactions were not significant, single effects of factors were retested using main effect ANOVAs. ANOVAs were conducted by general linear model procedures using sigma-restricted parameterization of categorical predictor variables (Satisitica 8.0, StatSoft, Inc.)

Table I. Combination of alternating Dark-Light temperatures and photoperiods tested and corresponding periods in the northern Mediterranean.

D-L temperatures photoperiod	10°/20°	15°/25°	20°/30°
10–14	Mid-spring: April	End of spring: May	Beginning of summer: June
12–12	Beginning of autumn: October	End of summer: September	No correspondence *in natura*

Results

Impact of salinity

J. acutus. With a 12–12 D-L photoperiod and a 10–20°C temperature alternation, the increase in salt concentration significantly increased the number of days before the first germination (average of 7 days at 0 mM NaCl and 18.4 days at 400 mM) as well as the mean germination time and reduced the germination speed (Figure 1, Table IIa). The germination rate decreased from almost 100% at 0 or 100 mM NaCl to about 30% at 400 mM NaCl (Figure 1, Table IIa).

J. maritimus. With a 12–12 D-L photoperiod and 10–20°C temperature alternation, the increase of salt also increased the number of days before germination (average of 9.9 days at 0 mM NaCl and 27.7 days at 400 mM NaCl) as well as the mean time of germination (Figure 2, Table IIb). The speed of germination showed a significant but slight decrease between 0 and 300 mM NaCl and a strong decrease between 300 and 400 mM NaCl (Figure 2, Table IIb). The germination rate decreased slowly from 55% to 26% between 0 and 300 mM NaCl, it reached only 4.3% at 400 mM NaCl (Figure 2, Table IIb).

Impact of temperature

J. acutus. The increase in temperature significantly modified the values of the four parameters tested (Table IIa). Interactions between temperature and salinity were significant for the first day of germination, the speed, and the germination rate, but not for the mean time of germination (Table IIa). Nevertheless, retesting of the effect of salinity and temperature on the mean time of germination by main effect ANOVA confirmed the significance for the two variables (Table IIIa). At the 12–12 photoperiod, the D-L temperatures 15–25 and 20–30 both reduced the number of days before the first germination at 0 mM NaCl (Figure 1, Table IIIa). We found the same significant effect for 100,

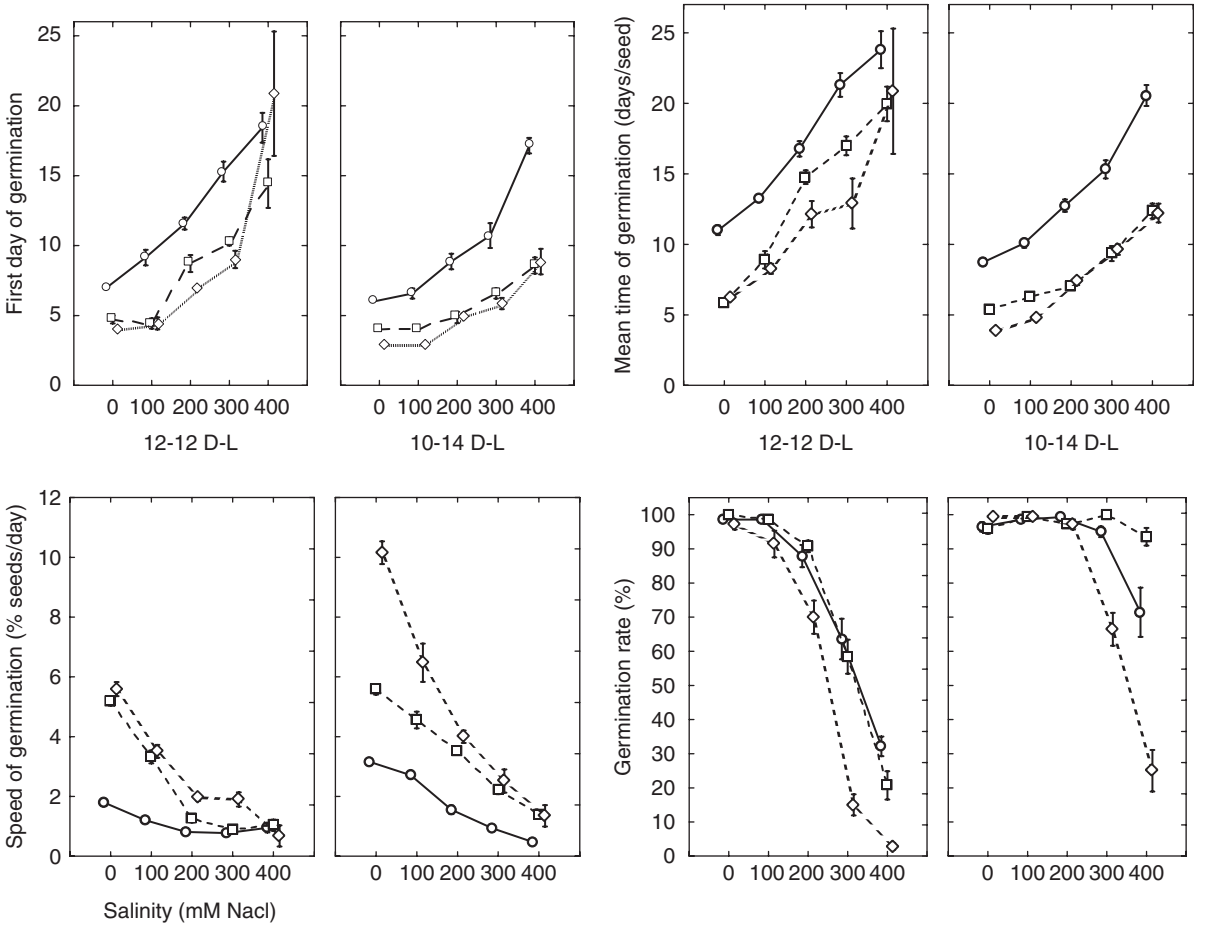


Figure 1. *Juncus acutus*: First day of germination, mean time germination, speed of germination, and germination rate, and their standard errors according to salinity, Dark-Light temperature alternation and Dark-Light photoperiod. Seeds were subjected to four salinities 0, 100, 200, 300, and 400 mM NaCl, three D-L temperatures 10–20°C, 15–25°C, 20–30°C and two D-L photoperiods (12–12 h, 10–14 h), with 7 jars × 20 seeds for each treatment.

Table II. Effects of salinity, Dark-Light temperature alternation, and D-L photoperiod alternation, and their interactions on the first day of germination, the speed of germination, the mean time germination, and the germination rate, for (a) *Juncus acutus* and (b) *Juncus maritimus*.

Species/variables	First day of germination	Speed of germination	Mean time of germination	Germination rate
(a) *Juncus acutus*				
Salinity	$F(4, 180) = 99.508$ $p < 0.0001$	$F(4, 180) = 346.56$ $p < 0.0001$	$F(4, 180) = 116.27$ $p < 0.0001$	$F(4, 180) = 385.32$ $p < 0.0001$
Temperature	$F(2, 180) = 54.406$ $p < 0.0001$	$F(2, 180) = 279.15$ $p < 0.0001$	$F(2, 180) = 89.902$ $p < 0.0001$	$F(2, 180) = 119.61$ $p < 0.0001$
Photoperiod	$F(1, 180) = 73.103$ $p < 0.00001$	$F(1, 180) = 252.63$ $p < 0.0001$	$F(1, 180) = 140.84$ $p < 0.0001$	$F(1, 180) = 333.20$ $p < 0.0001$
Salinity × temperature	$F(8, 180) = 2.3882$ $p < 0.05$	$F(8, 180) = 37.347$ $p < 0.0001$	$F(8, 180) = 0.71939$ n.s.	$F(8, 180) = 27.437$ $p < 0.0001$
Salinity × photoperiod	$F(4, 180) = 7.2$ $p < 0.0001$	$F(4, 180) = 20.163$ $p < 0.00001$	$F(4, 180) + 5.6820$ $p < 0.001$	$F(4, 180) = 73.137$ $p < 0.0001$
Temperature × photopériod	$F(2, 180) = 1.4687$ n.s.	$F(2, 180) = 29.086$ $p < 0.00001$	$F(2, 180) = 1.2699$ n.s.	$F(2, 180) = 4.1703$ $p < 0.05$
Temp × sal × phot	$F(8, 180) = 3.6605$ $p < 0.001$	$F(8, 180) = 9.6944$ $p < 0.00001$	$F(8, 180) = 1.83$ n.s.	$F(8, 180) = 10.957$ $p < 0.00001$
(b) *Juncus maritimus*				
Salinity	$F(4, 180) = 57.588$ $p < 0.000001$	$F(4, 180) = 103.05$ $p < 0.000001$	$F(4, 180) = 50.003$ $p < 0.000001$	$F(4, 180) = 59.430$ $p < 0.000001$
Temperature	$F(2, 180) = 44.182$ $p < 0.000001$	$F(2, 180) = 77.366$ $p < 0.000001$	$F(2, 180) = 40.888$ $p < 0.000001$	$F(2, 180) = 56.128$ $p < 0.000001$
Photoperiod	$F(1, 180) = 147.74$ $p < 0.000001$	$F(1, 180) = 1115.6$ $p < 0.000001$	$F(1, 180) = 314.32$ $p < 0.000001$	$F(1, 180) = 1266.2$ $p < 0.000001$
Salinity × temperature	$F(8, 180) = 1.2855$ n.s.	$F(8, 180) = 5.2021$ $p < 0.00001$	$F(8, 180) = 2.2771$ $p < 0.05$	$F(8, 180) = 1.0374$ n.s.
Salinity × photoperiod	$F(4, 180) = 22.723$ $p < 0.000001$	$F(4, 180) = 0.49885$ n.s.	$F(4, 180) = 12.472$ $p < 0.000001$	$F(4, 180) = 38.842$ $p < 0.000001$
Temperature × photoperiod	$F(2, 180) = 0.65289$ n.s.	$F(2, 180) = 17.947$ $p < 0.000001$	$F(2, 180) = 1.5515$ n.s.	$F(2, 180) = 6.0912$ $p < 0.01$
Temp × sal × phot	$F(8, 180) = 1.2053$ n.s.	$F(8, 180) = 1.5138$ n.s.	$F(8, 180) = 2.7056$ $p < 0.01$	$F(8, 180) = 4.0454$ $p < 0.001$

Note: F and p values were calculated by multi-factorial ANOVAs in a general linear model procedure.

200, and 300 mM NaCl but not for the highest salinity tested at the 20–30°C alternation, due to the high variation between replicates. The germination speed increased with the increase in temperatures (Figure 1, Table IIa). This increase was perceptible up to 300 mM NaCl at the 20–30°C alternation and only up to 200 mM NaCl for the 15°–25° alternation. The germination rate was close to 100% at 0 and 100 mM NaCl at the three D-L temperatures tested (Figure 1, Table IIIa). These rates were still higher than 50% at 300 mM NaCl and higher than 32% and 20% at 400 mM NaCl for the temperature alternations 10–20 and 15–25°C, respectively. The increase in temperatures to 20–30°C alternation amplified the diminution of the germination rate caused by the increase in salinity (Figure 1, Table IIIa) and the germination rate was only 15% and 2.9% at 300 and 400 mM NaCl, respectively, for the 20–30°C alternation.

Juncus maritimus. The increase in temperature significantly altered the four parameters tested (Table IIb). Interactions between temperature and salinity were significant for the speed and mean time of germination, but not for the first day of germination and the germination rate. Nevertheless, retesting of the effect of salinity and temperature by the main effect ANOVA confirmed a significant effect of the two variables on the first day of germination and the germination rate (Table IIIb). At the 12–12 photoperiod, the increase in D-L temperatures reduced the mean time of germination and increased the speed of germination but mainly for the lowest salinities (Figure 2). At 0 mM NaCl, this increase of D-L temperatures from 10–20 to 15–25°C significantly increased the germination rate from 55% to 78% but not from 10–20 to 20–30°C.

The mean time of germination strongly increased at the highest salinity for the temperature alternations 10–20 and 20–30°C (Figure 2). The decrease in the speed of germination with the increase in salt concentration was better contained at the D-L temperature of 10–20°C than at the two other alternations of temperature (Figure 2).

Impact of the photoperiod

Juncus acutus. The general model showed a strong impact of photoperiod on the four parameters tested (Table IIa). The interaction photoperiod × salinity

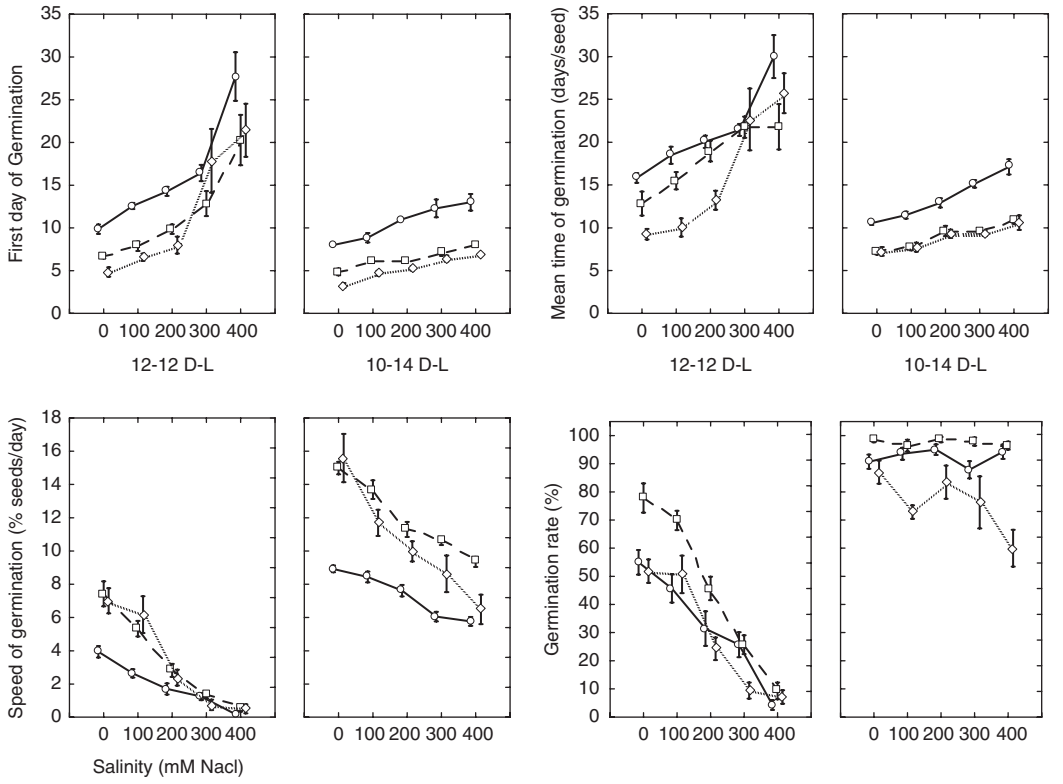


Figure 2. *Juncus maritimus*: First day of germination, mean time germination, speed of germination, and germination rate, and their standard errors according to salinity, Dark-Light temperature alternation, and Dark-Light photoperiod. Seeds were subjected to four salinities 0, 100, 200, 300 and 400 mM NaCl, three D-L temperatures 10–20°C, 15–25°C, 20–30°C and two D-L photoperiods (12–12 h, 10–14 h), with 7 jars × 20 seeds for each treatment.

× temperature was significant for the first day of germination, the speed of germination, and the germination rate but not for the mean time of germination. Nevertheless, retesting of the effect of salinity, temperature, and photoperiod on the mean time of germination by the main effects ANOVA confirmed a significant effect of the three variables (Table IIIa).

The increase in light duration (10–14 D-L photoperiod) reduce the duration before the first germination by 1, 2.5, 3.2, 6.6, and 1.3 days and the mean time of germination by 1, 2.5, 2.9, 4.8, and

Table III. Effects of salinity, Dark-Light temperature alternation, D-L photoperiod alternation (a) on the first day of germination and the mean time germination for *Juncus acutus*, (b) on the first day of germination, the speed of germination, the mean time germination, and the germination rate for *Juncus maritimus*.

Species/variables	First day of germination	Speed of germination	Mean time of germination	Germination rate
(a) *Juncus acutus*				
Salinity	$F(4, 180) = 99.508$ $p < 0.000001$		$F(4, 180) = 116.27$ $p < 0.01$	
Temperature	$F(2, 180) = 54.406$ $p < 0.000001$		$F(2, 180) = 89.902$ $p < 0.01$	
Photoperiod	$F(1, 180) = 73.103$ $p < 0.000001$		$F(1, 180) = 140.84$ $p < 0.01$	
(b) *Juncus maritimus*				
Salinity	$F(4, 180) = 57.588$ $p < 0.000001$	$F(4, 180) = 103.05$ $p < 0.01$	$F(4, 180) = 50.003$ $p < 0.000001$	$F(4, 180) = 59.430$ $p < 0.000001$
Temperature	$F(2, 180) = 44.182$ $p < 0.000001$	$F(2, 180) = 77.366$ $p < 0.01$	$F(2, 180) = 40.888$ $p < 0.000001$	$F(2, 180) = 56.128$ $p < 0.000001$
Photoperiod	$F(1, 180) = 147.74$ $p < 0.000001$	$F(1, 180) = 1115.6$ $p < 0.01$	$F(1, 180) = 314.32$ $p < 0.000001$	$F(1, 180) = 1266.2$ $p < 0.000001$

Note: F and p values were calculated by main effects ANOVAs in a general linear model procedure.

1.3 days, at 0, 100, 200, 300, and 400 mM NaCl (Figure 1). It increased the speed of germination at 0, 100, and 200 mM NaCl (Figure 1) and maintained the germination rate above 95% up to 300 mM NaCl and still above 70% at 400 mM NaCl (Figure 1).

We found the alternation of temperature 15–25°C to be the best temperature conditions for germination at the D-L photoperiod 10–14. With this alternation of temperature, the increase in the light duration increased the speed of germination, but mainly at 100, 200, and 300 mM NaCl (Figure 1), and maintained the germination rate close to 100% up to 300 mM NaCl. At 400 mM NaCl, we found it still at 94% against 21% at the 12–12 photoperiod (Figure 1). At the 20–30°C alternation, the increase in light duration also increased the speed of germination at the five salt concentrations tested. But in this case, the germination rate was maintained close to 100% only up to 200 mM NaCl and it decreased to 66% and 25% at 300 and 400 mM NaCl, respectively.

Juncus maritimus. With regard to *J. acutus*, the general model showed a strong impact of photoperiod on the four parameters tested (Table III). The interaction photoperiod × salinity × temperature was, in this case, significant for the mean time of germination and the germination rate only (Table IIb). Nevertheless, the retesting of the effect of salinity, temperature, and photoperiod on the first day of germination and the speed of germination by the main effect ANOVA confirmed a significant effect of the three variables (Table IIIb).

At the alternation of temperature 10–20°C, the increase in day duration (D-L photoperiod 10–14) reduced the mean time of germination and increased the germination rate to 90% or more at the four salt concentrations tested (compared to about 50% at 100 and 200 mM NaCl, and 27.5% and 4.3% at 300 and 400 mM NaCl, respectively, Figure 2).

With a 10–14 D-L photoperiod, the alternation of temperature 15–25°C, as for *J. acutus*, appeared to be the best conditions for the germination. This photoperiod ensured the maintenance of a high germination rate of *J. maritimus* at the three D-L temperatures tested up to 300 mM NaCl. In this case, the increase in the photoperiod reduced the mean germination time and the germination rate which reached more than 96% at all the salinity rates tested (Figure 2).

At the alternation of temperature 20–30°C, the increase in photoperiod also reduced the mean germination time (Figure 2) and increased the germination rate. However, it reached only 87%, 73%, 83%, 76%, and 60% at 0, 100, 200, 300, and 400 mM NaCl, respectively.

Discussion

The capacity to germinate seeds of *J. acutus* and *J. maritimus* collected in the Rhône delta was comparable to those obtained elsewhere by other authors for equivalent conditions (Boscaiu et al. 2001; Martínez-Sánchez et al. 2006; Vicente et al. 2007; Boscaiu et al. 2011).

The increase in salt concentration impacted the germination capacity of the two *Juncus* species. Salt led to an increase in the time before the germination and of the mean time of germination and a slowing down of the germination speed. This slowing down of the germination speed is likely to greatly limit the species recruitment and ability to compete in quickly changing environments, such as in coastal salt marshes (Bazzaz 1996).

Their germination rates, although they were slightly or much higher than those obtained in previous studies (Woodell 1985; Vicente et al. 2007; Boscaiu et al. 2011), followed the same pattern with the increase of salinity.

The increase in temperatures altered the responses of the two species. As hypothesized, we found the D-L temperature alternations 15–25°C and to a lesser extent 10–20°C, which corresponds to the northern Mediterranean spring or beginning of autumn, and potential relatively humid periods, more favorable to germination than the 20–30°C (summer) D-L alternation. Martínez-Sánchez et al. (2006) reported the same negative effect of 20–30°C compared to 15–25°C temperatures alternation on the speed and on the germination rate of *J. acutus*.

The role of the photoperiod in the germination process has already been demonstrated for many species (e.g. Mott & McComb 1975; Baskin & Baskin 1998; Noe & Zedler 2000; Munir et al. 2001). Here, the response of *J. acutus* and *J. maritimus* to salinity and to temperature differed strongly according to the two photoperiods tested. The increase in light duration from 12 to 14 h buffered the negative impact of salt on the germination process, whichever of the three alternations of temperature tested. The interactions between photoperiod and temperature and their impact on seed germination have long been discussed (Stearns & Olson 1958). Up to 300 mM NaCl, *J. acutus* like *J. maritimus* exposed to a 10–14 D-L photoperiod did not show a decrease in their germination rate for the alternation of temperature 10–20 or 15–25°C. A 10–14 D-L photoperiod with an alternation of temperatures 10–20 or 15–25°C between day and night corresponds to conditions met the most years in spring, a compromise between cool temperatures and relatively high maintenance of soil moisture.

Vegetation species in the Mediterranean need to develop strategies in response to the irregular annual

drought period which can start early in spring or later at the beginning of summer. The capacity to quickly germinate in spring, regardless of salinity, will give additional development time to seedlings, known to be a vulnerable phase (Engelbrecht et al. 2005), before having to face with high temperatures and drought. This ability is clearly a strong competitive advantage compared to plants which need to wait for "windows of germination" (Noe & Zedler 2001), which most of the time in Camargue will not arrive before the first autumnal rainfalls.

The relative similarity of the results between previous studies and ours under comparable conditions suggests for both *J. acutus* and *J. maritimus* that the results obtained in our case for conditions not tested elsewhere (10–14 D-L photoperiod) are broadly generalizable. This new finding on the key role of photoperiod seems of primary importance and may help to explain the presence of *J. acutus* and *J. maritimus* seedlings and, to a lesser extent, of rhizomes, at high salt concentrations. However, to determine exactly the scope, in demographic terms, of this ability to germinate in a saline environment in spring, additional studies should be conducted. The conditions of seed storage in our experiments did not correspond to the conditions of the soil seed bank. Germination tests *in natura* of the two *Juncus* species, depending on the photoperiod, are needed to validate the results obtained in the growth chamber. They must be supplemented by accurate tracking of the germination dynamic according to the seed bank and by monitoring of the capacity of young seedlings to survive and to develop depending on the salt concentration and water availability.

Acknowledgements

This work was supported by the Région Provence-Alpes-Côte d'Azur, the Foundation ProValat and the Foundation MAVA. We are grateful to Olivier Boutron, Diedre Flanagan, Patrick Grillas, Gaétan Lefèbvre, Léa Mishler, Marta Siliato and Loïc Willm for their help at different stages of the work.

References

Auld B, Medd RW. 1987. Weed: An illustrated botanical guide to the weeds of Australia. Melbourne: Inkata Press.

Baskin JM, Baskin CC. 1998. Seed: Ecology, biogeography, and evolution of dormancy and germination. Sand diego, CA: Academic Press.

Bazzaz FA. 1996. Plants in changing environments: Linking physiological population, and community ecology. Cambridge: Cambridge University Press.

Boscaiu M, Ballesteros G, Boira H, Vicente O, Boscaiu N. 2007. Ecophysiological studies in *Juncus acutus* L. and *J. maritimus* Lam. Contributii Botanice XLII: 42–46.

Boscaiu M, Ballesteros G, Naranjo MA, Vicente O, Boira H. 2011. Responses to salt stress in *Juncus acutus* and *J. maritimus* during seed germination and vegetative plant growth. Plant Biosyst 145(4): 770–777, doi:10.1080/11263504.2011.628446.

Brenchley JL, Probert RJ. 1998. Seed germination responses to some environmental factors in the seagrass *Zostera capricorni* from eastern Australia. Aquat Bot 62(3): 177–188, doi:10.1016/S0304-3770(98)00089-8.

Chiapusio GA, Sánchez M, Reigosa MJ, González M, Pellissier F. 1997. Do germination indices adequately reflect allelochemical effects on the germination process?. J Chem Ecol 23(11): 2445–2453, doi:10.1023/B:JOEC.0000006658.27633.15.

Come D. 1970. Les obstacles à la germination. Paris: Masson.

Cunningham GM, Mulham WE, Milthorpe PL, Leigh JH. 2011. Plants of Western New South Wales. Collinwood, VIC: CSIRO Publishing.

Davis MA, Thompson K. 2000. Eight ways to be a colonizer; two ways to be an invader. Bull Ecol Soc Am 81: 226–230.

Ekstam B, Johannesson R, Milberg P. 1999. The effect of light and number of diurnal temperature fluctuations on germination of *Phragmites australis*. Seed Sci Res 9(2): 165–170, doi:10.1017/S0960258599000185.

Engelbrecht BMJ, Kursar TA, Tyree T. 2005. Drought effects on seedling survival in a tropical moist forest. Trees 19(3): 312–321, doi:10.1007/s00468-004-0393-0.

Gómez Mercado F, del Moral Torres F, Giménez Luque E, de Haro Lozano S. 2012. Salinity tolerance of the hygrophilous plant species in the wetlands of the south of the Iberian Peninsula. Not Bot Horti Agrob 40: 18–28.

Greenwood ME, Macfarlane GR. 2006. Effects of salinity and temperature on the germination of *Phragmites australis*, *Juncus kraussii*, and *Juncus acutus*: Implications for estuarine restoration initiatives. Wetlands 26(3): 854–861, doi:10.1672/0277-5212(2006)26[854:EOSATO]2.0.CO;2.

Jefferies RL, Gottlieb D. 1982. Genetic differentiation of the microspecies *Salicornia europaea* L. (*sensu stricto*) and *S. ramosissima*. J Woods New Phytol 92(1): 123–129, doi:10.1111/j.1469-8137.1982.tb03368.x.

Jones V, Richards PW. 1954. *Juncus acutus* L. J Ecol 42(2): 639–650, doi:10.2307/2256896.

Khan MA, Ungar IA. 1997. Effects of light, salinity, and thermoperiod on the seed germination of halophytes. Can J Bot 75(5): 835–841, doi:10.1139/b97-093.

Loubet A. 2012. Modélisation de l'Hydrosystème Vaccarès: Contribution à une gestion adaptative des ressources en eau dans le delta du Rhône, France. Thèse de doctorat Université d'Aix-Marseille. Marseille, France.

Martínez-Sánchez JJ, Conesa E, Vicente MJ, Jiménez A, Franco JA. 2006. Germination responses of *Juncus acutus* (juncaceae) and *Schoenus nigricans* (cyperaceae) to light and temperature. J Arid Environ 66(1): 187–191, doi:10.1016/j.jaridenv.2005.11.004.

Mauchamp A, Mésleard F. 2001. Salt tolerance in *Phragmites australis* populations from coastal Mediterranean marshes. Aquat Bot 70(1): 39–52, doi:10.1016/S0304-3770(00)00140-6.

Mesléard F, Grillas P, Lepart J. 1991. Plant community succession in a coastal wetland after abandonment of cultivation: The example of the Rhône Delta. Vegetatio 94: 35–45.

Mott JJ, Mccomb AJ. 1975. The role of photoperiod and temperature in controlling the phenology of three annual species from an arid region of Western Australia. J Ecol 63(2): 633–641, doi:10.2307/2258741.

Munir J, Dorn LA, Donohue K, Schmitt J. 2001. The effect of maternal photoperiod on seasonal dormancy in *Arabidopsis thaliana* (*Brassicaceae*). Am J Bot 88(7): 1240–1249, doi:10.2307/3558335.

Noe GB, Zedler JB. 2000. Differential effects of four abiotic factors on the germination of salt marsh annuals. Am J Bot 87(11): 1679–1692, doi:10.2307/2656745.

Noe GB, Zedler JB. 2001. Spatio-temporal variation of salt marsh seedling establishment in relation to the abiotic and biotic environment. J Veget Sci 12(1): 61–74, doi:10.2307/3236674.

Otero C, Bailey AD. 2003. Europe's natural and cultural heritage. The European Estate: La Tour du Valat, France. Brussels: Friends of the Countryside.

Parson WT, Cuthbertson EJ. 2001. Noxious weeds of Australia. Canberra: CSIRO Publishing.

Partridge TR, Wilson JB. 1987. Germination in relation to salinity in some plants of salt marshes in Otago, New Zealand. New Zeal J Bot 25(2): 255–261, doi:10.1080/0028825X.1987.10410071.

Pino J, Vilà M, Álvarez N, Seguí JM, Guerrero C. 2009. Niche breadth rather than reproductive traits explains the response of wetland monocotyledons to land-cover change. Appl Veget Sci 12(1): 119–130, doi:10.1111/j.1654-109X.2009.01009.x.

Rozema J. 1975. The influence of salinity, inundation and temperature on the germination of some halophytes and non halophytes. Oecol Plant 10: 317–329.

Rubio-Casal AE, Castillo JM, Luque CJ, Figueroa ME. 2003. Influence of salinity on germination and seeds viability of two primary colonizers of Mediterranean salt pans. J Arid Environ 53(2): 145–154, doi:10.1006/jare.2002.1042.

Sánchez JM, Otero XL, Izco J. 1998. Relationships between vegetation and environmental characteristics in a salt-marsh system on the coast of Northwest Spain. Plant Ecol 136: 1–8.

Stearns F, Olson JS. 1958. Interactions of photoperiod and temperature affecting seed germination in *Tsuga canadensis*. Am J Bot 45(1): 53–58, doi:10.2307/2438321.

Ungar IA. 1991. Ecophysiology of vascular halophytes. Boca Raton, FL: CRC Press.

Vicente MJ, Conesa E, Álvarez-rogel J, Franco JA, Martínez-sánchez JJ. 2007. Effects of various salts on the germination of three perennial salt marsh species. Aquat Bot 87(2): 167–170, doi:10.1016/j.aquabot.2007.04.004.

Woodell SRJ. 1985. Salinity and seed germination patterns in coastal plants. Vegetatio 61(1–3): 223–229, doi:10.1007/BF00039828.

Zörb C, Sümer A, Sungur A, Flowers T, Özcan H. 2013. Ranking of eleven costal halophytes from salt marshes in Northwest Turkey according to their salt tolerance. Turkish J Bot 37: 1125–1133.