DE GRUYTER Open Life Sci. 2018; 13: 137–148

Research Article

Du Hyun Kim, Sim Hee Han*

Direct Effects on Seed Germination of 17 Tree Species under Elevated Temperature and CO_2 Conditions

https://doi.org/10.1515/biol-2018-0019
Received December 20, 2017; accepted March 28, 2018

Abstract: Effects on seed germination characteristics of 17 tree species were investigated under elevated temperature and CO_2. Seeds of 5 needle-leaf and 12 broad-leaf species were germinated under four conditions: 24°C + 400 μmol CO_2 mol air^{-1}, 24°C + 750 μmol CO_2 mol air^{-1}, 27°C + 400 μmol CO_2 mol air^{-1}, and 27°C + 750 μmol CO_2 mol air^{-1}. The elevated temperature and CO_2 affected germination percent (GP) of 7 tree species seeds. GPs of *Pinus densiflora*, *P. thunbergii*, *Betula ermanii*, and *Maackia amurensis* seeds were affected by the elevated temperature, while only that of *P. jezoensis* seed was influenced by the elevated CO_2. GPs of *Malus baccata* and *Zelkova serrata* seeds were influenced by both the elevated temperature and CO_2. In addition, the elevated temperature and CO_2 also affected mean germination time (MGT) of 12 tree species seeds. Particularly, MGTs of *P. thunbergii* and *Rhododendron tschonoskii* seeds were influenced by both factors. In conclusion, elevated temperature and CO_2 affected seed germination characteristics, which were reflected by significant differences among tree species. Specifically, these two factors exerted stronger influence on germination pattern such as MGT rather than seed germination percent.

Keywords: germination percent; mean germination time; needle-leaf; broad-leaf; seed germination characteristics

1 Introduction

In Korea, the ambient air CO_2 concentration is substantially higher than the global average. The average CO_2 concentration for 2016 was recorded as 409.9 ppm, which was an increase of 39.2 ppm (10.6%) relative to the annual average of 370.7 ppm for 1999, and 6.6 ppm higher than the global average of 403.3 ppm for the same year as documented by World Meteorological Organization (WMO) [1]. The mean yearly temperature for South Korea in 2016 was 13.6°C, which was 0.6°C higher than the recent 10 years (2007-2016) and 1.1°C higher than the current climatological normal (1981-2010) [2]. Baseline scenarios, those without additional mitigation (RCP 8.5), result in an increase in the average temperature of the Korean Peninsula to 6.0 degrees at the end of the 21st century [3].

Climatic change, such as warming and alteration of precipitation regimes, is causing shifts in species distributions [3, 4] and phenologies [5]. These changes can also alter forest composition; for example, warming could increase the growth rate of established individuals or select for warm-adapted species. Population demographics of woody plants established within intact successional plant communities are likely to be constrained by factors that alter seed germination and seedling establishment, and ultimately, recruitment of individuals into the population [6-8].

Plant seed germination is a crucial stage in the life cycle of plants, and the successful establishment of plants largely depends on successful germination [9]. Generally, seed germination tends to be highly unpredictable over space and time.

However, climate has a large influence on plant recruitment [10-12]. For example, with shortening winters [13], seeds may remain partially dormant in spring and need an extended time to germinate [14]. The alteration of temperature and water supply due to global climate change could preclude, delay, or enhance regeneration from seeds [15].

***Corresponding author: Sim Hee Han,** Department of Forest Genetic Resources, National Institute of Forest Science, Suwon 16631, Republic of Korea, E-mail: simhee02@korea.kr
Du Hyun Kim, Department of Life Resources Industry, Dong-A University, Busan 49315, Republic of Korea

Despite the considerable number of studies on the effects of climate change on plants [16], there have been few attempts to investigate its effect on plant regeneration [17]. Several environmental factors such as temperature, salinity, light, and soil moisture simultaneously influence seed germination [9, 18-21]. Among several factors, temperature has been considered as the most important. The variation in the optimal temperature for seed germination depends on the considered species, and for the majority of species, seed germination occurs over a wide range of temperatures [22]. This variation in the optimal temperature and the germination percent between species constitutes some adaptive strategies to harsh environmental conditions. It has been shown that temperatures above the thermal optimum often provoke an inhibition of germination and irreversible damage [9, 23].

In addition, plant regeneration from seed is largely governed by germinability and speed of germination. These components have received considerably less attention in CO_2 research relative to studies of vegetative or reproductive output responses. Moreover, the limited literature has not been rigorously examined for generalizable patterns of responses and/or potential mechanisms. Marty and BassiriRad [24] presented a meta-analysis summarizing the results of studies that have addressed the parental and direct effects of enriched CO_2 on seed germination success and germination percent. There is little empirical evidence that enriched CO_2 can have a direct effect on a germinating seed, but similar to parental responses, this direct effect on germination is quite inconsistent [25-29].

A study on historical climate change period showed that woody plants migrate along with climatic zones, but its moving velocity is estimated to be 4–200 km per 100 years. Therefore, except for tree species with a high migration velocity, they will not be able to catch up with the migration of climatic zones and becomes at high risk of extinction due to climate change [30].

In Korea, summer is getting longer, while winter is getting shorter. This phenomenon unquestionably stems from climate change driven by global warming, and it affects seed germination and regeneration of woody plants. When seeds of woody plants germinate without enough dormancy time, they do not regenerate and finally die under unsuitable environmental conditions after germination.

Therefore, it is important to evaluate the effects of temperature and CO_2 on vegetation, ecosystems, and certain tree species in order to secure a scientific basis for establishing actions to address adaptation and mitigation of climate change [31, 32].

This is especially true considering that there are few studies in relation to seed germination of native tree species under the elevated temperature and CO_2 concentration in Korea. Therefore, we evaluated the effects on seed germination characteristics of tree species under different temperatures and CO_2 concentrations.

2 Materials and methods

2.1 Plant materials

Mature seeds of 17 forest tree species (5 needle-leaf and 12 broad-leaf tree species), which are major tree species in Korea, were collected from natural or artificial forests on October 2015 (Table 1) and stored in a refrigerator at -18°C before the experiments. The viability of seeds evaluated by tetrazolium (TZ) assay was as in Table 2. For breaking dormancy, the seeds were stratified at 4°C for 60 days or soaked in hot water (100°C) for 60 s followed by cold tap water for 1 day before imposing the temperature and CO_2 treatments (Table 2).

2.2 Experimental design

The seed trial was carried out in four walk-in chambers (3 × 3 × 1.8 m) that allowed controllable conditions corresponding to each treatment at the Department of Forest Genetic Resources in the National Institute of Forest Science (NIFoS), Suwon City, Gyeonggido, Korea.

The temperature and CO_2 concentration in each chamber varied depending on the treatment: T1 as a control (24°C, ambient air CO_2), T2 (27°C, ambient air CO_2), T3 (24°C, enriched air CO_2), and T4 (27°C, enriched air CO_2). The temperature and CO_2 concentration employed in the experiment were based on the annual mean temperature (24°C) during the growing season of May to September and annual mean CO_2 level (400 µmol CO_2 mol air^{-1}) in Korea, and the projected temperature and CO_2 level (27°C, 750 µmol CO_2 mol air^{-1}) at the end of the 21st century (2071–2100) according to the IPCC scenario [33]. The air in the chambers was circulated through charcoal filters and CO_2 was mixed into the air stream. During the whole experimental period, the relative humidity was maintained at 68 ± 1% and illumination at a photon flux density of 400 µmol m^{-2} s^{-1} during a 16-h photoperiod.

Table 1. Seed collection sites and annual mean (minimum, maximum) temperature of 17 tree species

Scientific name	Abbreviation	Seed collection sites	Annual mean temperature (℃) 1981-2010	Annual mean temperature (℃) 2015	Remarks
Chamaecyparis pisifera (Siebold & Zucc.) Endl.	*Cpi*	Yeosu	14.0 (11.3, 18.0)	15.3 (12.5, 18.6)	Introduced
Larix kaempferi (Lamb.) Carriere	*Lka*	Chungju	11.2 (5.9, 17.7)	12.9 (7.5, 19.0)	Introduced
Picea jezoensis (Siebold & Zucc.) Carriere	*Pje*	Mt. Jiri	Not collected	8.5 (0.7, 14.0)	Native
Pinus densiflora Siebold & Zucc.	*Pde*	Suwon	12.0 (7.5, 17.2)	13.6 (9.0, 19.1)	Native
Pinus thunbergii Parl.	*Pth*	Yeosu	14.0 (11.3, 18.0)	15.3 (12.5, 18.6)	Native
Albizia kalkora Prain	*Aka*	Mokpo	13.9 (10.3-18.6)	14.8 (11.5, 18.8)	Native
Betula ermanii Cham.	*Ber*	Mt. Jiri	Not collected	8.5 (0.7, 14.0)	Native
Corylopsis gotoana var. *coreana* (Uyeki) T.Yamaz.	*Cgoc*	Suwon	12.0 (7.5, 17.2)	13.6 (9.0, 19.1)	Native
Fraxinus rhynchophylla Hance	*Frh*	Suwon	12.0 (7.5, 17.2)	13.6 (9.0, 19.1)	Native
Maackia amurensis Rupr.	*Mam*	Chungju	11.2 (5.9, 17.7)	12.9 (7.5, 19.0)	Native
Malus baccata (L.) Borkh.	*Mba*	Suwon	12.0 (7.5, 17.2)	13.6 (9.0, 19.1)	Native
Prunus padus L.	*Ppa*	Chungju	11.2 (5.9, 17.7)	12.9 (7.5, 19.0)	Native
Rhododendron mucronulatum Turcz.	*Rmu*	Suwon	12.0 (7.5, 17.2)	13.6 (9.0, 19.1)	Native
Rhododendron mucronulatum var. *ciliatum* Nakai	*Rmuc*	Mt. Jiri	Not collected	8.5 (0.7, 14.0)	Native
Rhododendron schlippenbachii Maxim.	*Rsc*	Suwon	12.0 (7.5, 17.2)	13.6 (9.0, 19.1)	Native
Rhododendron tschonoskii Maxim.	*Rts*	Mt. Jiri	Not collected	8.5 (0.7, 14.0)	Native
Zelkova serrata (Thunb.) Makino	*Zse*	Imsil	11.2 (5.5, 18.0)	12.5 (7.0, 19.1)	Native

Table 2. Initial viability, dormancy type, pretreatment method and substrates of 17 tree species seeds

Scientific name	Viability (%)	Dormancy	Pretreatment	Substrate	References
Chamaecyparis pisifera (Siebold & Zucc.) Endl.	20	No	NT	petri dish	[52]
Larix kaempferi (Lamb.) Carriere	86	Shallow	CS	petri dish	[52]
Picea jezoensis (Siebold & Zucc.) Carriere	55	Shallow	CS	petri dish	[52]
Pinus densiflora Siebold & Zucc.	70	No	NT	petri dish	[52]
Pinus thunbergii Parl.	100	No	NT	petri dish	[52]
Albizia kalkora Prain	30	Hard seedcoat	SWC	soil	[63]
Betula ermanii Cham.	49	Shallow	CS	petri dish	[52]
Corylopsis gotoana var. *coreana* (Uyeki) T.Yamaz.	66	Shallow	CS	soil	[64]
Fraxinus rhynchophylla Hance	57	Embryo/Hard seedcoat	CS	soil	[52]
Maackia amurensis Rupr.	25	No	NT	soil	[65]
Malus baccata (L.) Borkh.	69	Embryo	CS	soil	[52]
Prunus padus L.	46	Embryo/Hard seedcoat	CS	soil	[52]
Rhododendron mucronulatum Turcz.	61	No	NT	petri dish	[52]
Rhododendron mucronulatum var. *ciliatum* Nakai	81	No	NT	petri dish	[52]
Rhododendron schlippenbachii Maxim.	75	No	NT	petri dish	[52]
Rhododendron tschonoskii Maxim.	65	No	NT	petri dish	[52]
Zelkova serrata (Thunb.) Makino	50	Embryo	CS	soil	[66]

NT: non-pretreatment, CS: cold stratification at 4°C for 60 days, SWC: soaking in hot water (100°C) for 60 s and then cold tap water for 1 day, Soil = peat moss : perlite = 1 : 1

2.3 Seed germination test

After pretreatments and stratifications, the seeds of the different treatments were left to germinate in the light/dark (16 h/8 h a day) in a sand pot (1 cm depth from the soil surface) or in a 90 mm Petri dish with five replications. Each containing 50 seeds was evaluated for germination. The sand pots and Petri dishes were constantly rearranged to avoid positional bias once a week and the four chambers were switched once a month to reduce chamber effects on seed germination.

Seeds in the Petri dish were considered to have germinated once the radicle had protruded by 1 mm, and seeds in the soil pot were considered to have germinated when new stem tips were observed on the soil surface every day for 60 days after sowing.

Germination percent (GP) was determined using the following equation: $GP = SG/TS \times 100$, where GP = percent germination, SG = seeds germinated, and TS = total seeds planted. Mean germination time (MGT) was calculated using the following formula: $MGT = \Sigma(n \times d)/N$, where n = number of seeds germinated on each day, d = number of days from the beginning of test, and N = total number of seeds germinated at the termination of the experiment.

2.4 Statistical analysis

All data were statistically analyzed using analysis of variance of a completely randomized design. Means were compared using the Duncan multiple range test (DMRT) at the 5% level. Statistical analyses were conducted using SAS System for Windows, Version 8.01 (SAS Institute, USA).

3 Results

3.1 Germination Percent (GP)

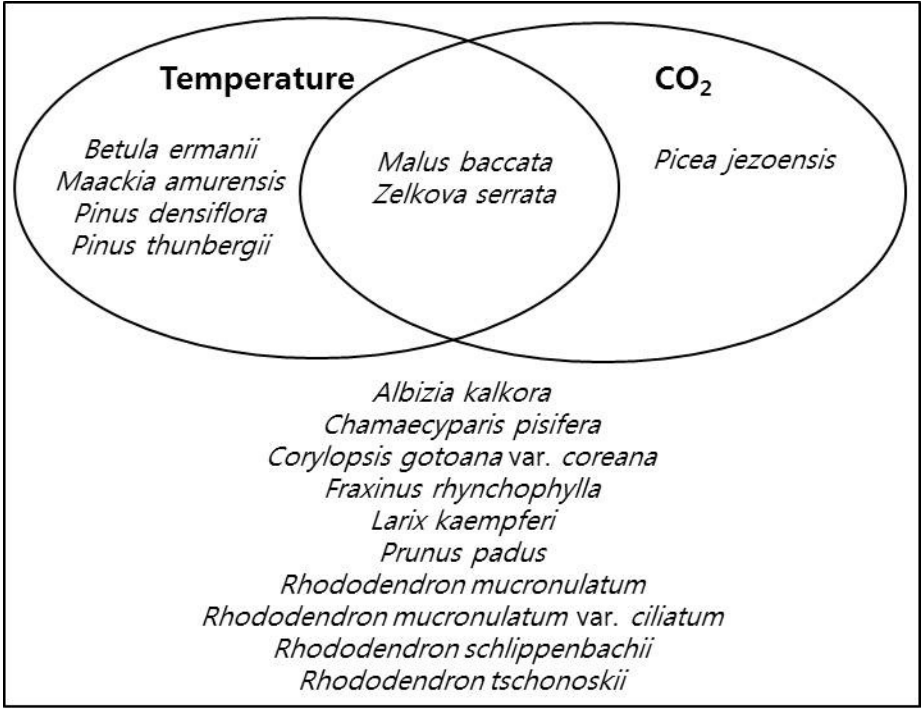
The higher temperature and enriched CO_2 had a positive or negative influence on GP of 17 tree seeds (Table 3, Figure 1). GP of two needle-leaf seeds (*P. densiflora* and *P. thunbergii*) and two broad-leaf seeds (*B. ermanii* and *M. amurensis*) were significantly affected by the higher temperature, and only the *P. jezoensis* seed was significantly changed by the enriched CO_2 ($p < 0.05$). The changes of GP in response to the elevated temperature and CO_2 were observed in two broad-leaf seeds (*M. baccata* and *Z. serrata*) of the 17 tree species.

Table 3. Effects of the elevated temperature and CO_2 concentration on germination percent of seventeen tree species seeds

Scientific name	F value		
	Temperature	CO_2	Temperature × CO_2
Chamaecyparis pisifera (Siebold & Zucc.) Endl.	0.15n.s.	2.02n.s.	0.02n.s.
Larix kaempferi (Lamb.) Carriere	0.21n.s.	1.24n.s.	0.52n.s.
Picea jezoensis (Siebold & Zucc.) Carriere	3.70n.s.	5.78*	4.08n.s.
Pinus densiflora Siebold & Zucc.	5.20*	4.11n.s.	0.58n.s.
Pinus thunbergii Parl.	26.53***	0.89n.s.	2.32n.s.
Albizia kalkora Prain	0.20n.s.	3.59n.s.	1.83n.s.
Betula ermanii Cham.	7.67*	0.28n.s.	2.94n.s.
Corylopsis gotoana var. *coreana* (Uyeki) T. Yamaz.	1.62n.s.	2.63n.s.	1.34n.s.
Fraxinus rhynchophylla Hance	4.63n.s	1.06n.s.	0.71n.s.
Maackia amurensis Rupr.	5.24*	0.03n.s.	1.52n.s.
Malus baccata (L.) Borkh.	13.11**	12.46**	1.25n.s.
Prunus padus L.	2.05n.s.	2.05n.s.	4.82*
Rhododendron mucronulatum Turcz.	2.23n.s.	0.10n.s.	0.92n.s.
Rhododendron mucronulatum var. *ciliatum* Nakai	0.35n.s.	0.04n.s.	0.04n.s.
Rhododendron schlippenbachii Maxim.	0.17n.s.	0.01n.s.	0.52n.s.
Rhododendron tschonoskii Maxim.	0.04n.s.	2.61n.s.	0.83n.s.
Zelkova serrata (Thunb.) Makino	47.06***	11.76**	8.30*

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; n.s., non-significance

(A) Germination percent



(B) Mean germination time

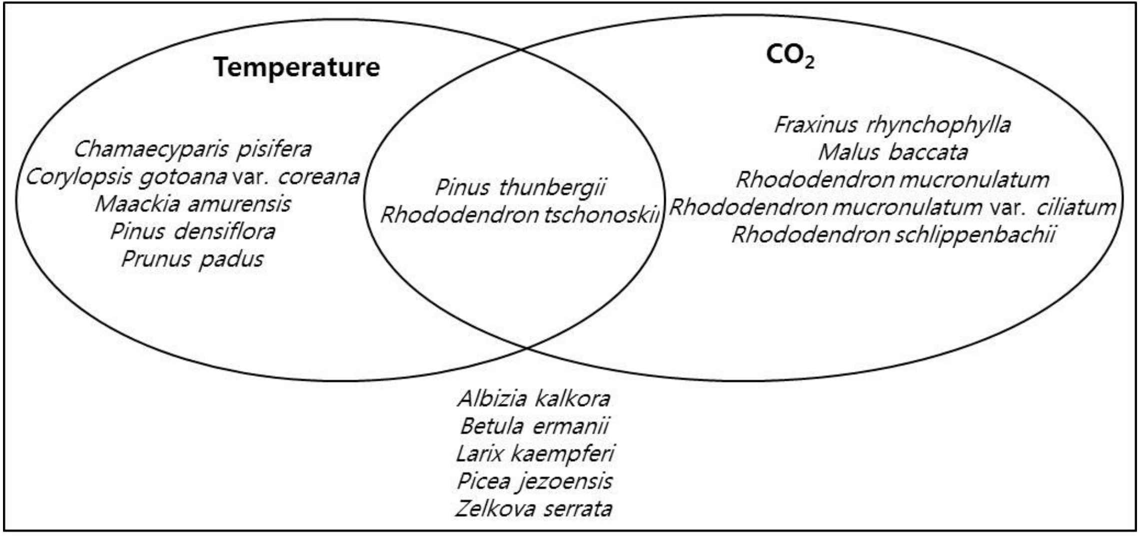


Figure 1. Tree species responses on seed germination percent and mean germination time under the elevated temperature and CO_2 concentration

Effects of the elevated temperature and CO_2 are described in Figure 2. Germination of *Chamaecyparis pisifera* and *Larix kaempferi* seeds was not affected at all by increased temperature and CO_2 concentration. GP of *P. jezoensis* seed was the lowest under the higher temperature and the enriched CO_2 (27°C + 750 µmol CO_2 mol air^{-1}) ($p < 0.05$) conditions. It was not affected by the elevated CO_2 concentration under the ambient temperature (24°C) but was significantly lower under enriched CO_2 and higher temperature (27°C). GP of *P. densiflora* seed was the lowest when both temperature and CO_2 were elevated (27°C + 750 µmol CO_2 mol air^{-1}). The enriched CO_2 influenced the reduction of GP, which was significantly higher at the elevated temperature (27°C) than at the ambient temperature (24°C) ($p < 0.05$). At the ambient CO_2, the higher temperature (27°C) induced the lower GP, and the effect of temperature change was more clearly evident under the enhanced CO_2. GP of *P. thunbergii*

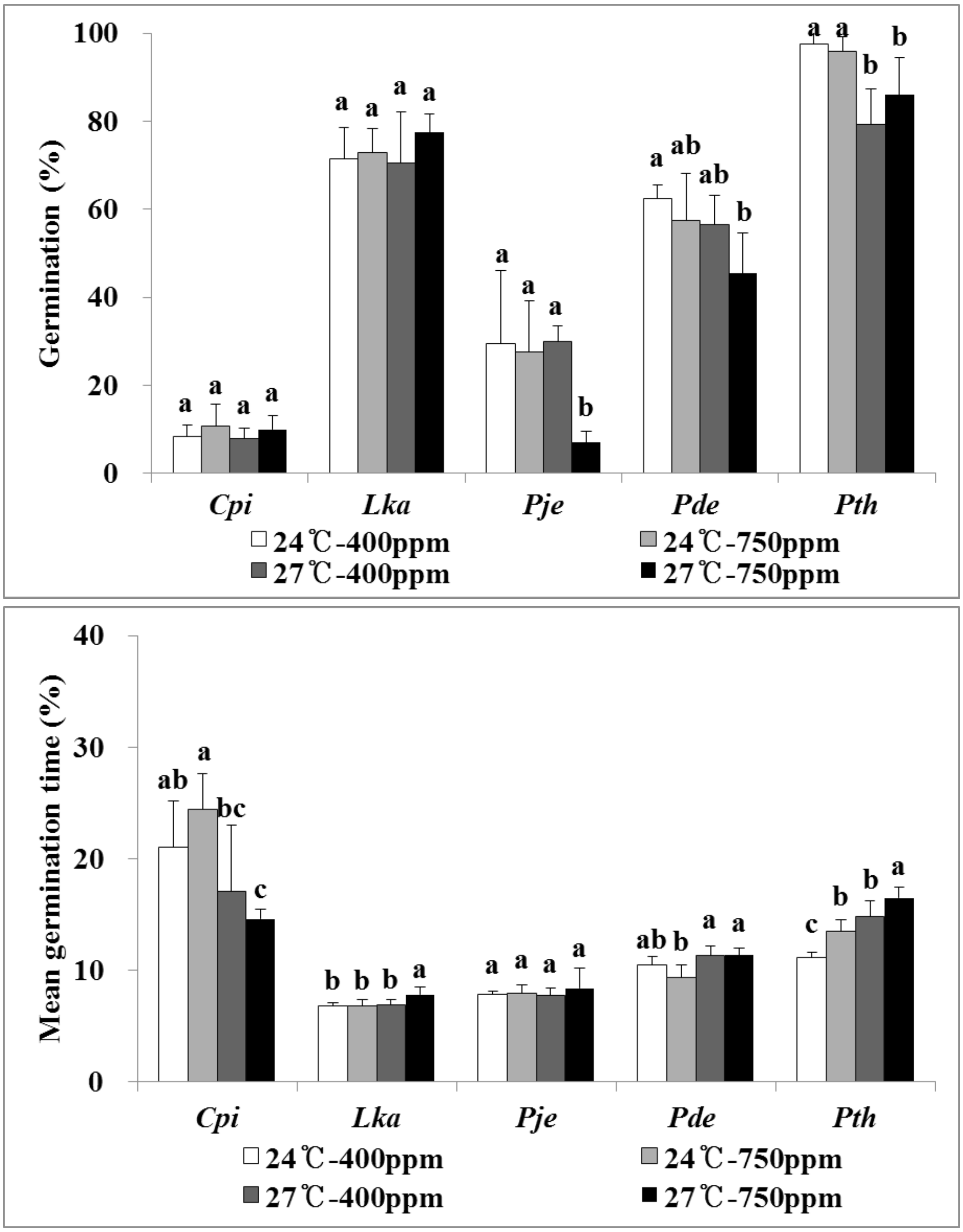


Figure 2. Seed germination percent (top) and mean germination time (bottom) of five needle-leaf tree species under the elevated temperature and CO_2 concentration. All the values are mean of five replicates ± standard deviation (SD); the same letters are not significantly different at the 5% probability level by the Duncan's multiple range tests.

seed was higher at the ambient temperature (24°C) than at the higher temperature (27°C), and there was no effect under the different CO_2 concentrations.

Germination pattern of broad-leaf seeds was significantly different from those of needle-leaf seeds ($p < 0.05$) (Figure 3). GP of *B. ermanii* seed was higher under the higher temperature (27°C), whereas there was no effect by the enhanced CO_2. The temperature effect on seed germination was clearer under the ambient CO_2 (400 µmol CO_2 mol air^{-1}) than the enriched CO_2 (750 µmol CO_2 mol air^{-1}). GP of *M. baccata* seed was influenced by the change of both temperature and CO_2 concentration ($p < 0.05$). Particularly, it was lower under the higher temperature (27°C) and was observed to be more significant under the elevated CO_2 (750 µmol CO_2 mol air^{-1}). The GP of *Z. serrata* seed was highly sensitive to the changes of both temperature and CO_2 concentration, and was significantly lower under the conditions of higher temperature and CO_2 concentration. In particular, the effect of CO_2 concentration was stronger at the ambient temperature (24°C) than at the elevated temperature (27°C).

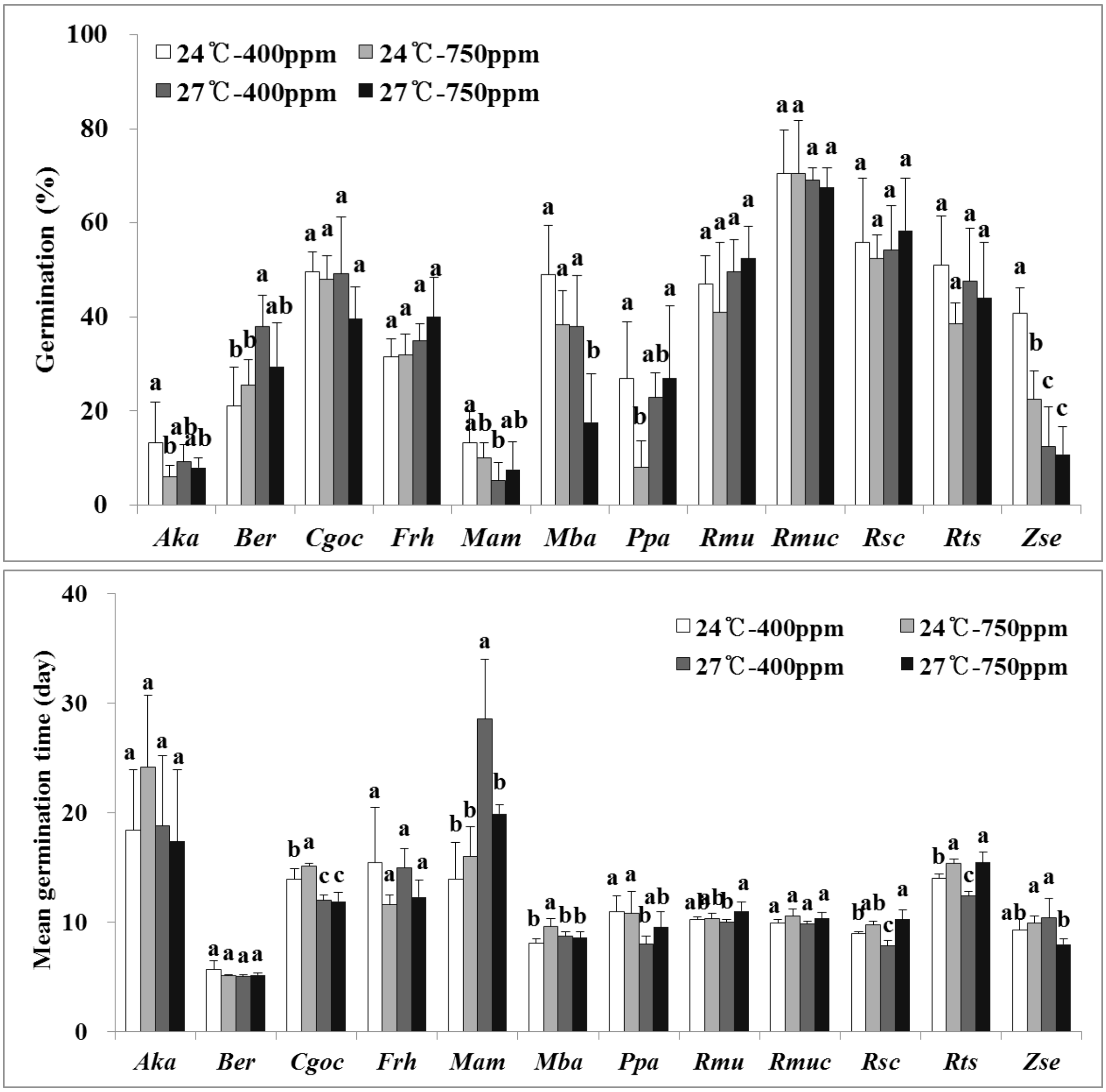


Figure 3. Seed germination percent (top) and mean germination time (bottom) of twelve broad-leaf tree species under the elevated temperature and CO_2 concentration. All the values are mean of five replicates ± standard deviation (SD); the same letters are not significantly different at the 5% probability level by the Duncan's multiple range tests.

3.2 Mean Germination Time (MGT)

MGTs of three needle-leaf tree seeds (*C. pisifera*, *P. densiflora* and *P. thunbergii*) were significantly influenced by the change of temperature ($p < 0.05$). In particular, MGT of *P. thunbergii* seed was affected by the changes of both temperature and CO_2 concentration (Table 4, Figure 1).

MGT of *C. pisifera* seed was lower under the higher temperature (27°C) regardless of CO_2 concentration (Figure 2). In contrast, MGT of *L. kaempferi* seed was the highest under the higher temperature and enriched CO_2 (27°C + 750 μmol CO_2 mol air^{-1}) conditions, and that of *P. densiflora* seed was higher under the higher temperature (27°C) regardless of CO_2 concentration (Figure 2). In addition, MGT of *P. thunbergii* seed was the lowest under the ambient temperature and CO_2 (24°C + 400 μmol CO_2 mol air^{-1}) and the highest under the higher temperature and enriched CO_2 (27°C + 750 μmol CO_2 mol air^{-1}) conditions

In the case of broad-leaf tree species, MGTs of *Corylopsis gotoana* var. *coreana*, *Maackia amurensis* and *Prunus padus* seeds were affected by the alteration of temperature, while those of *Fraxinus rhynchophylla*, *Malus baccata*, *Rhododendron mucronulatum*, *R. mucronulatum* var. *ciliatum* and *R. schlippenbachii* seed were influenced by the change of CO_2 concentration (Table 4). On the other hand, MGT of *R. tschonoskii* seed was significantly affected by the change of both temperature and CO_2

Table 4. Effects of the elevated temperature and CO_2 concentration on mean germination time of seventeen tree species seeds

Scientific name	**F value**		
	Temperature	**CO_2**	**Temperature × CO_2**
Chamaecyparis pisifera (Siebold & Zucc.) Endl.	14.80**	0.06n.s.	2.78n.s.
Larix kaempferi (Lamb.) Carriere	4.39n.s.	3.61n.s.	2.59n.s.
Picea jezoensis (Siebold & Zucc.) Carriere	0.09n.s.	0.41n.s.	0.30n.s.
Pinus densiflora Siebold & Zucc.	10.28**	1.53n.s.	1.82n.s.
Pinus thunbergii Parl.	54.90***	19.84***	0.58n.s.
Albizia kalkora Prain	1.71n.s.	0.84n.s.	2.23n.s.
Betula ermanii Cham.	1.67n.s.	1.09n.s.	2.76n.s.
Corylopsis gotoana var. *coreana* (Uyeki) T. Yamaz.	69.18***	3.46n.s.	4.49n.s.
Fraxinus rhynchophylla Hance	0.00n.s.	5.11*	0.16n.s.
Maackia amurensis Rupr.	18.48***	1.54n.s.	6.27*
Malus baccata (L.) Borkh.	0.54n.s.	8.83**	10.44**
Prunus padus L.	9.21*	1.07n.s.	1.48n.s.
Rhododendron mucronulatum Turcz.	0.63n.s.	4.83*	3.00n.s.
Rhododendron mucronulatum var. *ciliatum* Nakai	0.40n.s.	5.85*	0.04n.s.
Rhododendron schlippenbachii Maxim.	1.42n.s.	35.55***	8.62*
Rhododendron tschonoskii Maxim.	7.84*	59.27***	9.92**
Zelkova serrata (Thunb.) Makino	0.70n.s.	3.28n.s.	8.64**

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; n.s., non-significance

concentration. Meanwhile, MGTs of *M. amurensis*, *M. baccata*, *R. schlippenbachii*, *R. tschonoskii* and *Z. serrata* seeds responded to the interaction between temperature and CO_2 concentration (Table 4).

MGT of *C. gotoana* var. *coreana* seed was the highest under ambient temperature and enriched CO_2 (24°C + 750 µmol CO_2 mol air^{-1}) and the lowest under the higher temperature (27°C) regardless of CO_2 concentration (Figure 3). MGT of *M. amurensis* seed was more sensitive to temperature change than to CO_2 change, and it was the highest under higher temperature and ambient CO_2 (27°C + 400 µmol CO_2 mol air^{-1}). MGT of *M. baccata* seed was the highest under ambient temperature and enriched CO_2 (24°C + 750 µmol CO_2 mol air^{-1}) and that of *P. padus* seed was the lowest under the higher temperature and ambient CO_2 (27°C + 400 µmol CO_2 mol air^{-1}) conditions. MGT of *R. mucronulatum* seed was the lowest under the higher temperature and ambient CO_2 (27°C + 400 µmol CO_2 mol air^{-1}) conditions, but the highest under higher temperature and enriched CO_2 (27°C + 750 µmol CO_2 mol air^{-1}). MGTs of *R. schlippenbachii* and *R. tschonoskii* seeds were also the lowest in the higher temperature and the ambient CO_2 (27°C + 400 µmol CO_2 mol air^{-1}) conditions and the highest under higher temperature and enhanced CO_2 (27°C + 750 µmol CO_2 mol air^{-1}). Lastly, the MGT of *Z. serrata* seed was the lowest under the higher temperature and enriched CO_2 (27°C + 750 µmol CO_2 mol air^{-1}) conditions.

4 Discussion

Each individual species has a base and ceiling temperature that represents the extremes at which germination can occur. Below and above these extremes no germination can occur [34]. If climate change results in temperatures that exceed the ceiling for a species, then that species will not be able to germinate; thus, affecting its survivability.

In our study, seed germination of 6 species were affected by the higher ambient temperature (Figure 1), and GP of 5 tree seeds, except for *B. ermanii*, was reduced at the higher temperature. In addition, elevated temperature affected MGTs of 7 species of 17 tree seeds. MGTs of *P. densiflora*, *P. thunbergii*, and *M. amurensis* seed were higher under the higher temperature, but MGTs of *C. pisifera*, *C. gotoana* var. *coreana* and *P. padus* seed were lower under the higher temperature.

Several researchers have shown that the optimal temperature for germination and seedling growth depends on the species [35, 36]. Generally, temperature plants germinate between 0°C and 35°C whereas tropical plants germinate between 10°C to 45°C. Within the species, optimal temperature varies significantly between the genotypes [37], and high temperature tolerance of seed contributes to the attributes of the species [38].

Our findings also showed a variety of species responses to the increase in temperature, as was the case in previous studies. This means that the optimum temperature range for seed germination in 17 species is different. This is due to the different seed shapes (seed size and weight) and physiological characteristics found in each species.

In our results, three species (*P. densiflora*, *P. thunbergii* and *M. amurensis*) seeds that showed lower GP had higher MGT at the higher temperature (Figure 2), which means delayed seed germination at the higher temperature. In particular, seeds of *Pinus* species were highly sensitive to higher temperature and lost their germinability due to decay under the higher temperature. In an accelerated aging test of *Pinus* seeds, high temperature accelerated pine seed aging [39]. This suggests that the failure to germinate was more likely a consequence of seed mortality rather than of delayed or aborted germination. It is generally known that the higher the temperature, exposure to any temperature beyond the optimum range for germination can negatively affect seed germination, as in the above three species [34].

Germination substrate can also affect seed germination. In our study, the seeds of *M. baccata* and *Z. serrata* germinated in sand decreased in GP at higher temperatures (Figure 3). Many studies have shown that seeds germinated in the soil have seen a decrease in germination percent at higher temperatures [40]. Several factors under high soil temperature are considered key to germination reduction: maximum temperature attained [41, 42], soil moisture and seed water content [43], seed structure, anatomy and morphology (e.g. size, seed coat) [44], and seed dormancy dynamics [41]. However, the relative importance of any individual factor is difficult to assess, and maximum temperature and heat duration are considered foremost to seed germination reduction [45]. Much of the literature assumes an inverse relationship between temperature and duration [46]. The long term exposure of the seeds at higher temperatures, as shown in our experiments, may be the main cause of the decline in seed germination.

As shown above, high temperature has a detrimental effect on seed germination causing thermos-inhibition [47], and temperature causing thermo-dormant changes varies with the genotype [48]. In general, high temperatures reinforce dormancy or may even induce it [49]. A drastic change in temperature will also have a significant effect on germination due to the temperature dependence of hormones and enzymes. If the temperature window is breached, then these enzymes may become inactive [50].

However, unlike the above results, high temperatures sometimes break internal dormancy and stimulate germination [51]. In our study, *B. ermanii* seeds have increased their GP at high temperature (Figure 3). This is also due to the different temperature ranges of optimum germination for *Betula* species. Birch seeds such as *B. ermanii* require relatively high temperatures to germinate. The optimal germination temperature range for birch seeds is 30°C for 8 hours and 20°C for 16 hours [52]. Further, several reasons have been given for the enhancement of seed germination by high temperature. Among these are fracturing of hard seed coats, stimulation of seed embryos, and desiccation of seed coats [53].

High temperatures also increase the speed of germination [34]. This is because high temperatures can speed up the chemical reaction in seed germination [54]. In our results, the lower MGT of *C. gotoana* var. *coreana* and *P. padus* seeds with impermeable hard seed coat were more pronounced at the elevated temperature (Figure 3). However, germination speed can differ according to species, soil structures, sowing methods and especially temperature and soil moisture rations [54].

CO_2 has been shown to stimulate the germination of various seeds at relatively high concentration [55]. Doubling the CO_2 concentration resulted in an increase in the speed and final percent of germination, for *Medicago sativa*, *Amaranthus hybridus* and *Chenopodium album* [25].

Unlike the above results, in our study, an increase in CO_2 concentrations did not contribute positively to seed germination. CO_2 enrichment affected seed GPs of only three species (*M. baccata*, *Z. serrata*, and *P. jezoensis*) out of 17 tree species (Figure 1). Seed germination of the three species was significantly lower under CO_2 enrichment (Figure 2). As such, the effects of seed germination on CO_2 changes appear to vary from species to species. Corbineau and Côme [56] were suggested that CO_2 does not always have a beneficial effect on seed germination. Several reports mention that at high concentration it inhibits the germination of some seeds. In addition, Omer and Horyath [57] suggested that increased CO_2 concentration does not significantly affect the seed germination of many plants, but could cause variations in seed germination patterns as a result of our study.

CO_2 enhancement significantly influenced the seed MGTs of 7 tree species, and seeds of 6 tree species, except *F. rhynchophylla*, showed significantly higher MGT under CO_2 enhancement (Figure 3). Similar to the results of our study, previous studies have shown that elevated CO_2 concentration can have different influences on seed germination and emergence among different species [25]. In particular, our studies show that *F. rhynchophylla* seed has a positive effect of a reduction in the MGT from high CO_2 unlike other species, but it is not easy to find the cause. However, these species were germinated in the soil unlike other species, and they had different types of dormancy.

In addition, the effect of CO_2 concentration on seed germination may even differ among genotypes of the same species, and there is a strong interaction between genotype and treatment. This means that genetic variation for a selective response to changes in CO_2 concentration may be present in natural populations [26].

Although the germination response to CO_2 has been suggested to be generally positive because of an enhancement in ethylene production due to CO_2 [58], many studies have shown contradictory results, similar to our study results [59]. Summing up, the effect of CO_2 enrichment on seed germination is very different among different species, and their effects may be positive [60], neutral [61], or negative [26], with a strong dependence on the species studied [62]. No significant interaction was observed between CO_2 and temperature on the germination response [25], and this was also re-confirmed in our study.

In conclusion, increased temperature and CO_2 had a direct effect on seed germination characteristics, but the direct effect of the increase in CO_2 on seed germination was relatively minor. Also, two factors exerted stronger influences on germination pattern (such as MGT) rather than seed GP of woody plants. On the other hand, the germination effects of seeds from changes in temperature and CO_2 concentration varied greatly depending on the species. Various factors appear to be involved in the interspecific differences, including seed morphological structure, dormancy type, germination substrate, and optimum germination temperatures. These results indicate that if the increase in temperature has negative effects total germination and germination speed, persistence of individual species will be altered and the distribution of species could change. Similarly, if increasing temperatures have a differential positive effect on germination of some species, then these species will promote their fitness and also change their distribution. This has incredible ecological and economic effects for the local ecosystems and surrounding areas. However, more accurate and more data is needed to predict the species distribution changes due to temperature and CO_2 changes. In other words, additional research should be continued in order to more accurately interpret the effects of seed germination on species, considering various factors including natural conditions.

Acknowledgements: This study was supported by the Dong-A University research fund.

Conflict of interest: Authors state no conflict of interest

References

[1] WMO, The state of greenhouse gases in the atmosphere based on global observations through 2016, WMO Greenhouse Gas Bulletin, 2017

[2] Korea Meteorological Administration, Annual Climatological Report, 2016

[3] IPCC, Climate Change 2014, Mitigation of climate change, 2015

[4] Lenoir J., Gegout J.C., Marquet P.A., de Ruffray P., Brisse H., A significant upward shift in plant species optimum elevation during the 20th century, Science, 2008, 320, 1768-1771

[5] Sherry R.A., Zhou X.H., Gu S.L., Arnone J.A., Schimel D.S., Verburg P.S., et al., Divergence of reproductive phenology under climate warming, Proc. Natl. Acad. Sci. USA, 2007, 104, 198-202.

[6] Grubb P.J., The maintenance of species-richness in plant communities: The importance of the regeneration niche, Biol. Rev., 1977, 52, 107-145

[7] Harper J.L., Population biology of plants, Academic Press, London, UK, 1977

[8] Christie D.A., Armesto J.J., Regeneration microsites and tree species coexistence in temperate rain forests of Chiloe Island, Chile, J. Eco., 2003, 91, 776-784

[9] Gorai M., Neffati M., Germination responses of *Reaumuria vermiculata* to salinity and temperature, Ann. Appl. Biol., 2007, 151, 53-59

[10] Lloret F., Peñuelas J., Estiarte M., Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean type community, Global Change Biol., 2004, 10, 248-258

[11] Fay P.A., Schultz M.J., Germination, survival, and growth of grass and forb seedlings: effects of soil moisture variability, Acta Oecol., 2009, 35, 679-684

[12] Dalgleish H.J., Koons D.N., Adler P.B., Can life-history traits predict the response of forb populations to changes in climate variability, J. Eco., 2010, 98, 209-217

[13] Dong W., Jiang Y., Yang S., Response of the starting dates and the lengths of seasons in mainland China to global warming, Clim. Change, 2010, 99, 81-91

[14] Walck J.L., Baskin J.M., Baskin C.C., A comparative study of the seed germination biology of a narrow endemic and two geographically wide spread species of Solidago (Asteraceae), 1. Germination phenology and effect of cold stratification on germination, Seed Sci. Res., 1997, 7, 47-58

[15] Walck J.L., Hidayati S.N., Dixon K.W., Thompson K., Poschlod P., Climate change and plant regeneration from seed, Glob. Change Biol., 2011, 17, 2145-2161

[16] Pautasso M., Dehnen-Schmutz K., Holdenrieder O., Pietravalle S, Salama N., Jeger M.J., Lange E., et al., Plant health and global change: some implications for landscape management, Biol. Rev., 2010, 85, 729-755

[17] Hedhly A., Hormaza J.I., Herrero M., Global warming and sexual plant reproduction, Trends in Plant Sci., 2009, 14, 30-36

[18] Ungar I.A., Seed germination and seed-bank ecology of halophytes. In: J. Kigel, G. Galili (Ed.), Seed Development and Germination. New York, NY, USA: Marcel Dekker Inc., 1995, 599-627

[19] Huang Z., Zhang X.S., Zheng G.H., Gutterman Y., Influence of light, temperature, salinity and storage on seed germination of *Haloxylon ammodendron,* J. Arid Environ., 2003, 55, 453-464

[20] El-Keblawy A., Al-Rawai A., Effects of salinity, temperature and light on germination of invasive *Prosopis juliflora* (Sw.) D.C., J. Arid Environ., 2005, 6, 555-565

[21] El-Keblawy A., Al-Rawai A., Effects of seed maturation time and dry storage on light and temperature requirements during germination in invasive *Prosopis juliflora,* Flora, 2006, 201, 135-143

[22] Neffati M., Caractérisation morphologique de certaines espèces vég tales nord-africaines, Implications pour l'amélioration pastorale, PhD thesis, Gent University, Belgium, 1994

[23] Gorai M., Vadel M.A., Neffati M., Seed germination characteristics of *Phragmites communis*: Effects of temperature and salinity, Belg. J. Bot., 2006, 139: 78–86

[24] Marty C., BassiriRad H., Seed germination and rising atmospheric CO_2 concentration: a meta-analysis of parental and direct effects, New Phytol., 2014, 202, 401-414

[25] Ziska L.H., Bunce J.A., The influence of elevated CO_2 and temperature on seed germination and emergence from soil, Filed Crops Res., 1993, 34, 147-157

[26] Andalo C., Godele B., Lefranc M., Mousseau M., Till-Bottraud I., Elevated CO_2 decreases seed germination in *Arabidopsis thaliana*, Global Change Biol., 1996, 2, 129-135

[27] Leishman M.R., Sanbrooke K.J., Woodfin R.M., The effects of elevated CO_2 and light environment on growth and reproductive performance of four annual species, New Phytol., 1999, 144, 455-462

[28] Mohan J.E., Clark J.S., Schlesinger W.H., Genetic variation in germination, growth, and survivorship of red maple in response to subambient through elevated atmospheric CO_2, Global Change Biol., 2004, 10, 233-247

[29] Classen A.T., Norby R.J., Campany C.E., Sides K.E., Weltzin J.F., Climate change alters seedling emergence and establishment in an old-field ecosystem, PLoS ONE 2010, 5, 1-8

[30] Davis M.B., Lags in vegetation response to greenhouse warming, Clim. Change, 1989, 15, 75-82

[31] Box E.O., Crumpacker D.W., Hardin E.D., Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida, Clim. Change, 1999, 41, 213-248

[32] Yates D.N., Kittel T.G., Cannon R.F., Comparing the correlative Holdridge model to mechanistic biogeographical models for assessing vegetation distribution response to climate change, Clim. Change, 2000, 44, 59- 87

[33] IPCC, Climate Change 2007, The physical science basis, Cambridge University Press, 2007

[34] Finch-Savage W.E., Leubner-Metzger G., Seed dormancy and the control of germination, New Phytol., 2006, 171, 501-523

[35] Bierhuizen J.F., Wagenvoort W.A., Some aspects of seed germination in vegetables. 1. The determination and application of heat sums and minimum temperature for germination, Scientia Hort., 1974, 2, 213-219

[36] Angus J.F., Cunningham R.B., Moncur R.B., Mackenzie M.W., Phasic development in field crops I. Thermal response in the seedling phase, Field Crops Res., 1980, 3, 365-378

[37] Monteith J.R., Climatic variation and the growth of crops, Quart. J. R. Met. Soc., 1981, 107, 749-774

[38] Yuan X., Wen B., 2018. Seed germination response to high temperature and water stress in three invasive Asteraceae weeds from Xishuangbanna, SW China, PloS ONE, 2018, 13, e0191710

[39] Han S.H., Koo Y.B., Kim C.S., Oh C.Y., Song J.H., Viability determination of *Pinus rigida* seeds using artificially accelerated aging, Kor. J. Agri. For. Meteorol., 2006, 8, 10-14

[40] Koduru S., Grierson D.S., Afolyan A.J., Effects of high temperatures on seed germination of *Solanum aculeastrum*, Asian J. Plant Sci., 2006, 5, 353-356

[41] Thompson A.J., Jones N.E., Blair A.M., The effect of temperature on viability of imbibed weed seeds. Ann. Appl. Biol., 1997, 130, 123-134

[42] Melander B., Kristensen J.K., Soil steaming effects on weed seedling emergence under the influence of soil type, soil moisture, soil structure and heat duration, Ann. Appl. Biol., 2011, 158, 194-203

[43] Egley G.H., High-temperature effects on germination and survival of weed seeds in soil, Weed Sci., 1990, 38, 429-435

[44] Horowitz M., Taylorson R.B., Hardseededness and germinability of Velvetleaf (*Abutilon theophrasti*) as affected by temperature and moisture, Weed Sci., 1984, 32, 111-115

[45] Vidotto F., De Palo F., Ferrero A., Effect of short-duration high temperatures on weed seed germination, Ann. Appl. Biol., 2013, 163, 454-465

[46] Dahlquist R.M., Prather T.S., Stapleton J.J., Time and temperature requirements for weed seed thermal death, Weed Sci., 2007, 55, 619-625

[47] Parera C.A., Qiao P., Cantliffe D.J., Enhanced celery germination at stress temperature via solid matrix priming, Hort. Sci., 1993, 28, 20-22

[48] Desai, B.B., Kotecha P.M., Salunkhe D.K., Seeds handbook: biology, production, processing and storage, Marcel Dekker Inc., New York, 1996

[49] Kruk B.C., Benech-Arnold R.L., Functional and quantitative analysis of seed thermal responses in postrate knotweed (*Polygonum aviculare*) and common purslane (*Portulaca oleracea*), Weed Sci., 1998, 46, 83-90

[50] Peterson M.E., Daniel R.M., Danson M.J., Eisenthal R., The dependence of enzyme activity on temperature: determination and validation of parameters, Biochem. J., 2007, 402, 331-337

[51] de Villalobos A.E., Pelaez D.V., Boo R.M., Mayor M.D., Elia O.R., Effect of high temperatures on seed germination of *Prosopis caldenia* Burk, J. Arid Environ., 2002, 52, 371-378

[52] Bonner F.T., Karrfalt R.P., The woody plant seed manual, USDA Forest Service, Agriculture Handbook 727, 2008

[53] Baskin C.C., Baskin J.M., Seeds: ecology, biogeography, and evolution of dormancy and germination, 1st ed., San Diego, CA, USA: Academic Press, 1998

[54] Balkaya A., Modelling the effect of temperature on the germination speed in some legume crops, J. Agron., 2004, 3, 179-183

[55] Corbineau F., Bagniol S., Come D., Sunflower (*Helianthus annuus* L.) seed dormancy and its regulation by ethylene, Israel J. Bot., 1990, 39, 313-325

[56] Corbineau F., Côme D., Control of seed germination and dormancy by the gaseous environment, In: J. Kigel, G. Galili (Ed.), Seed Development and Germination, New York, Basel, Hong Kong, Marcel Dekker, Inc., 1995

[57] Omer L.S., Horvath S.M., Potential effects of elevated carbon dioxide levels on seed germination of three native plant species, Bot. Gaz., 1983, 144, 477-480

[58] Esashi Y., Ooshima Y., Michiharu A., Akiko K., Satoh S., CO_2-enhancement of C_2H_4 production in tissues of imbibed cockle bur seeds, Aust. J. Plant Physiol., 1986, 14, 417-429

[59] Ward J.K., Strain B.R., Elevated CO_2 studies: present, past and future, Tree Physiol., 1999, 19, 211-220

[60] Wulff R.D., Alexander H.M., Intraspecific variation in the response to CO_2 enrichment in seeds and seedlings of *Plantago lanceolate,* Oecologia, 1985, 66, 458-460.

[61] Garbutt K., Williams W.E., Bazzaz F.A., Analysis of the differential response of five annuals to elevated CO_2 during growth, Ecology, 1990, 71, 1185-1194

[62] Hussain M., Kubiske M.E., Connor K.F., Germination of CO_2-enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO_2 enrichment, Funct. Ecol., 2001, 15, 344-350

[63] Koffa S.N. 1983. Temperature: its effect on the pre-germination of *Albizia falcataria*, Canopy Int., 1983, 9, 5

[64] Roh M.S., Lee A.K., Suh J.K., Bordelon C.M., Interspecific variations in seed germination of *Corylopsis*, Scientia Hort., 2008, 118, 347-350

[65] Pai J.G.B., Graves W.R., Seed source affects seedling development and nitrogen fixation of *Maackia amurensis*, J. Environ. Hort., 1995, 13, 142-146

[66] Yang J.C., Kuo S.R., Lin T.P., Intermediate storage behavior and the effect of prechilling on germination of Japanese Zelkova (*Zelkova serrata*) seeds, Seed Sci. Technol., 35, 99-110