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버드나무와 갈대의 정착과 경쟁에 대한 실험적 연구

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Abstract

An experimental study on the establishment and competition of *Salix koreensis* and *Phragmites australis*

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The process of vegetation change from perennial herb to woody plant have been observed in many wetlands. For understanding the vegetational succession, it is important to know ecological characteristics at early life stage of plants and interspecific competition according to environmental condition. The goal of this study was to predict the process of initial establishment for a year from seed recruitment according to different environment condition for *Salix koreensis*, a woody plant and *Phragmites australis*, a perennial herb, which are common wetland species in Korea. This study quantifies the effects of water level, light intensity and seed storage time on germination, survival and growth of early seedlings and competition of two species.

The initial establishments from seed to 1-year-old seedlings of two species coincided each other temporally and spatially. The effects of water level (0 ㎝ and +2 ㎝) and relative light intensity (100%, 30% and 0%) on seed germination rate of two species were tested. Germination rate of *S. koreensis* varied at different relative light intensity, and that of *P. australis* was not influenced by light intensity and water level. Germination rate of both species were relatively high in all treatment (*S. koreensis*: 76.5%-97.4%, *P. australis*: 60.9%-71.5%), so flooding and shading were not limiting factor at germination of two species. Seed viability of *S. koreensis* was lost within a few days (16 days), and all seedlings originated from old seeds (10 days) died. Seedlings growth rate of both species showed peak from mid June to mid August, and *P. australis* growed quickly and largely than *S. koreensis* (final height ratio of *S. koreensis* to *P. australis* without both flooding and shading = 0.70). We examined the effect of water level (-4㎝, +1㎝, +2㎝ and +4㎝) and relatively light intensity (100% and 30%) on survival and growth of young seedlings (1 ㎝ in height). Water level (-10㎝, +4㎝ and +12 ㎝) and relatively light intensity (100% and 30%) on survival and growth of old seedlings (about 40 days in age) was also tested. When seedlings are very young (1 ㎝ in height), any *S. koreensis* seedlings could not survive under flooding of twice level as its height, but 30% of *P. australis* seedlings overcame the same flooding. In the case of about 40-day-old seedlings, flooding level of 12 ㎝ reduced the survival and growth of *S. koreensis* seedlings, but did not influence on *P. australis* seedlings. On the contrary to flooding, shading had relatively stronger influence on *P. australis* than *S. koreensis*. Shading of 70% affected survival and growth of both species irrespective of its age, but relatively more harmful to *P. australis* than *S. koreensis*. Especially, under shading of 70%, all young *P. australis* seedlings (1 ㎝ in height) could not overcome water level twice their heights, and old *P. australis* seedlings could not flower. Without both of flooding and shading, *P. australis* had relatively dominant than *S. koreensis* in competitive situation of two species. When flooding was given, *P. australis* had more relatively competitive ability, and when shading was given, *S. koreensis* did. *S. koreensis* seedlings were taller than *P. australis* under -10 ㎝-water level and 30%-light intensity, whereas *P. australis* was dominant under the others treatment.

This study shows that the competition of two species in initial establishment process is changed according to environmental conditions. Unless appropriate moisture condition for germination is formed in a few days (about eight days), *S. koreensis* could not establish from seed. Flooding has an adverse affect on establishment of both species, but is more harmful to *S. koreensis* than *P. australis,* especially right after germination. On the contrary, in shaded understory, growth of *P. australis* seedlings is worse than *S. koreensis*.

keywords : competition, establishment, flooding,
Phragmites australis, *Salix koreensis*, shading

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Introduction

Recently, the role of ecology in predicting the future status of ecosystem based on the current environmental changes has been emphasized (Molles 2008; Coreau et al. 2009). In that context, we can say that succession model that enables us to understand and predict the changes in community is ecologically meaningful. To establish the succession model, it is very important to understand the responses of individual species to certain environmental conditions. Huston and Smith (1987) proposed that we can understand how communities are formed by using a combination of life history traits and physiological traits. Ecological application based on the life history traits often leads to successful restoration case (Mahoney & Rood 1998). In wetlands, the "Environmental Sieve Model" is one of the succession model based on life history traits (van der Valk 1981). At this model, environmental factors function as a sieve, which strain aquatic plant species so that only specific species with adaptability to certain environment can establish.

Environmental factors can restrict the distribution of plants not only in spatial range but also in temporal range (Grubb 1977; Leek, Simpson & Parker 2008). That is to say, it is important that not only whether there is or not a certain environment, but when the species is caught in certain environment, because there can be difference of environmental condition favoured by plants at different stage of life cycle within a species (Rabinowitz 1978; Shipley et al. 1989).

Life cycle of plants is divided into many stages with elasticity, but it can be simply divided into four stages: seed germination, seedlings, juvenile and reproductive adult (Enright, Franco & Silvertown 1995; Leek, Simpson & Parker 2008). Occasionally, it is thought that stage of seed germination and seedlings are more important for three different reasons. First, plants are highly vulnerable and are placed in the greatest danger of mortality when they are in the ungerminated embryo, cotyledon stages and little seedlings (Kozlowski 1979). Second, "regeneration niche", containing requirement for germination success and seedling survival, being different from "habitat niche" of mature plants, is emphasized in order to explain the interaction of ecologically similar species in plant ecology (Grubb 1977; Niiyama 1990). Third, recruitment of new individual by seeds is essential to upgrade the genetic quality of communities (Kozlowski & Pallardy 1997). Therefore characteristics related to seed germination and seedling survival and growth are very important in the success of establishment of plant community (Harper 1977; Kellogg et al., 2003). Namely, success in germination and seedling survival mean success from seed bank to seedlings and seedlings to establishment, respectively.

Previous experiments of life history traits at seed germination and seedling stages have been carried out in each species independently. Because these experiments have not been performed under the same spatial and temporal conditions, it is hard to do the interspecific comparison accurately, as a result, it is not easy to predict direction of succession (Day, Doyle & Draugelis-Dale 2006). Besides environmental ranges preferred by ecologically similar species trend to overlap each other, it is hard to find delicate trait difference between species by independent studies (Kwon et al 2007; Lee et al 2007). So it is necessary to design experimental studies, comparing species appearing together, under identical conditions at the same period of time according to life cycle stages for ecological prediction. Additionally, competition experiment with different environmental conditions can be also considered.

Wetlands ecology are appropriate to study the succession based on life cycle traits and its adaptation because there are frequent environmental changes in wetland ecosystem, and those changes would cause direct and massive impact on the species composition, richness, and production (Mitsch & Gosselink 2007). Water regime is a major factor to determine patterns of community development in wetland (van der Valk 1981). Variation in flooding levels affects regeneration and plant distribution by controlling germination and seedling survival (Ferreira & Stohlgren 1999; Day, Doyle & Draugelis-Dale 2006). So, many existing experimental studies of wetland plants have dealt with water regime at stage of seed germination or seedling growth (Keddy & Ellis 1985; Coops & Velde 1995; Armstrong et al. 1999; Mauchamp, Blanch & Grillas 2001; Guilloy et al. 2011).

Light is also thought as an important abiotic factor such as water regime. Light is necessary for germination of some species, and each species requires different amount of that (Pons, 1992; Copeland and McDonald, 2001). Some studies related to light have conducted about wetland plants (Ekstam, Johannesson & Milberg 1999; Scanga 2011). Sometimes difference of intercepted light is a result of vegetation change by canopy alteration (Niinemets 2010), therefore plants' response to light is important in research of succession.

Seed longevity is also important traits to establish successfully in plant life history. Long lifespan of seeds increases the temporal opportunity that seeds meet an appropriate environment, seed longevity has important ecological implications in succession (Murdoch & Ellis, 1992; Kozlowski & Pallardy 1997).

Salix species, a woody plant and *Phragmites australis*, a perennial herb are typical wetland plants. Both of them inhabit wetland widely and commonly (Patten 1998; Mauchamp & Méth 2004; Day, Doyle & Draugelis-Dale 2006), and have large size (Haslam 1972; Lee 2002) and have strong ecological influence (Bliss & Cantlon 1957; Fiala 1976; Roman, Niering & Warren 1984; Johnson et al. 1985; Rejmánková 2011). Both species are not only used in wetland restoration or creation, but also considered as invasive and undesirable plants (Cronk & Fennessy 2001; Mitsch & Gosselink 2007). *S. koreensis*, dominant tree of *Salix* species in Korea (Lee et al. 2001), and *P. australis* frequently emerge in the same area in Korean wetlands (Kim & Ju 2005; Lee, Marrs & Lee 2011).

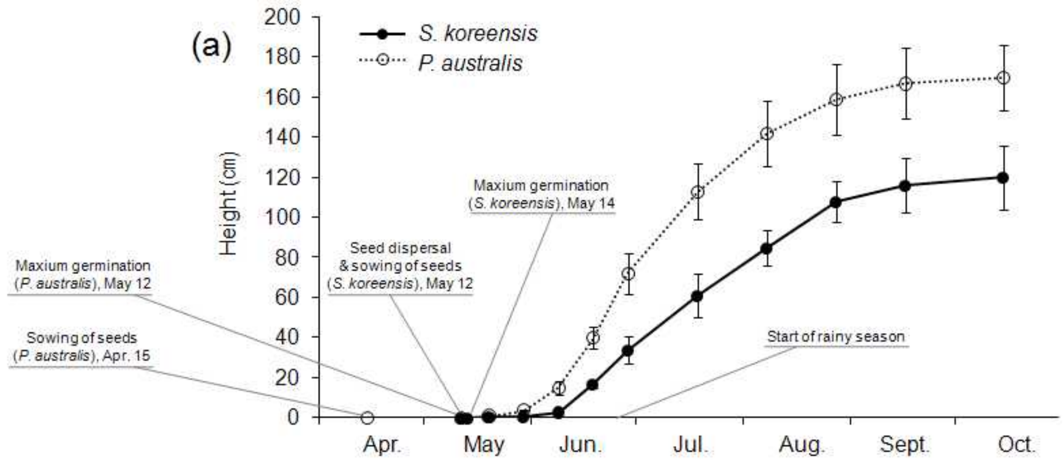
According to some studies about vegetation development in wetland, vegetation change from perennial herb to woody plant have been observed (van der Valk & Bliss 1971; Lee, You & Robinson 2002; Kim et al. 2010). Therefore comparing *S. koreensis* and *P. australis* is meaningful in study about wetland succession for understanding factors influencing that vegetation change process.

According to three stages: seed germination, young seedlings (below about 20-day-old) and old seedlings (about 40-day-old), this study quantifies the effects of water level, light intensity and seed storage time on growth and survival of *S. koreensis*, *P. australis* and their competition, under identical experiment at the same time. The goal of this study was to understand the process of initial establishment for a year from seed recruitment for *S. koreensis* and *P. australis* according to different environment condition. The specific objectives were to determine whether (1) interaction of *S. koreensis* and *P. australis* occur at initial establishment; (2) seed longevity differ between species; (3) light intensity, water level and their interaction affect germination rate, survival and growth of young seedlings (below 20-day-old) and old seedlings (above 40-day-old) of *S. koreensis* and *P. australis*; (4) light intensity, water level and their interaction affect competition; (5) the effects differ at different stages and species.

Materials and methods

1. Experiment overview

Experiments of fully crossed factorial design were conducted according to the growth stages of *S. koreensis* and *P. australis* to investigate the initial establishment for a year (Figure 1). Experiments for two species were carried out at the time, and growth stage was divided into four levels: (1) seed germination; (2) seedling survival (right after germination); (3) young seedling growth (1-6 ㎝ in height); (4) old seedling growth (at beginning rainy season). In every experiment, I used seedlings same in height to minimize the possible influences of difference in initial height. Experimental treatments were composed of light intensity, water level, elapsed time after seeds dispersal and interspecific competition of two species, and applied by appropriate levels according to growth stage. Additionally, experiments for soil seed bank and germination period of two species were performed to confirm spatial and temporal possibility of competition between two species.



(b)

Experiment	State of materials	Species	Experimental treatment				Period
			Light intensity	Water level	Elapsed time after seed dispersal	Interspecific competition	
Seed bank	Soil	-					←→
Germination period	Seed	*S. koreensis*					←→
	Seed	*P. australis*					←→
Germination rate	Seed	*S. koreensis*	○	○	○		←→
	Seed	*P. australis*	○	○	○		←→
Seedling survival	Right after germination	*S. koreensis*			○		←→
Young seedling growth	1.0 (0.7~1.3) ㎝- height	*P. australis*	○	○			←→
	1.0 (0.7~1.3) ㎝- height	*S. koreensis*	○	○			←→
	6.0 (5.0~7.0) ㎝ - height	*P. australis*	○	○			←→
Old seedling growth (rainy season)	28 (25~31) ㎝ - height	*S. koreensis*	○	○		○	←→
	63 (57~69) ㎝ - height	*P. australis*	○	○		○	←→

Figure 1. (a) Growth curve in height of *S. koreensis* and *P. australis* seedlings that grew in the experimental field (mean values ± SD, n = 20 for each species). Seedlings that height is close to mean height at each time were used in experiments. (B) Experimental set-up conducted according to growth stage for the establishment and competition of *S. koreensis* and *P. australis*, showing experimental treatment and period. The periods are connected to X axis of the figure 1 (b).

1.1. Reference site

Reference site of the experiment was riverine wetland, Wangsuk stream, Namyangju City, Gyeonggi Province, Korea (N 37° 37′25″ E 127° 08′37″). River width near the site was 30-50 m, *S. koreensis* and *P. australis* communites were wide spread, and flooding happened periodically. In order to reflect the environmental conditions of reference site into our experimental set as similar as possible, seeds of *S. koreensis* and soil seed bank were collected in that field and soil texture, soil nutrients and relative light intensity of field were measured.

1.2. Experimental place

Experiment for germination rate was conducted at growth chamber in which the maximum photosynthetic photon flux density (PPFD) was 50 $\mu mol \cdot m^{-2} \cdot sec^{-1}$. The experiments for germination period and old seedling growth (at beginning rainy season) were conducted in the experimental field at Seoul National University, Seoul City, Korea (N 37° 27′ 29″ E 127° 57′ 10″), where was 24 ㎞ away from the reference site. The annual mean temperature and precipitation in Seoul City was 12.1℃ and 2043.5 ㎜ in 2010 (Figure 2). The experiments for soil seed bank, seedling survival (right after germination) and young seedlings growth (1-6 ㎝ in height) were conducted in a greenhouse at Seoul National University. The greenhouse was constructed of glass, which transmit 99% of solar radiation, and temperature during the experiment ranged from 14 to 38℃.

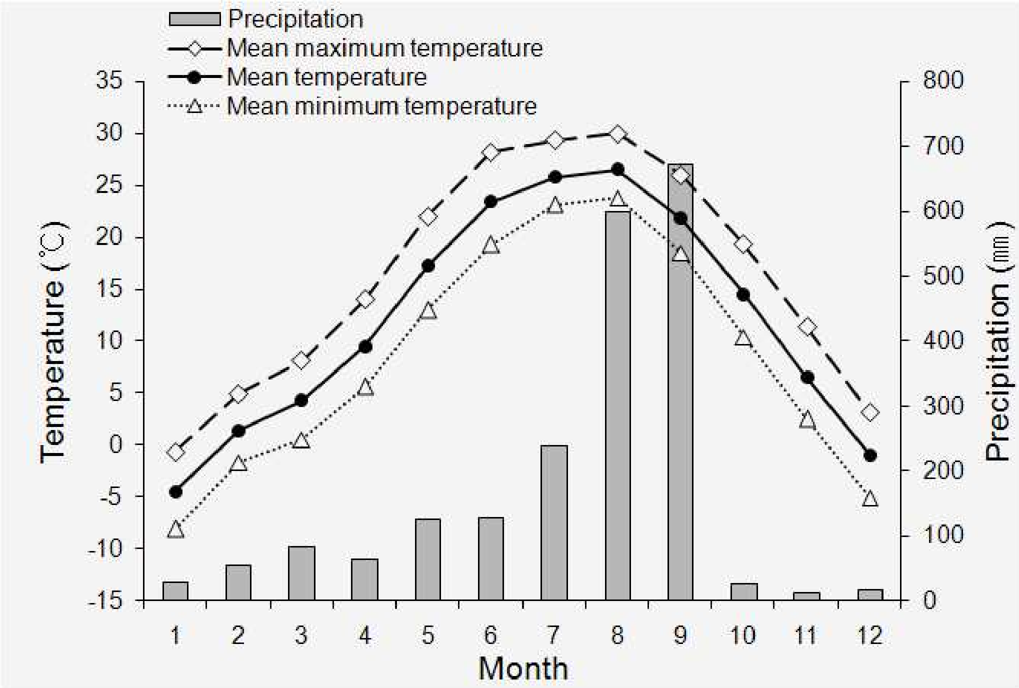


Figure 2. Climate diagram of Seoul, Korea (Korea Meteorological Administration 2010).

1.3. Decision of light intensity levels for treatment

Light intensity treatment was applied in several experiments to test the effect of shading in habitat on seed germination and seedling establishment. Relative light intensity (Photosynthetic photon flux density) was measured to decide intensity of shading by portable photometer (LI-250A Light Meter with Quantum (PAR) Sensors, LI-COR Inc., USA). Four quadrats (20 ㎝ × 20 ㎝) were randomly established under the crown of four trees species (*S. koreensis*, *S. subfragilis*, *S. pseudolasiogyne* and *Acer tataricum* subsp. *ginnala*) which are common wetland woody plants in Korea. Relative light intensity was determined as the percentage of light intensity in established quardrats relative to that out of crown, and measurements were carried out three times a day (10 a.m., 1 p.m., and 4 p.m.) during a cloudless period. The mean relative light intensity was

29.7% (SD = 20.8, n = 48), and this result was in accordance with McLeod, Reed & Nelson (2001), who reported relative light intensity was 32.1% under *S. nigra* crown. Consequently shading nets blocking 70% light intensity were used in the experiments.

1.4. Soil used in the experiments

Soil was used as growing substrate in all experiment except the germination rate experiment in which filter paper was used. Soil was made of 1:1 mixtures of bed-soil (for rice seedbed, Dongbuhannong, Korea) and river sand. The total nitrogen and available phosphorus of mixed soil were 74.9 ㎎/㎏ and 25.4 ㎎/㎏, respectively (referred to hereafter as soil). Soil texture was sandy loam, and it corresponded with measurement value in reference site and previous study about habitat characteristics of *Salix* species (Lee et al. 2001). Soil used in soil seed bank experiment was sterilized at 100℃ for a day.

2. Plant material

Seeds of *S. koreensis* were collected on May 12, 2010 in reference site. Branches with catkins were cut when the seeds had begun to be released, and collected *S. koreensis* seeds were used in experiments immediately. Seeds of *P. australis* were obtained from a local native plant nursery nearby reference site in November, 2009. Thereafter, *P. australis* seeds were stored dry at 5℃ with being sealed in refrigerator till being used in the experiments.

Part of seeds of two species was used in the experiments of germination rate and germination period, and the remainders were scattered on the soil in 20 pots (41 ㎝ wide, 21 ㎝ long and 11 ㎝ high) for each species on April 15, 2010 (*P. australis*) and May 12, 2010 (*S. koreensis*). A pot was placed in a bucket (51 ㎝ wide, 35 ㎝

long and 14 ㎝ high). When the seedlings emerged too densely, thinning were applied by cutting the shoots to about 3 ㎝ apart. Water level (distance from the soil surface to the water surface) was maintained as -4 ㎝ by adding tap water to bucket till the end of the experiments. Thereafter we measured height (distance from the soil surface to the top of seedlings) of healthy 20 individual seedlings randomly at intervals of 10 days (to 50-day-old) and 20 days (to the end of the experiments). Seedlings that height is close to the mean height each time were used in the experiments of seedling growth.

3. Soil seed bank

Seedling emergence experiment was performed that is widely used to investigate soil seed bank (Dalling et al. 1995; Kim & Ju 2006) in the greenhouse. Soil samples were collected by volume of 20 ㎝ × 20 ㎝ and 5 ㎝ depth of each six replicate quadrats located randomly at *S. koreensis* and *P. australis* community (coverage: 80% of *S. koreensis*, 25% of *P. australis*) in the reference site on March 10, 2010. The samples were stored at 5℃ with being sealed in refrigerator. On April 1, 2010, each sample was prepared for experiment by removal of root and stem, and placed in six trays (51 ㎝ wide, 35 ㎝ long and 14 ㎝ high) that were filled with sterile soil to 5 ㎝ high. Thereafter the soil were watered periodically, emergent seedlings were identified, counted and removed at intervals of 20 days till October 15, 2010.

4. Germination Period

The 600 seeds of each species were sowed in six pots (21 ㎝ wide, 21 ㎝ long and 18 ㎝ high), filled with soil to top, on April 15, 2010 (*P. australis*) and May 12, 2010 (*S. koreensis*) in the experimental field. The 100 seeds was sowed in a pots that was placed in a bucket (40 ㎝ wide, 24 ㎝ long and 28 ㎝ high). Water level were maintained -4 ㎝ by watering during the experiments. A seed was regarded as germinated if the cotyledons were verified with the naked eye, and germinated seeds were counted at intervals of 2 days for 30 days, by which time germination had ceased. Part of the seedlings were used in the experiments of seedling growth after finishing the period of germination experiment.

5. Germination rate

5.1. Germination rate at different light intensity and water level

Germination rate experiment was conducted in 12-h light / 12-h dark rhythm in a growth chamber under the photosynthetic photon flux density (PPFD) of 50 $\mu mol \cdot m^{-2} \cdot sec^{-1}$ during the light phase. And the relative humidity was 60% in the growth chamber during the experiment. The temperature was 23℃ and 13℃ during light and dark phase, respectively, determined by the mean maximum and minimum temperature of a week before and after seed dispersal of *S. koreensis*.

Fully crossed factorial design was used to test the effect of light intensity and water level on germination rate for each species. The light intensity treatment had three levels consisting of 100%, 30% and 0%, controlled by shading net blocking 70% of light intensity and dark box. The water level treatment had two levels consisting of 0 ㎝ and +2 ㎝. The seeds of two species were placed on the filter paper moistened with distilled water in petri dishes (9 ㎝ in diameter and 4 ㎝ high) on May 12, 2010, right after seed dispersal of *S. koreensis*. 70-80 seeds of *S. koreensis* were distributed on a petri dish, and in the case of *P. australis*, 50-60 seeds were placed. Total 30 petri dishes were prepared for the experiment, and 5 petri dishes were assigned for each treatment lastly. By adding distilled water periodically, moist state of filter paper and water level of +2 ㎝ were maintained of each water level treatments.

A *S. koreensis* seed was regarded as germinated if the seedlings developed cotyledons, hypocotyl and root (Maroder et al. 2000), while a *P. australis* seed was if the radicle, or coleoptile had protruded at least 1㎜ (Ekstam & Forseby 1999). Germinated seeds were counted and removed to prevent epidemics at two days interval. The experiments were conducted for 30 days, by which time germination had ceased.

5.2. Germination rate according to elapsed time after seed dispersal

Germination rate response to elapsed time after seed dispersal was examined. The elapsed time after seed dispersal treatment in *S. koreensis* had 11 levels consisting of 0, 2, 4, 6, 8, 10, 12, 14, 16, 18 and 20 days. The seeds were stored at room temperature without being sealed till the experiment was initiated. In the case of *P. australis* had two levels consisting of 1 year and 2 years, and the seeds were stored dry at 5℃ with being sealed in refrigerator till being used in experiment. The 0 day-treatment of *S. koreensis* and 1 year-treatment of *P. australis* were begun on May 12, 2010. Five replicates were used for each treatment, and all treatments were conducted under 100%-light intensity and 0 ㎝-water level condition, and the experimental procedure was equal to the above experiment of germination rate at different light intensity and water level.

6. Seedling survival

Seedling survival rate of *S. koreensis* according to elapsed time after seed dispersal was examined in greenhouse. The elapsed time after seed dispersal treatment had eight levels consisting of 0, 2, 4, 6, 8, 10, 12 and 14 days. Many seeds were sowed in 5 pots (41 ㎝ wide, 21 ㎝ long and 11 ㎝ high), filled with soil to top, on May 12, 2010, right after seed dispersal (0 day-treatment). In the case of 2 days-treatment, seeds were sowed on May 14, two days after seed dispersal. In the same way, 4-14 days-treatment were prepared.

A pot was placed in each bucket (51 ㎝ wide, 35 ㎝ long and 14 ㎝ high), and water level was maintained as -4 ㎝ by adding tap water to bucket till the end of the experiments. By thinning emergent seedlings, 20 individuals remained per pot. In other words, 20 seedlings were used of each of five replicates per treatment (eight levels). Left 20 individuals were observed for 20 days, and number of survived individual was counted. A seedling was regarded as survived when the normal leaves had developed in 20 days after germinated. This experiment were not conducted in the case of *P. australis*.

7. Young seedling growth

Seedlings of *P. australis* were eight days old when the mean height was 1.0 ㎝ on May 20, 2010. On the other hand, it was 20 days when the mean height of *S. koreensis* seedlings reach 1.0 ㎝, on June 3, 2010. At that time *P. australis* seedlings were 22 days old and mean 6.0 ㎝ tall. Fully crossed factorial design was used to test the effect of light intensity and water level on each 3 cases: 1.0 ㎝-tall *S. koreensis*, 1.0 ㎝-tall *P. australis* seedlings and 6.0 ㎝-tall *P. australis*. The light intensity treatment had two levels consisting of

100% and 30%. And the water level treatment had 4 levels consist~~ing~~ of −4 cm, +1 cm, +2 cm and +4 cm. Each treatment (2×4) was replicated 20 individual seedlings.

160 seedlings were transplanted, of similar size (1.0 cm-tall-seedlings: between 0.7 and 1.3 cm, 6.0 cm-tall-seedlings: between 5.0 cm and 7.0 cm), in the 80 pots (15 cm in diameter and 13 cm high), filled with soil to top. Two seedlings were planted in each pot, and five pots were placed in a bucket (51 cm wide, 35 cm long and 14 cm high), so total 16 buckets were used. The half of the buckets were shaded by shading nets blocking 70% of light intensity (30%-light intensity treatment), and the other half were exposed to full sunlight (100%-light intensity treatment). And in each of a fourth of buckets, water level was maintained −4 cm, +1 cm, +2 cm and +4 cm (−4 cm, +1 cm, +2 cm and +4 cm-water level treatment, respectively) by adding tap water during the experiment. Lastly eight (2 × 4) treatments were combined, and two buckets (20 individual) were assigned for each treatment.

The two initial parameters (height and normal leaf number) of 1.0 cm-tall *S. koreensis* seedlings were measured for all individual right after the experimental installation. There were no significant diffe rence on height ($p = 0.971$) and normal leaf number ($p = 0.409$) between different treatments. And the three initial parameters (height of the longest shoot, leaf number on the longest shoot and shoot number per genet) of *P. australis* seedlings were measured in the same way. There were no significant difference on height ($p = 0.770$) between treatments, and all seedlings had a leaf and a shoot of 1.0 cm-tall seedlings. In the case of 6.0 cm-tall seedlings, there were no significant difference on height ($p = 0.238$) between treatments and all seedlings had three leaves and a shoot. All experiments were performed in greenhouse, and water level was maintained initial condition to Oct. 15, 2010, the end of the experiment.

The same parameters with initial condition for each species were measured at intervals of 10 days (to 40-day-old) and 20 days (to 100-day-old) during experiment. And we harvested all seedlings of both species on October 15, 2010, and nine parameters (survival rate, height, leaf number, bud number, diameter of root collar, leaf dry weight, stem dry weight, root dry weight and below : above-ground ratio) and 10 parameters (survival rate, height of the longest shoot, cumulative height, leaf number on the longest shoot, shoot number per genet, diameter of the thickest shoot, aboveground dry weight, belowground dry weight and below : above-ground ratio) were measured at all *S. koreensis* and *P. australis* seedlings, respectively. Aboveground meant leaf and aerial shoot, and belowground meant rhizome and root in the case of *P. australis* seedlings. Biomass was determined by weighing harvested seedlings washed free of all soil, dried to a constant weight at 60℃.

8. Old seedling growth

Seedlings of *S. koreensis* and *P. australis* grown in the experimental field were mean 28 ㎝ tall (42-day-old) and 63 ㎝ tall (44-day-old), respectively on June 25, 2010 when the rainy season began. Fully crossed factorial design was used to test the effect of light intensity, water level and interspecific competition on seedlings growth of two species.

The light intensity treatment had two levels consisting of 100% and 30%, controlled by shading net blocking 70% of light intensity. And the water level treatment had three levels consisting of -10 ㎝, +4 ㎝ and +12 ㎝. And the competition treatment had two levels consisting of pure planting and mixed planting, according to the replacement principle (de Wit 1960; de Wit, Tow & Ennik; Fowler 1982). Pure planting treatment meant that only a species was planted in a pot, while mixed planting treatment meant meant two species planted at one-to-one ratio together. In both of the two treatments, density of individual was adjusted 362.8/㎡ by planting 16 individuals seedlings in a pot of which top area was 441 ㎠. We decided the value by reflecting result of soil seed bank experiment (Table 3) and the previous researches that density of 1-year-old *Salix* species seedlings was 250/㎡ (Kim, Nam & Han 2007) and 249-3,864 /㎡ (Sacchi & Price 1992), and density of 1-year-old *P. australis* seedlings was 20-1,300/㎡ (Lee, Marrs & Lee 2011) in riverine wetland. Each treatment (2×3×2) was replicated five times.

720 seedlings of each species were transplanted, of similar size (*S. koreensis* seedlings: between 25 and 31 ㎝, *P. australis* seedlings: between 57 and 69 ㎝), in the pots (21 ㎝ wide, 21 ㎝ long and 18 ㎝ high), filled with soil to top. We prepared 90 pots, and planted 16 individual seedlings of *S. koreensis* in each of 30 pots, a third of total pots, seedlings of *P. australis* did in the same way (pure planting-competition treatment). In the remaining 30 pots, 8 individual seedlings of each species were planted together in zigzags each other (mixed planting-competition treatment). Eventually 16 individuals no distinguished between species were planted in each and all pots. And two pots planted purely of each species and a pot planted by mixture were placed in a bucket (92 ㎝ wide, 66 ㎝ long and 35 ㎝ high), so total 30 buckets were used. The half of the buckets were shaded by shading nets (30%-light intensity treatment), and the other half were completely exposed to sunlight (100%-light intensity treatment). And in each of a third of buckets, water level were maintained -10 ㎝, +4

cm and +12 cm (-10 cm, +4 cm and +12 cm-water level treatment, respectively) by adding tap water during the experiment. Lastly 12 (2 × 3 × 2) treatments were combined, and five buckets were assigned for each treatment.

The two initial parameters (height and leaf number) of *S. koreensis* seedlings were measured for all individual right after experimental installation. There were no significant difference between treatments on height ($p = 0.777$) and leaf number ($p = 0.899$). And the three initial parameters (height of the longest shoot, leaf number on the longest shoot and shoot number per genet) of *P. australis* seedlings were measured in the same way. There were no significant difference between treatments on height of the longest shoot ($p = 0.588$), leaf number on the longest shoot ($p = 0.539$) and shoot number per genet ($p = 0.713$), too. All experiments were performed in the experimental field, and water level was maintained initial condition to October 15, 2010, the end of the experiment. And We harvested all seedlings after ending experiment, and the same parameters with the above-mentioned experiment of young seedling growth (1-6 cm in height) were measured (flowering rate was added at *P. australis*).

9. Statistical analysis

For all measured value of the experiments, One or Multi-way ANOVA and Tukey WSD post hoc multiple comparison test at the 0.05 significance level (SPSS 17.0), except dead seedlings of seedlings growth experiment.

Results

1. Soil seed bank

At the end of the experiment, total 38 species were emerged from the soil depth of 0–5 ㎝ at *S. koreensis* and *P. australis* communities in the reference site (Table 1). Species with the highest density of seedlings is *Centipeda minima* (2,483 ± 959㎡) and, *P. australis* seedlings showed the 13th highest density (304 ± 69/㎡). On the other hand, *S. koreensis* seedlings were not emerged.

2. Germination period

P. australis seeds germinated for the first time at 17 days after seeds sowed (0.3%) (Figure 3). The largest number of *P. australis* seeds germinated on May 12, 27 days after sowed, 37.8% of seeds germinated per day. Whereas 36.6% of *S. koreensis* seeds germinated at a day after sowed. It was on May 14, at two days after sowed, that the largest number of *S. koreensis* seeds germinated, and 45.2% of seeds germinated per day. The gap of date maximum germination occurred between 2 species was two days. The cumulative germination rate was 87.3% and 70.5% of *S. koreensis* and *P. australis* seeds, respectively.

Table 1. Number of seedlings emerged from the soil depth of 0-5 ㎝ at *S. koreensis* and *P. australis* communities (coverage: 80% of *S. koreensis*, 25% of *P. australis*) in riverine of Wangsuk stream (n = 6).

Species	Mean density (No./㎡)	SE
Centipeda minima	2,483	959.4
Lindernia dubia	1,117	434.0
Alopecurus aequalis	1,050	224.5
Beckmannia syzigachne	683	197.2
Lindernia procumbens	663	221.7
Panicum bisulcatum	463	138.4
Erigeron annuus	379	71.9
Capsella bursapastoris	375	88.2
Alyssum martimum	371	89.8
Isachne globosa	358	117.6
Persicaria hydropiper	317	69.0
Stellaria alsine var. *undulata*	313	71.4
Phragmites australis	304	69.8
Rorippa palustris	121	33.9
anunculus sceleratus	117	11.4
Persicaria thunbergii	108	28.6
Potentilla supina	96	15.1
Miscanthus sacchariflorus	58	26.9
Echinochloa crusgalli var. *oryzicola*	54	11.8
Persicaria nodosa	38	18.0
Equisetum arvense	38	16.7
Digitaria ciliaris	38	15.5
Ambrosia artemisiifolia	33	12.2
Artemisia princeps	33	13.9
Trigonotis peduncularis	29	15.1
Cyperus difformis	29	11.8
Mazus pumilus	29	18.8
Commelina communis	29	18.8
Veronica undulata	29	10.2
Aeschynomene indica	25	13.1
Bromus japonicus	25	17.1
Stellaria aquatica	21	13.5
Typha angustifolia	21	16.3
Cyperus hakonensis	21	11.8
Trifolium repens	21	13.5
Leersia japonica	17	12.2
Humulus japonicus	17	8.2
Rumex crispus	13	8.6

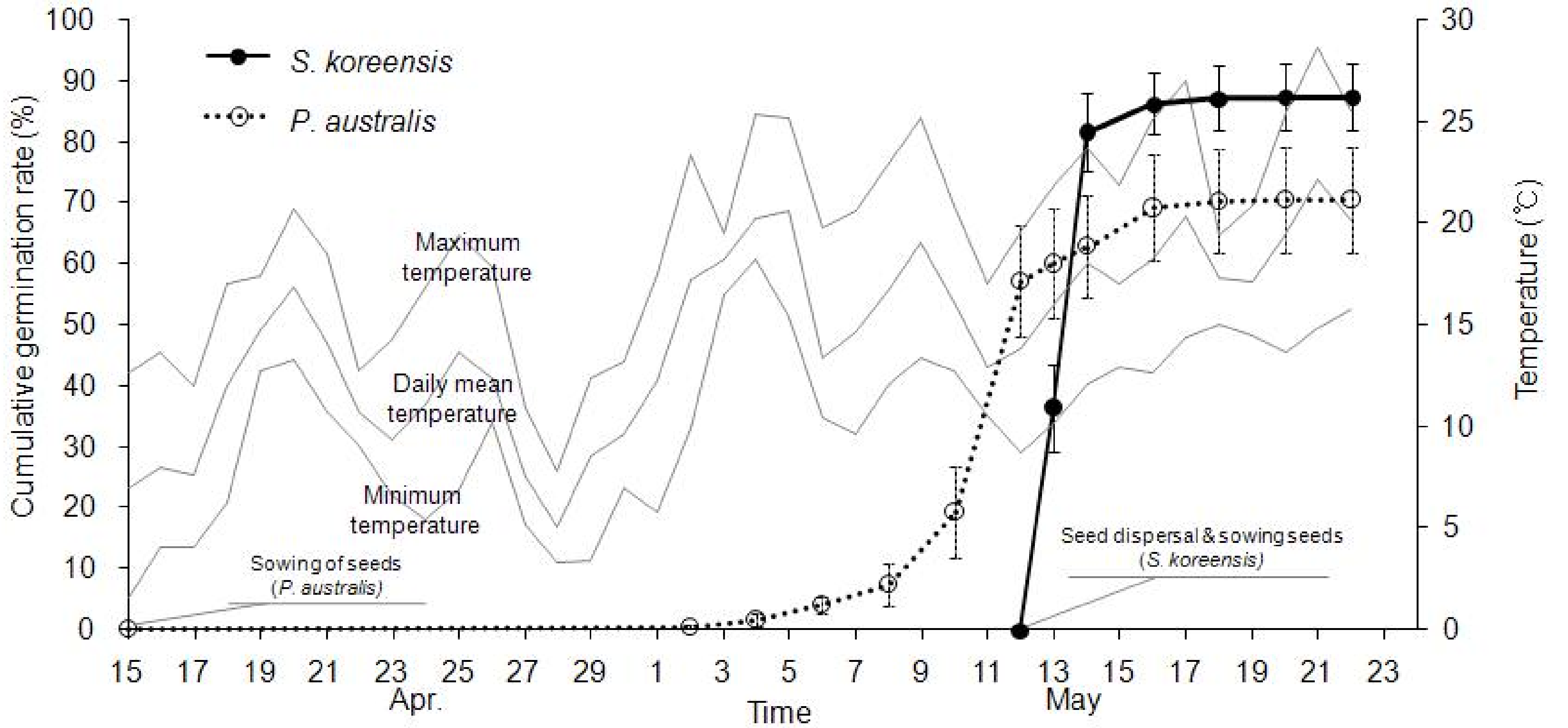


Figure 3. Cumulative germination rate of *S. koreensis* and *P. australis* seeds with time in the experimental field (mean values ± SD, n = 6 for each species). 100 seeds were used for each replicates.

3. Germination rate

3.1. Germination rate at different light intensity and water level

Mean final germination rate by treatment combination for *S. koreensis* ranged between 76.5% and 97.4% (Figure 4). Light intensity significantly affected the germination rate of *S. koreensis* seed ($p<0.001$) without light intensity × water level interactive effect (Table 2). Mean germination rate of *S. koreensis* significantly declined with decrease of light intensity from 100% to 30% and 0%. The mean final germination rate of *S. koreensis* at 0%-light intensity was 20% lower than that at 100%-light intensity. In darkness, although seeds germinated, seedlings were thin and the two cotyledons were not opened, while those in shadelessness seemed healthy, and the two cotyledons were opened widely. Final germination rate of *S. koreensis* were not different at different water level significantly.

Mean final germination rate by treatment combinations for *P. australis* ranged between 60.9% and 71.6% (Figure 5). There was no significant difference in *P. australis* germination rate by light intensity and water level treatment at the 0.05 level (Table 3).

Table 2. Analysis of variance for the effect of light intensity (100%, 30% and 0%) and water level (0 ㎝ and +2 ㎝) on final germination rate of *S. koreensis*.

Source of variation	d.f.	F-value	
		Final germination rate	
Light intensity	2, 24	60.10	***
Water level	1, 24	0.88	ns
Light intensity × Water level	2, 24	0.61	ns

ns: Not sgnificant at 0.05 level.
***: Significant at <0.001 level.

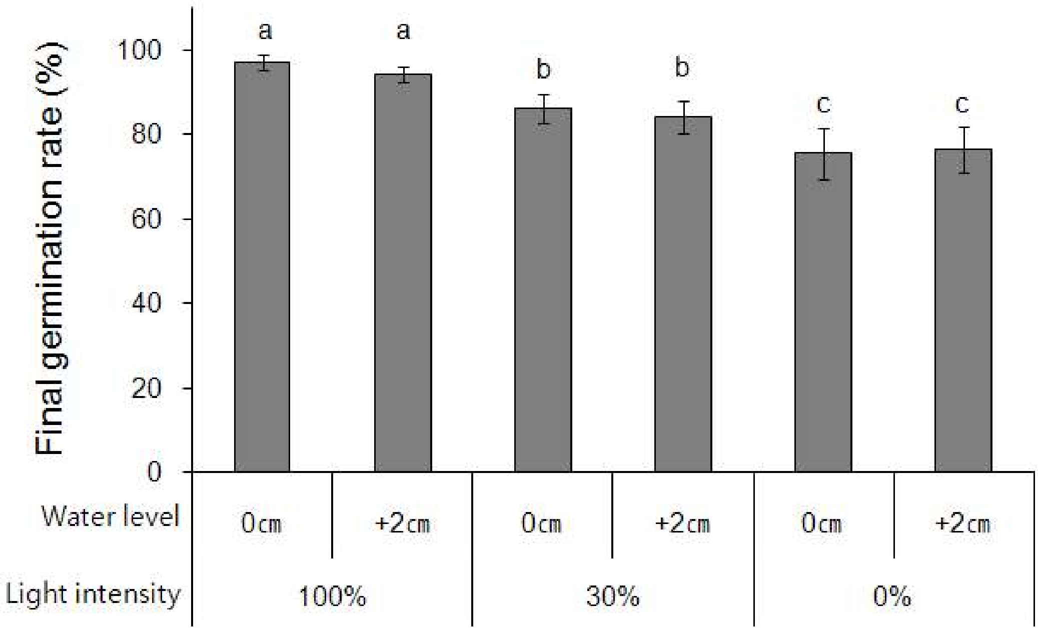


Figure 4. Final germination rate of *S. koreensis* at different light intensity and water level treatments (mean values ± SD, n = 5 for each treatment). 70-80 seeds were used for each replicates. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

Table 3. Analysis of variance for the effect of light intensity (100%, 30% and 0%) and water level (0 ㎝ and +2 ㎝) on final germination rate of *P. australis*.

Source of variation	d.f.	F-value
		Final germination rate
Light intensity	2, 24	1.18 ns
Water level	1, 24	0.20 ns
Light intensity × Water level	2, 24	1.13 ns

ns: Not sgnificant at 0.05 level.

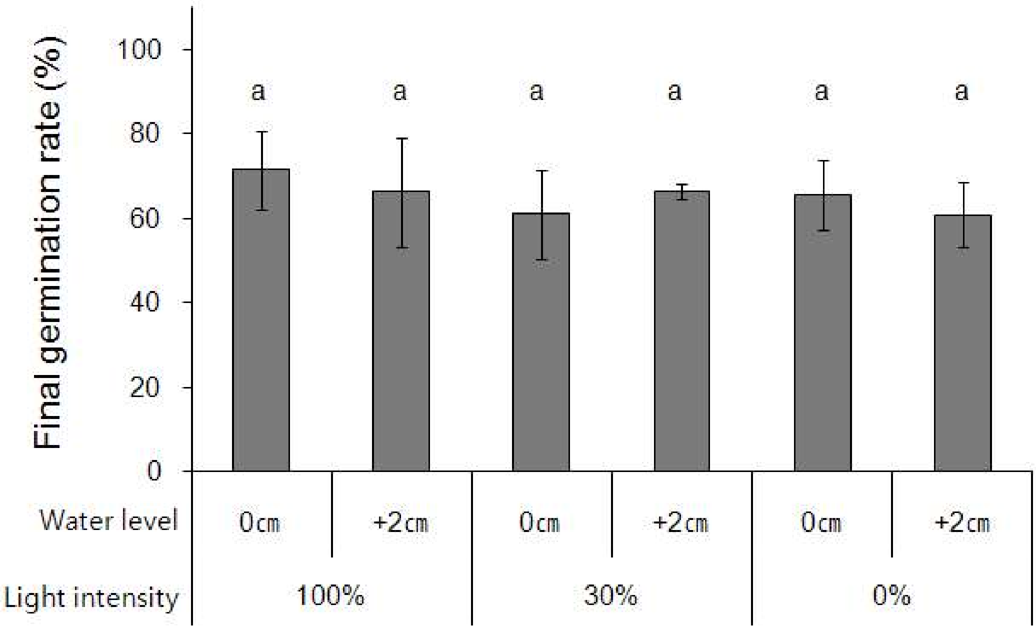


Figure 5. Final germination rate of *P. australis* at different light intensity and water level treatments (mean values ± SD, n = 5 for each treatment). 50-60 seeds were used for each replicates. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

3.2. Germination rate according to elapsed time after seed dispersal

With increase of elapsed time after seed dispersal, final germination rate of *S. koreensis* significantly decreased ($p<0.001$) (Figure 6). Final germination rate of *S. koreensis* fell to less than 50% at 8 days-after seed dispersal treatment. When 16 days passed after seed dispersal, *S. koreensis* seeds did absolutely not germinate.

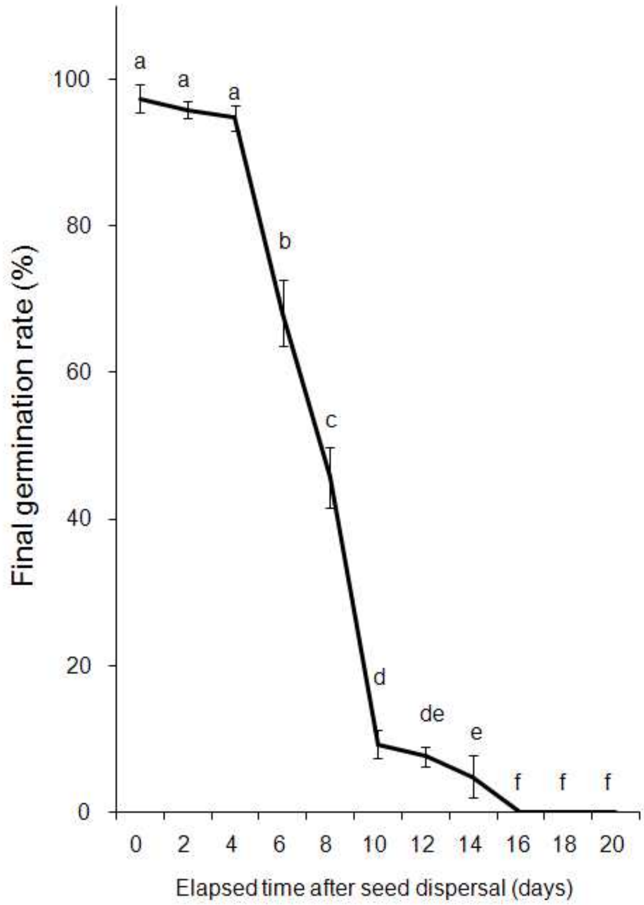


Figure 6. Changes in final germination rate of *S. koreensis* according to elapsed time after seed dispersal under 100%-light intensity and 0 ㎝-water level condition (mean values ± SD, n = 5 for each treatment). 70-80 seeds were used for each replicates. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

Like *S. koreensis*, *P. australis* seed final germination rate significantly decreased with increase of elapsed time after seed dispersal ($p<0.001$) (Figure 7), but the scale of time was different. As elapsed time after seed dispersal lengthen from a year to two years, final germination rate of *P. australis* decreased from 71.6% to 35.4%.

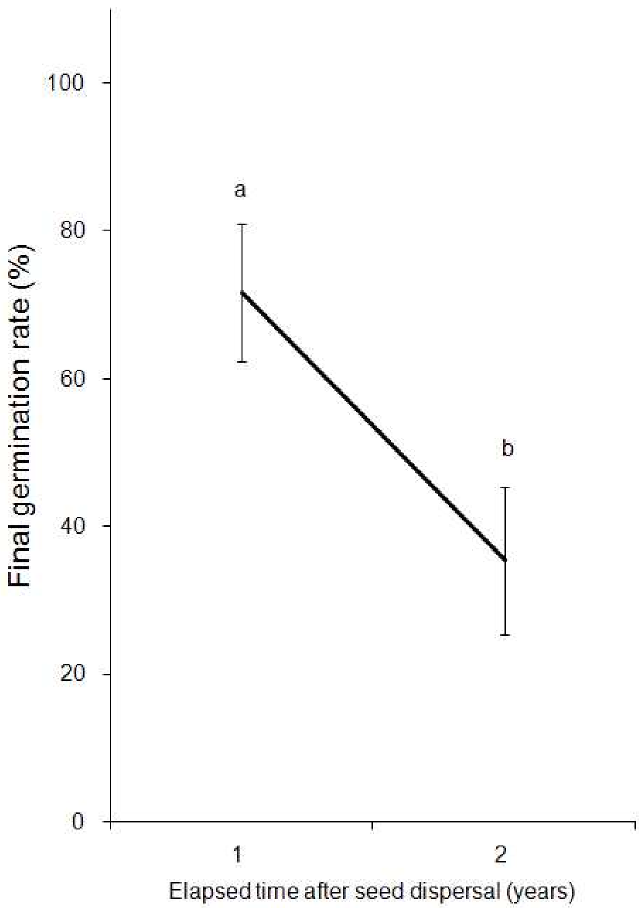


Figure 7. Changes in final germination rate of *P. australis* according to elapsed time after seed dispersal under 100%-light intensity × 0 ㎝-water level condition (mean values ± SD, n = 5 for each treatment). 70-80 seeds were used for each replicates. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

4. Seedling survival

With increase of elapsed time after seed dispersal, final survival rate of *S. koreensis* seedlings significantly decreased ($p<0.001$) (Figure 8). Even though seeds germinated, all seedlings had no normal leaf and didn't grow at all in 20 days, if the seeds had begun to germinate at 10 days after seed dispersal.

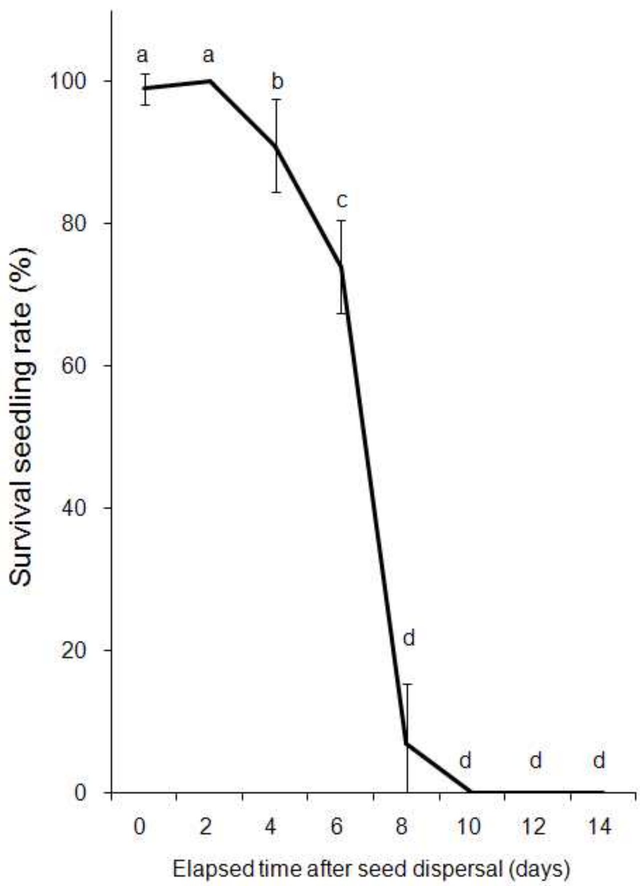


Figure 8. Changes in final survival rate right after germination according to elapsed time after seed dispersal of *S. koreensis* seedlings under 100%-light intensity and -4 ㎝-water level condition (mean values ± SD, n = 5 for each treatment). 20 seedlings were used for each replicates. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

5. Young seedling growth

5.1. *Salix koreensis*

All 20-day-old *S. koreensis* seedlings (1 ㎝ in height) died at water level that was double or more than seedlings height (+2 ㎝ and + 4 ㎝-water level treatments) (Figure 9). The cotyledon and stem of seedlings submerged completely turned black after about three weeks. At the same water level as seedlings height, survival rate was 80% at 100%-light intensity and 55% at 30%-light intensity, and all seedlings survived at water table was at the surface of soil.

The entire parameters of *S. koreensis* were significantly different at harvest between light intensity treatment except below : above-ground ratio ($p<0.001$) (Table 4). The mean values of height, leaf number, bud number, diameter of root collar, leaf dry weight, stem dry weight and root dry weight at 30%-light intensity were 62.7%, 65.0%, 64.7%, 63.6%, 82.8%, 81.3% and 87.2%, respectively, lower than those at 100%-light intensity.

And there were significant difference between -4 ㎝ and +1 ㎝ -water level for diameter of root collar ($p<0.01$), stem dry weight ($p<0.05$) and root dry weight ($p<0.05$) at harvest. As water level was higher from 0 ㎝ to +1 ㎝, the mean diameter of root collar, stem dry weight, and root dry weight decreased by 16.6%, 22.3% and 24.2%, respectively, within 100%-light intensity treatment. But within 30%-light intensity, there was not significant difference between 0 ㎝ and +1 ㎝-water level for those parameters.

The height and leaf number under +1 ㎝-water level treatment were significantly lower than 0 ㎝-water level treatment until August, but the gaps between two of water level treatments were gradually narrowed within 100%-light intensity. So final mean height and leaf number were not different between 0 ㎝ and +1 ㎝-water level (Figure 10).

There was no significant difference between below : above-ground ratio of *S. koreensis* seedlings at all treatments combination.

Table 4. Analysis of variance for the effect of light intensity (100% and 30%) and water level (-4 ㎝ and +1 ㎝) on growth of 20-day-old *S. koreensis* seedlings (mean seedlings height: 1 ㎝). +2 ㎝ and +4 ㎝-water level treatments were excluded from analysis, because all seedlings died under this conditions.

Source of variation	d.f.	F-value							
		Height	Leaf number	Bud number	Diameter of root collar	Leaf dry weight	Stem dry weight	Root dry weight	Below : above -ground ratio
Light intensity	1, 63	948.28 ***	780.70 ***	957.89 ***	452.34 ***	148.44 ***	147.27 ***	189.07 ***	3.88 ns
Water level	1, 63	1.68 ns	0.30 ns	1.95 ns	10.68 **	0.53 ns	3.98 *	5.66 *	0.21 ns
Light intensity × Water level	1, 63	0.20 ns	0.01 ns	0.42 ns	7.82 **	0.41 ns	3.10 ns	3.92 ns	0.00 ns

ns: Not sgnificant at 0.05 level.
*: Significant at 0.01-0.05 level.
**: Significant at 0.001-0.01 level.
***: Significant at <0.001 level.

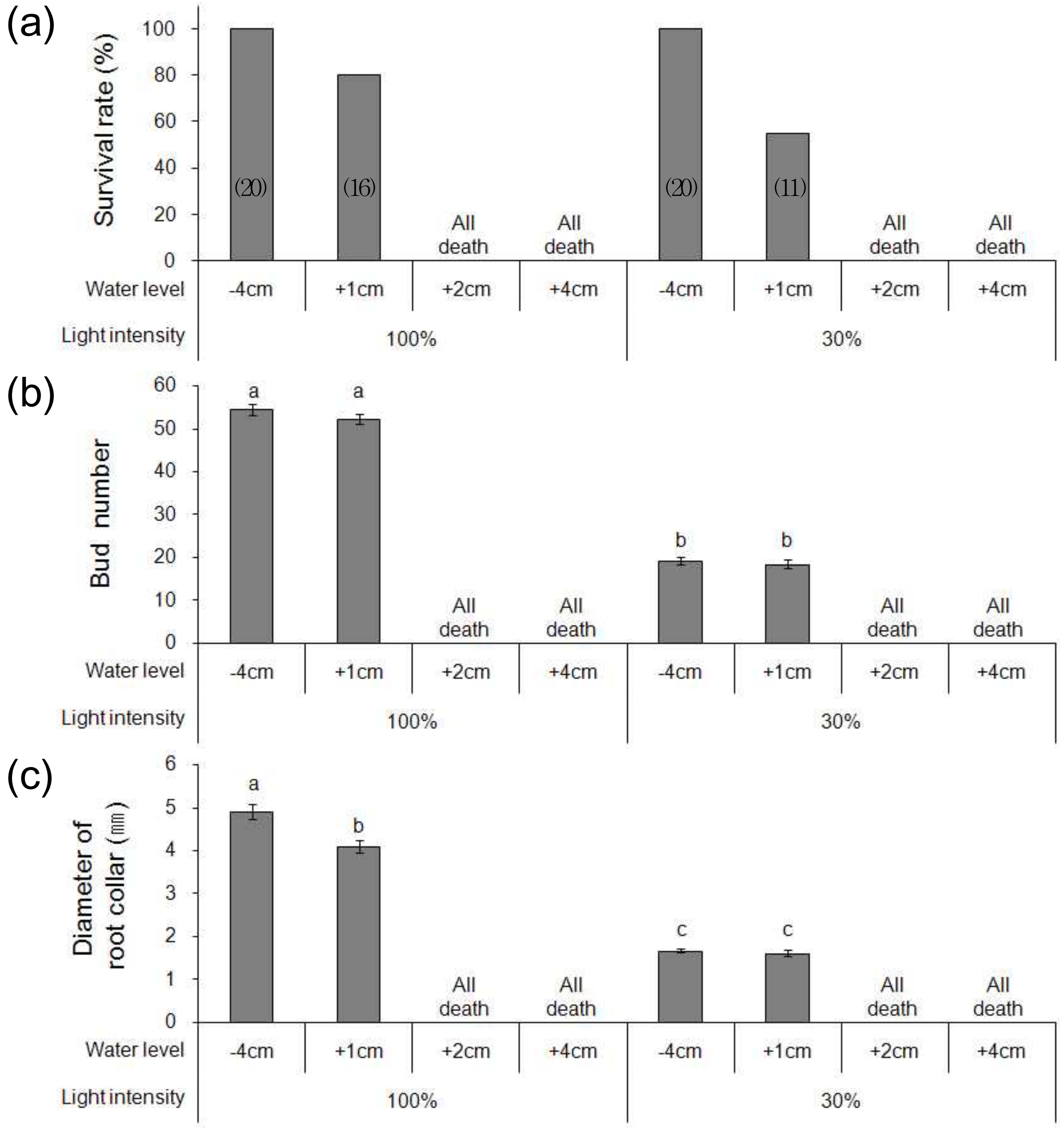


Figure 9. Final survival rate (a), bud number (b), diameter of root collat (c), leaf dry weitght (d), stem dry weight (e), root dry weight (f) and below : above-ground ratio (g) of 20-day-old *S. koreensis* seedlings (mean seedlings height: 1 ㎝) at different light intensity and water level treatments at the end of the experiment (mean values ± SE). The number in parentheses refer to replication number, except dead individuals. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

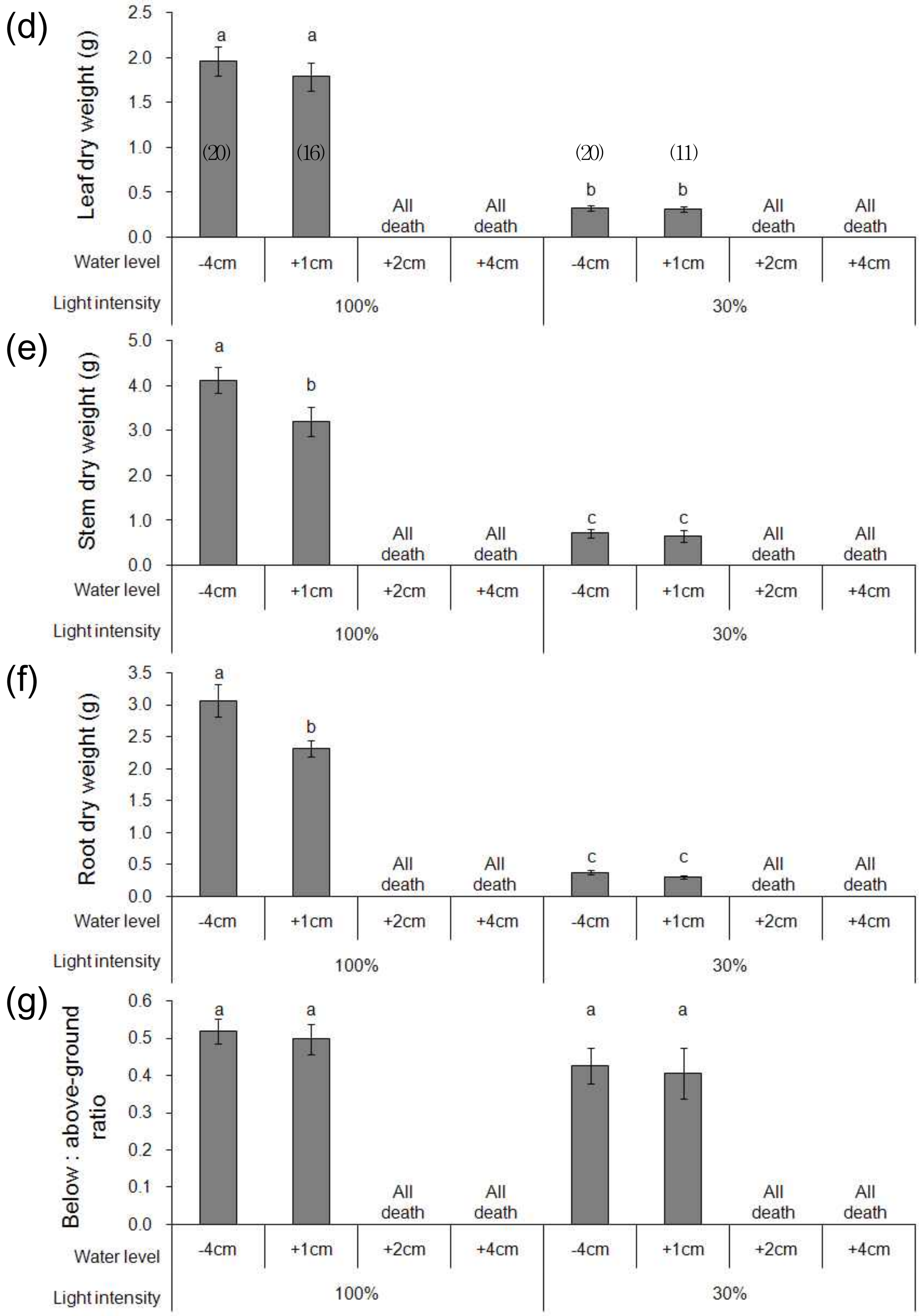


Figure 9. Continued (caption in page 31).

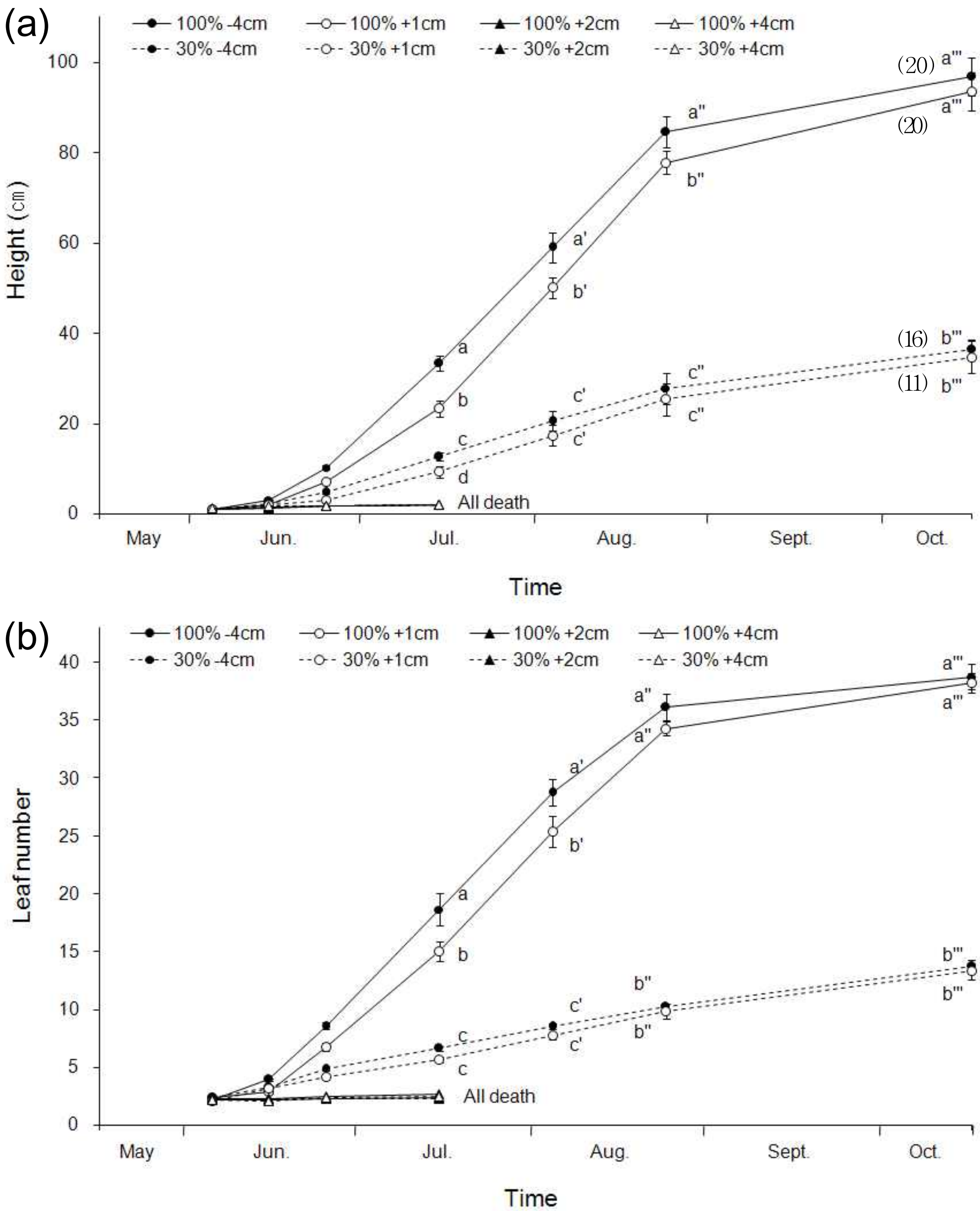


Figure 10. Growth curve on height (a), leaf number (b) of 20-day-old *S. koreensis* seedlings (mean seedlings height: 1 ㎝) at different light intensity and water level treatments (mean values ± SE). The number in parentheses refer to replication number, except dead individuals. Different letters indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

5.2. *Phragmites australis*

All 8-day-old *P. austrails* seedlings (1 ㎝ in height) died at water level that was four times length of the seedlings height (+4 ㎝-water level) (Figures 11). And at water level that was double of the seedlings height (+2 ㎝-water level), all 8-day-old seedlings died under 30%-light intensity condition while 35% of seedlings survived under full sunlight. In the case of water level that was same or less than seedlings height, all or part of seedlings survived for both of 8 and 22-day-old seedlings (1 ㎝ and 6 ㎝ in height, respectively). Overall, survival rate was lower under 30%-light intensity than under 100%-light intensity within the same water level condition. Especially, 22-day-old seedlings had a low survival rate (50%) at 30%-light intensity × -4 ㎝-water level treatment (66% flooding of seedlings height).

The all parameters of *P. australis* were significantly different at harvest between light intensity treatment except below : above-ground ratio ($p<0.001$) (Table 5). The mean values at 30%-light intensity were 88.5%, 96.6%, 58.7%, 75.6%, 60.8%, 94.9% and 96.4%, respectively, lower than those at 100%-light intensity for height of the longest shoot, cumulative height, leaf number on the longest shoot, shoot number per genet, diameter of the thickest shoot, aboveground dry weight and belowground dry weight (Figures 11 and 12).

There were significant water level × age interactive effect on the height of the longest shoot ($p<0.001$), cumulative height ($p<0.001$), shoot number per genet ($p<0.01$), aboveground dry weight ($p<0.001$) and belowground dry weight ($p<0.001$) of *P. australis* seedlings at harvest. The pairwise comparisons showed that seedlings at +2 ㎝ -water level × 8 day-age treatment were significantly shorter in hight than the other treatments combination within 100%-light intensity at harvest, and seedlings showed the same tendency as height on cumulative height, shoot number per genet, diameter of the thickest shoot, aboveground dry weight and belowground dry weight. Leaf number on the longest shoot of 8-day-old seedlings were significantly lower at +2 ㎝-water level than those at 0 ㎝ and +1 ㎝ -water level until August, but the gaps were gradually narrowed within 100%-light intensity, so there was no significant difference between water level treatment at harvest.

There was no significant difference between below : above-ground ratio of *P. australis* seedlings at all treatments combination.

Table 5. Analysis of variance for the effect of light intensity (100% and 30%), water level (-4 ㎝, +1 ㎝, +2 ㎝ and +4 ㎝) on growth of 8 and 22-day-old *P. australis* seedlings (mean seedlings height: 1 ㎝ and 6 ㎝, respectively).

Source of variation	d.f.	F-value							
		Height of the longest shoot	Cumulative height	Leaf number on the longest shoot	Shoot number per genet	Diameter of the thickest shoot	Above ground dry weight	Below ground dry weight	Below : above -ground ratio
Light intensity	1, 199	6456.51 ***	5137.03 ***	883.14 ***	1495.63 ***	748.88 ***	2198.18 ***	916.93 ***	1.23 ns
Water level	3, 199	4.04 **	15.60 ***	1.16 ns	3.83 *	2.07 ns	16.22 ***	10.70 ***	0.28 ns
Age	1, 199	14.49 ***	35.08 ***	1.43 ns	6.50 *	4.56 *	38.90 ***	16.13 ***	0.17 ns
Light intensity × Water level	3, 199	0.98 ns	0.52 ns	0.27 ns	0.26 ns	0.04 ns	0.40 ns	0.86 ns	0.04 ns
Light intensity × Age	1, 199	1.22 ns	0.09 ns	0.01 ns	0.13 ns	0.08 ns	0.17 ns	0.09 ns	0.01 ns
Water level × Age	2, 199	15.48 ***	27.56 ***	1.24 ns	5.27 **	2.92 ns	31.28 ***	12.26 ***	0.05 ns
Light intensity × Water leve × Age	1, 199	0.04 ns	0.00 ns	0.04 ns	0.02 ns	0.01 ns	0.11 ns	0.00 ns	0.02 ns

ns: Not sgnificant at 0.05 level.
*: Significant at 0.01-0.05 level.
**: Significant at 0.001-0.01 level.
***: Significant at <0.001 level.

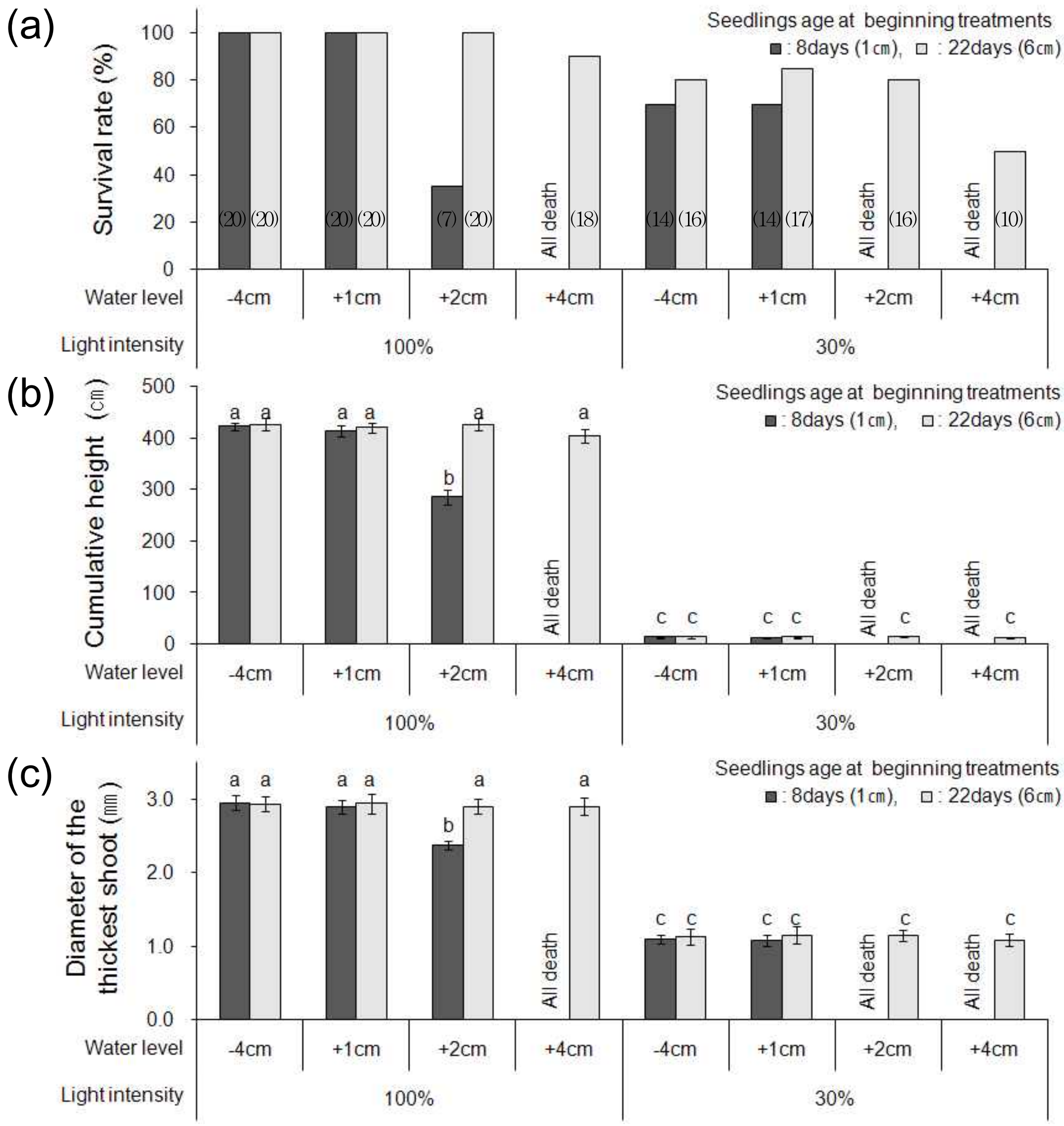


Figure 11. Final survival rate (a), cumulative height (b), diameter of the thickest shoot (c), aboveground dry weight (d), belowground dry weight (e) and below : above -ground ratio (f) of 8 and 22-day-old *P. australis* seedlings (mean seedlings height: 1 ㎝ and 6 ㎝, respectively) at different light intensity and water level treatments at the end of the experiment (mean values ± SE). The number in parentheses refer to replication number, except dead individuals. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

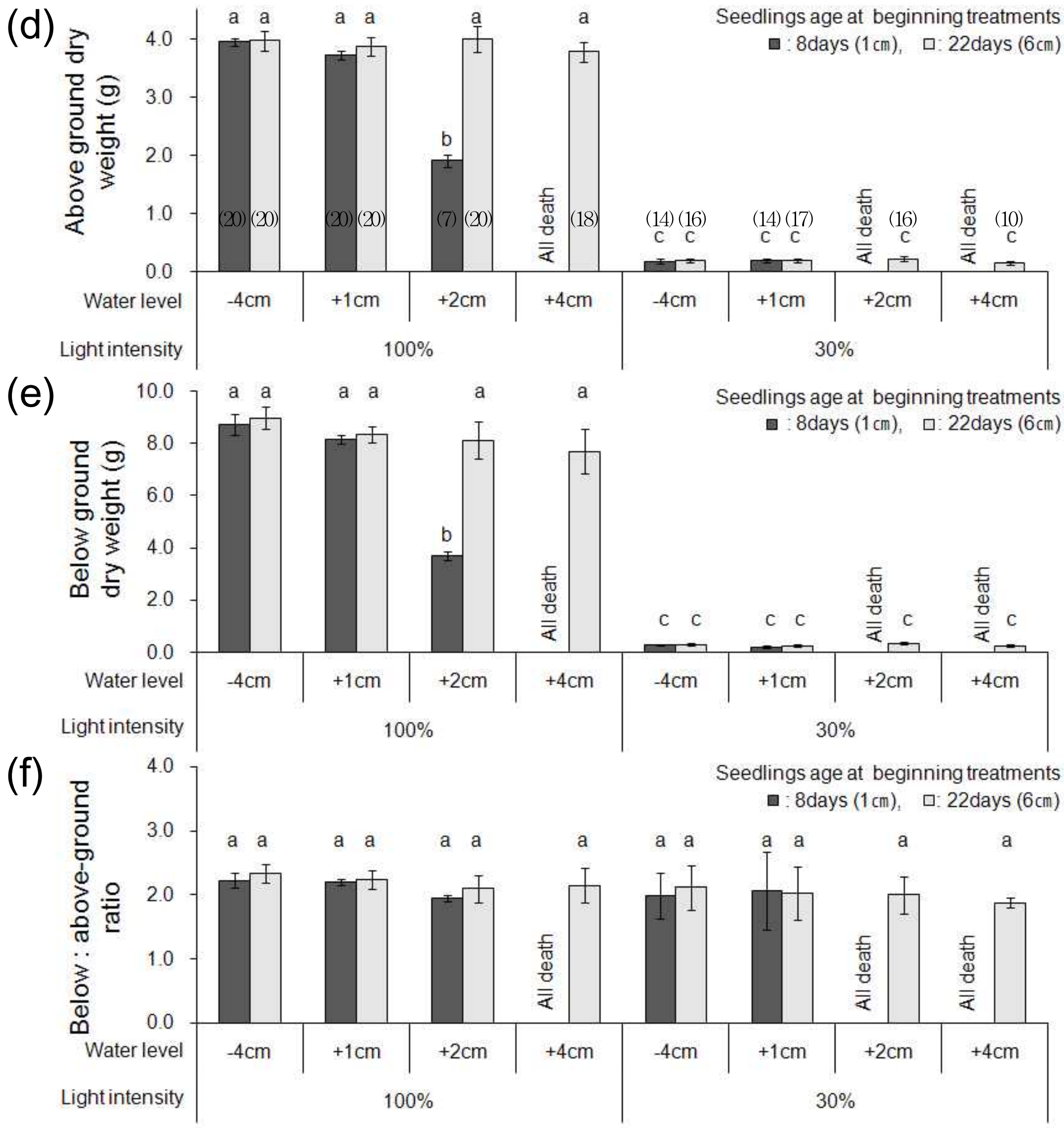


Figure 11. Continued (caption in page 37).

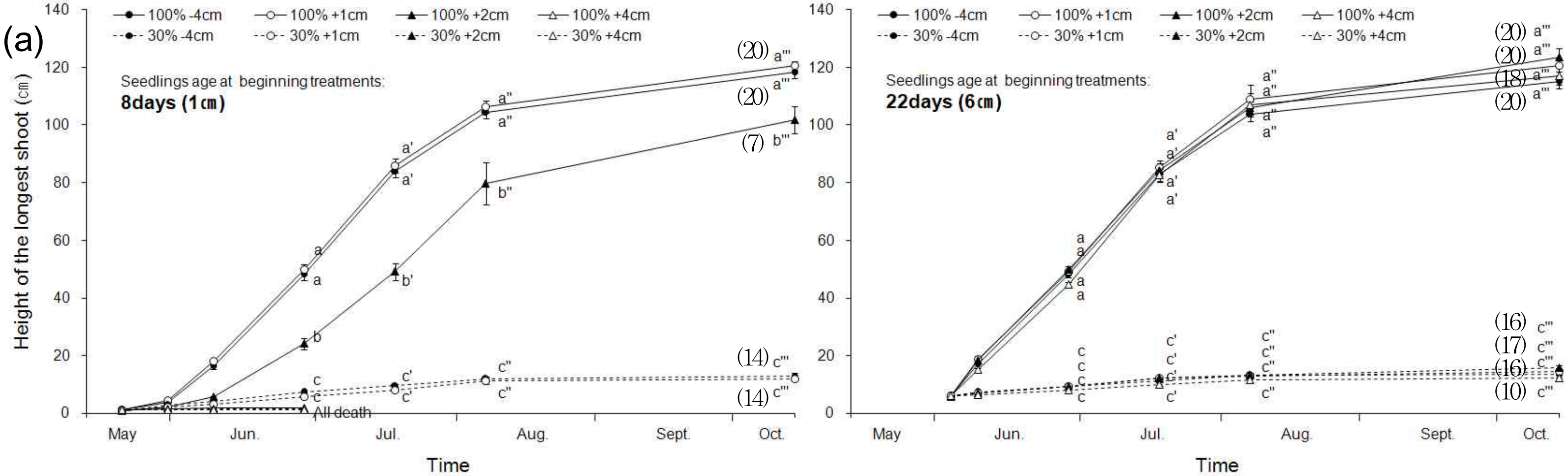


Figure 12. Growth curve on height of the longest shoot (a), leaf number on the longest shoot (b) and shoot number per genet (c) of 8 and 22-day-old *P. australis* seedlings (mean seedlings height: 1 ㎝ and 6 ㎝, respectively) at different light intensity and water level treatments (mean values ± SE). The number in parentheses refer to replication number, except dead individuals. Different letters indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

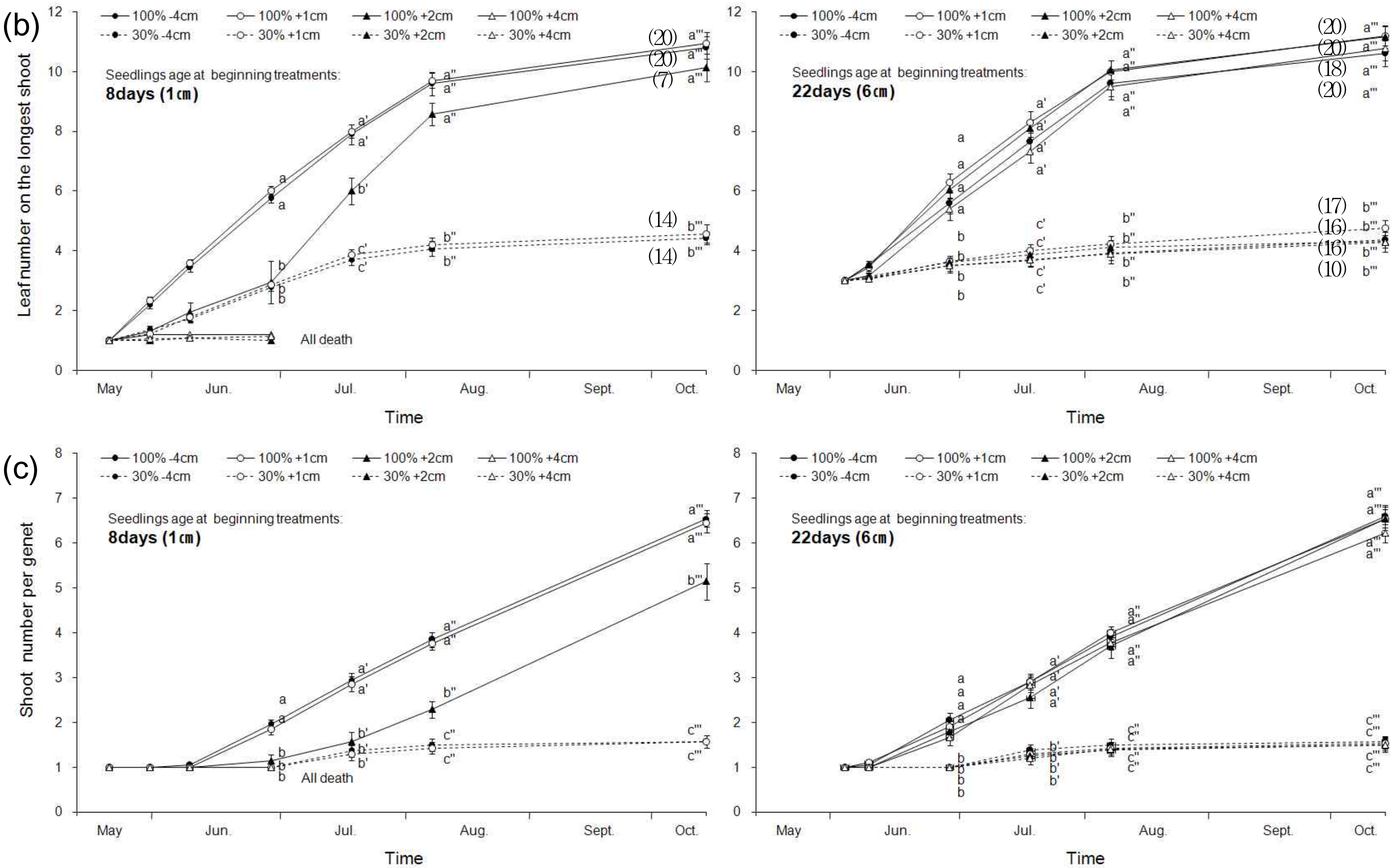


Figure 12. Continued (caption in page 39).

6. Old seedling growth

6.1. *Salix koreensis*

42-day-old *S. koreensis* seedlings (28 ㎝ in height) had mean survival rate and height across all combined treatments ranging from 50.0% to 100.0% and 39.3 ㎝ to 124.1 ㎝, respectively (Figure 13). And similar tendency was seen according treatments on all parameters of seedlings growth.

There were significant difference between light intensity treatments on height ($p<0.01$), leaf number ($p<0.001$), diameter of root collar ($p<0.01$), leaf dry weight ($p<0.001$), stem dry weight ($p<0.001$) and root dry weight ($p<0.001$) of *S. koreensis* seedlings (Table 6). And light intensity treatment had significant interactive effects with water level treatment on only three parameters associated with leaf: leaf number ($p<0.05$), bud number ($p<0.05$) and leaf dry weight ($p<0.05$), while having significant interactive effects with competition treatment on all parameters. With decrease of light intensity from 100% to 30%, growth amount of *S. koreensis* seedling decreased by 20.6% on height, 29.6% on leaf number, 30.0% on diameter of root collar, 44.8% on leaf dry weight, 55.4% on stem dry weight and 57.3% on root dry weight on equal water level condition within pure planting condition. But in the case of within mixed planting condition, as light intensity declined, seedlings growth tended to slightly increase under -10 ㎝ and +4 ㎝-water level condition, and no changed under +12 ㎝-water level. And light intensity treatment had no effect on survival rate and bud number.

There were significant difference among three water level treatments on all parameters: survival rate, height, leaf number, bud number, diameter of root collar, leaf dry weight, stem dry weight and root dry weight ($p<0.001$) of *S. koreensis* seedlings. And water level treatment had significant interactive effects with light intensity treatment on three parameters and with competition treatment on three parameter: survival rate ($p<0.01$), stem dry weight ($p<0.001$) and root dry weight ($p<0.001$). Overall, with the increase of water level from -10 ㎝ to +12 ㎝, survival rate of *S. koreensis* seedlings declined by 31.0%, and growth amount decreased by 41.4% on height, 33.1% on leaf number, 30.3% on bud number, 47.2% on diameter of root collar, 57.5% on leaf dry weight, 72.0% on stem dry weight and 85.9% on root dry weight on equal light intensity and competition condition. But the decrements according to the changing water level were bigger under mixed planting than under pure planting.

As to competition treatments, there were significant difference between way of planting on all parameters ($p<0.001$) of *S. koreensis* seedlings, just like water level treatment. And competition treatment had significant two-way interactive effects with light intensity and water level treatment on survival ($p<0.01$), but had no three-way interaction. *S. koreensis* survival rate of mixed planting was lower than that of pure planting on equal water level condition within 100%-light intensity condition. In contrast, in the case of 30%-light intensity, survival rate was not influenced by competition treatment under low water level condition (-12 ㎝ and +4 ㎝).

There were significant three-way interactive effect on seven growth parameters of *S. koreensis* seedlings ($p<0.001$): height, leaf number, bud number, diameter of root collar, leaf dry weight, stem dry weight and root dry weight. Amount of seedlings growth of pure planting was similar or higher in comparison with mixed planting under 30%-light intensity × -10 ㎝-water level and 30%-light intensity × +4 ㎝-water level treatments. But under the other conditions, *S. koreensis* growth amount of mixed planting were lower than that of pure planting.

While below : above-ground ratio were influenced by water level and competition treatment significantly ($p<0.001$), it was not influenced by light intensity.

Table 6. Analysis of variance for the effect of light intensity (100% and 30%), water level (-10 ㎝, +4 ㎝ and +12 ㎝) and competition (pure and mixed planting with *P. australis*) on growth of 42-day-old *S. koreensis* seedlings (mean seedlings height: 28 ㎝).

Source of variation	d.f.	F-value								
		Survival rate	Height	Leaf number	Bud number	Diameter of root collar	Leaf dry weight	Stem dry weight	Root dry weight	Below : above-ground ratio
Light intensity	1, 48	2.41 ns	7.84 **	25.94 ***	2.35 ns	13.10 **	18.60 ***	70.49 ***	72.50 ***	0.46 ns
Water level	2, 48	83.63 ***	114.04 ***	79.85 ***	29.69 ***	253.10 ***	109.40 ***	166.76 ***	512.71 ***	179.46 ***
Competition	1, 48	63.41 ***	116.26 ***	187.51 ***	154.37 ***	224.62 ***	201.51 ***	270.36 ***	401.98 ***	72.20 ***
Light intensity × Water level	2, 48	1.38 ns	1.32 ns	3.38 *	4.00 *	0.00 ns	4.83 *	1.82 ns	4.82 ns	0.32 ns
Light intensity × Competition	1, 48	11.65 **	44.37 ***	117.91 ***	77.39 ***	212.91 ***	157.64 ***	157.64 ***	279.76 ***	7.55 **
Water level × Competition	2, 48	7.26 **	1.68 ns	0.66 ns	0.30 ns	0.35 ns	1.07 ns	12.62 ***	44.36 ***	1.17 ns
Light intensity × Water level × Competition	2, 48	0.99 ns	10.24 ***	13.26 ***	11.77 ***	26.18 ***	13.50 ***	34.91 ***	83.23 ***	1.82 ns

ns: Not sgnificant at 0.05 level.
*: Significant at 0.01-0.05 level.
**: Significant at 0.001-0.01 level.
***: Significant at <0.001 level.

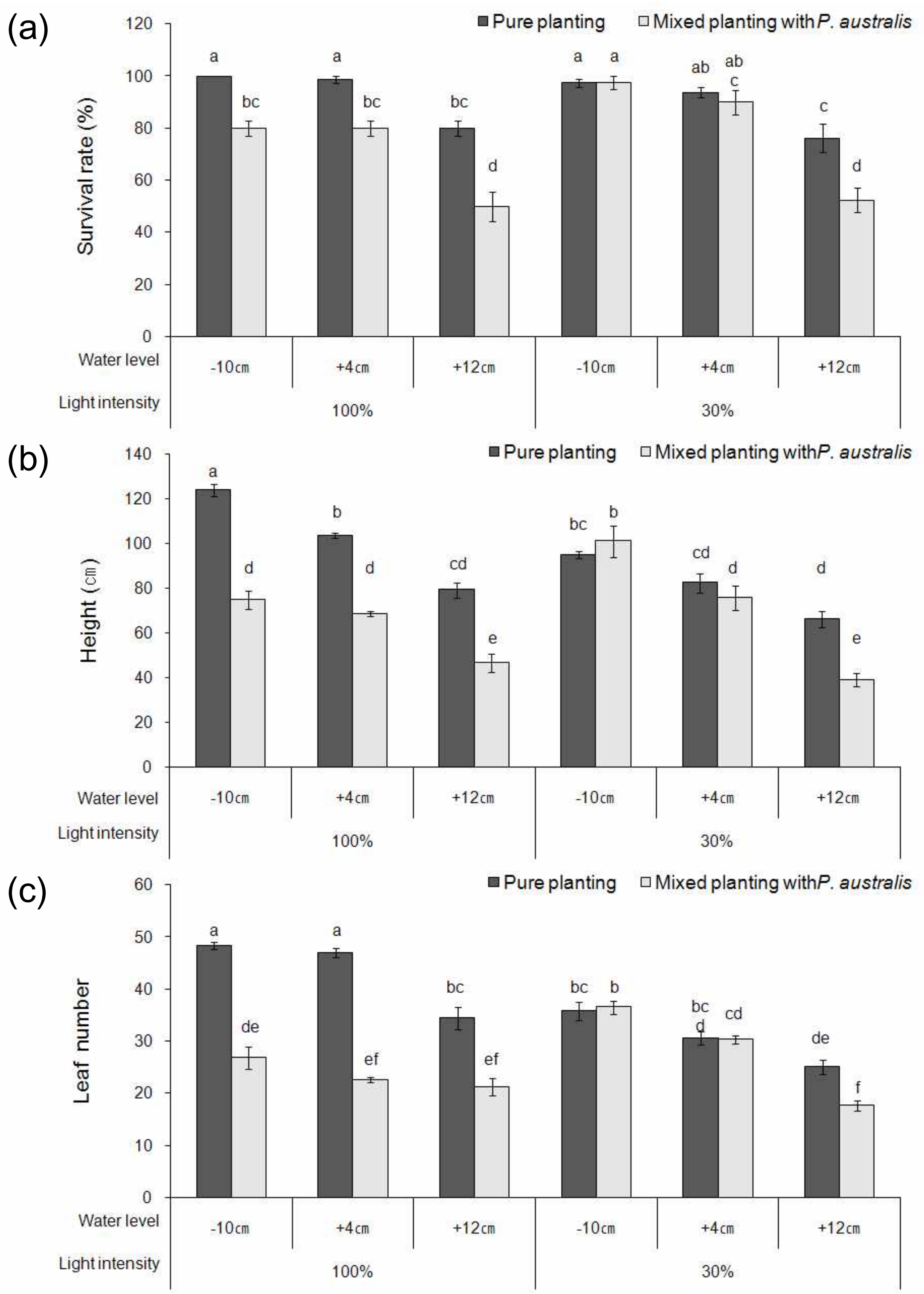


Figure 13. Final survival rate (a), height (b), leaf number (c), bud number (d), diameter of root collat (e), leaf dry weitght (f), stem dry weight (g), root dry weight (h) and below : above-ground ratio (i) of 42-day-old *S. koreensis* seedlings (mean seedlings height: 28 ㎝) at different light intensity, water level and competition treatments at the end of the experiment (mean values ± SE, n = 5 for each treatment). 16 and 8 seedlings were used for each replicates of pure and mixed-planting treatment, respectively. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

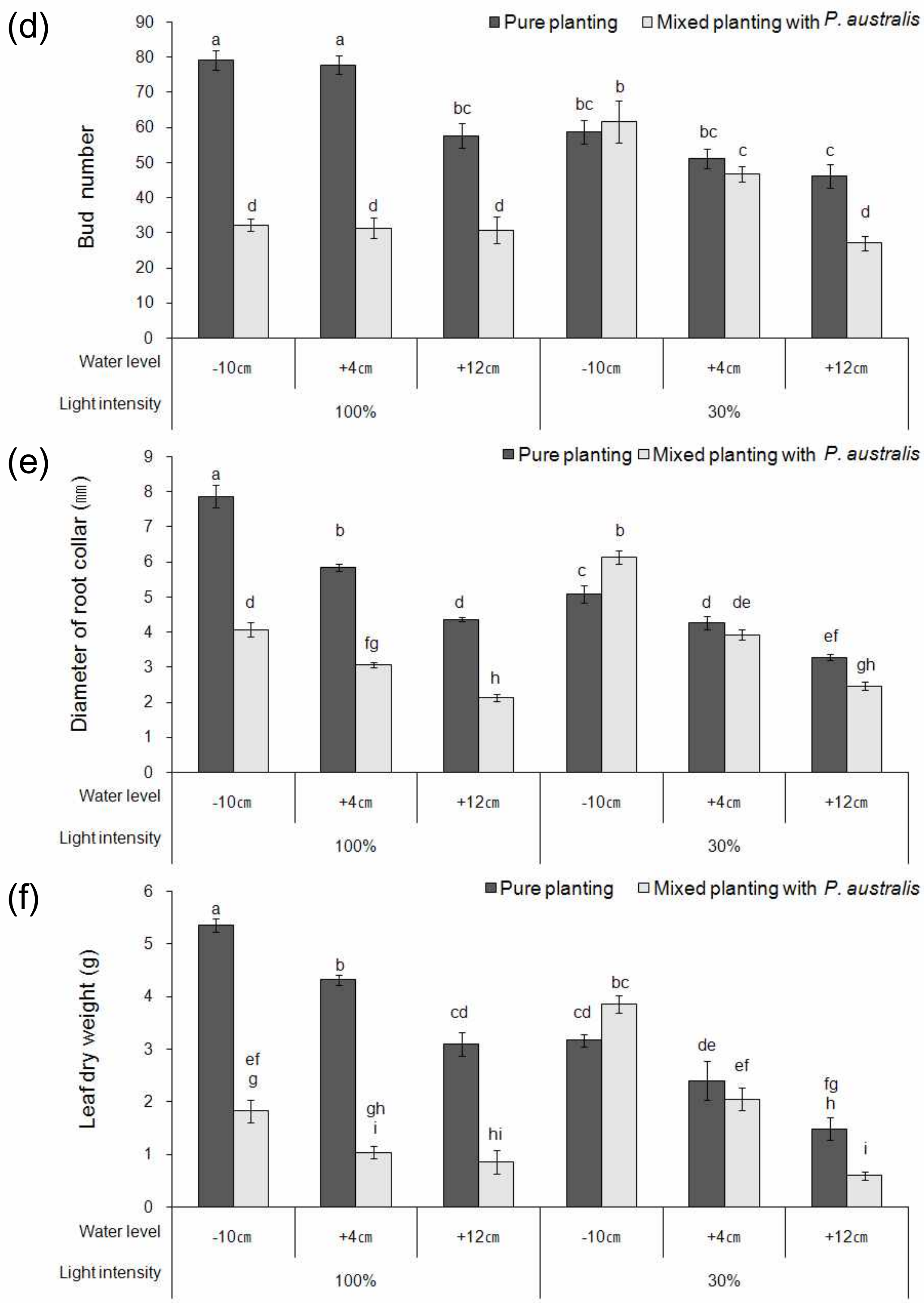


Figure 13. Continued (caption in page 45).

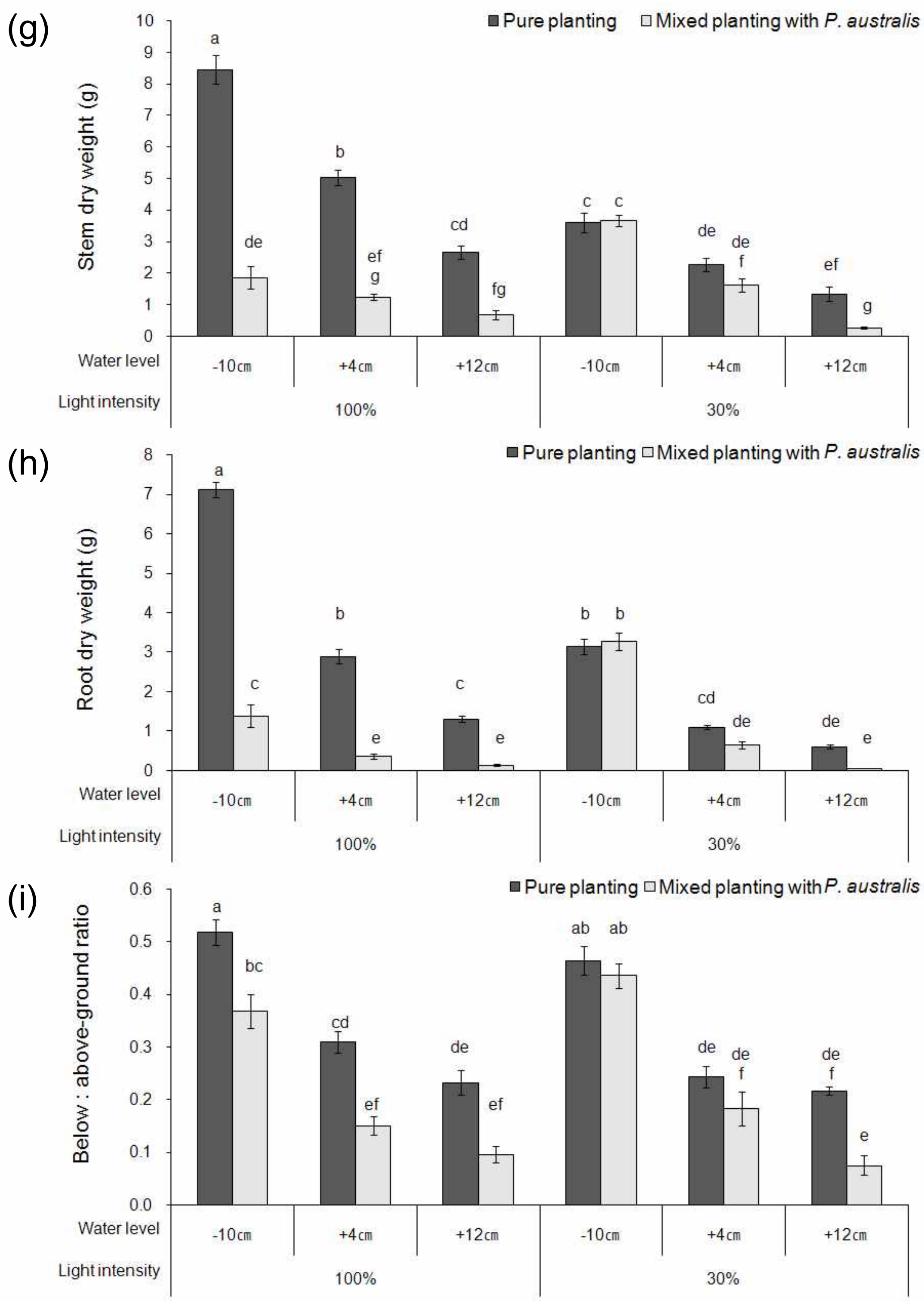


Figure 13. Continued (caption in page 45).

6.2. *Phragmites australis*

44-day-old *P. australis* seedlings (63 ㎝ in height) had mean survival rate and height by all treatments combination ranging from 67.5% to 100.0% and 56.1 ㎝ to 206.4 ㎝, respectively (Figure 14). Final survival rate showed that differences between light intensity, water level, competition, and their 2-way and 3-way interactive effects were significant ($p < 0.001$) (Table 7). Mean survival rate of *P. australis* seedlings was 67.5% under 30%-light intensity × -10 ㎝ water level condition, while being above 90.0% under the other conditions. Flowering rate showed that differences between light intensity ($p<0.001$), competition ($p<0.01$), and their two-way interaction ($p<0.01$) were significant. Under 70% shading condition, all seedlings did not have an inflorescence. But under full sunlight, a few seedlings had inflorescences across all water level and competition conditions, and flowering rate was higher in mixed planting than in pure planting.

And similar tendency was seen according treatments on all parameters of seedlings growth. There were significant difference between light intensity treatments on height of the longest shoot ($p<0.001$), cumulative height ($p<0.001$), leaf number on the longest shoot ($p<0.01$), shoot number per genet ($p<0.001$), diameter of the thickest shoot ($p<0.001$), aboveground dry weight ($p<0.001$) and belowground dry weight ($p<0.001$) of *P. australis* seedlings. And light intensity treatment had relatively strong interactive effect with competition treatment (on 7 growth parameters: height of the longest shoot, cumulative height, leaf number on the longest shoot, shoot number per genet, diameter of the thickest shoot, aboveground dry weight and belowground dry weight) in comparison with water level treatment (on only 3 growth parameters: shoot number per genet, aboveground dry weight and belowground dry weight). With decrease of light intensity from 100% to 30%, growth amount of *P. australis* seedling decreased by 52.6% on height of the longest shoot, 48.7% on cumulative height, 0.7% on leaf number on the longest shoot, 29.5% on shoot number per genet, 20.7% on diameter of the thickest shoot, 9.7% on aboveground dry weight and 68.0% on belowground dry weight at equal water level treatment within pure planting condition. But in the case of within mixed planting condition, the decrements according to decreasing light intensity were bigger, growth amount decreased by 62.7%, 73.1%, 12.6%, 44.5%, 37.8%, 79.6% and 80.4% on each growth parameters, respectively.

There were significant difference between water level treatments on height of the longest shoot ($p<0.01$), cumulative height ($p<0.01$), shoot number per genet ($p<0.01$), diameter of the thickest shoot ($p<0.001$) and aboveground dry weight ($p<0.001$) of *P. australis* seedlings. Difference of water level between −10 ㎝ and +12 ㎝ did not affect leaf number on the longest shoot and belowground dry weight of *P. australis* significantly.

Water level treatment had relatively strong interactive effects with competition treatment (on six growth parameters: height of the longest shoot, cumulative height, shoot number per genet, diameter of the thickest shoot, aboveground dry weight and belowground dry weight) in comparison with light intensity treatment (on three growth parameters: shoot number per genet, aboveground dry weight and belowground dry weight). Within pure planting condition, growth amount of seedlings tended to be similar among three water level conditions. In contrast, in the case of mixed planting, as water level increased from −10 ㎝ to +12 ㎝, growth amount of seedling increased by 17.2% on height of the longest shoot, 31.6% on cumulative height, 18.0% on shoot number per genet, 27.2% on diameter of the thickest shoot and 57.2% on aboveground dry weight on equal light intensity condition.

There were significant difference between competition treatments on all growth parameters of *P. australis* ($p<0.001$). And competition treatment had strong interactive effects with both light intensity treatment (on seven growth parameters: height of the longest shoot, cumulative height, leaf number on the longest shoot, shoot number per genet, diameter of the thickest shoot, aboveground dry weight and belowground dry weight) and water level treatment (on six growth parameters: height of the longest shoot, cumulative height, shoot number per genet, diameter of the thickest shoot, aboveground dry weight and belowground dry weight). Amount of seedlings growth of mixed planting was lower than pure planting under 30%-light intensity × -10 ㎝ water level treatment. But under the other treatments, *P. australis* growth amount of mixed planting tended to be similar or higher than that of pure planting.

Below : above-ground ratio was influenced by water level ($p<0.001$) without significant interactive effect with the other treatments.

Table 7. Analysis of variance for the effect of light intensity (100% and 30%), water level (-10 ㎝, +4 ㎝ and +12 ㎝) and competition (pure and mixed planting with *S. koreensis*) on growth of 44-day-old *P. australis* seedlings (mean seedlings height: 63 ㎝).

Source of variation	d.f.	F-value									
		Survival rate	Flowering rate	Height of the longest shoot	Cumulative height	Leaf number on the longest shoot	Shoot number per genet	Diameter of the thickest shoot	Above ground dry weight	Below ground dry weight	Below : above -ground ratio
Light intensity	1, 48	63.48 ***	29.47 ***	1728.03 ***	692.37 ***	7.54 **	561.33 ***	265.38 ***	1312.59 ***	2419.80 ***	0.80 ns
Water level	2, 48	13.51 ***	1.55 ns	5.71 **	7.32 **	3.05 ns	5.41 **	10.06 ***	23.12 ***	0.10 ns	14.73 ***
Competition	1, 48	33.57 ***	13.80 **	20.52 ***	128.53 ***	16.28 ***	249.04 ***	46.73 ***	144.79 ***	190.15 ***	0.89 ns
Light intensity × Water level	2, 48	13.51 ***	1.55 ns	1.86 ns	2.48 ns	0.23 ns	5.66 **	1.99 ns	3.58 *	8.39 **	0.22 ns
Light intensity × Competition	1, 48	33.57 ***	13.80 **	47.31 ***	146.87 ***	6.31 *	85.64 ***	42.83 ***	119.67 ***	212.88 ***	0.10 ns
Water level × Competition	2, 48	13.51 ***	1.55 ns	6.21 **	6.49 **	2.55 ns	11.91 ***	13.31 ***	27.38 ***	22.81 ***	1.40 ns
Light intensity × Water level × Competition	2, 48	13.51 ***	1.55 ns	2.61 ns	3.23 *	0.33 ns	2.05 ns	7.41 **	5.63 **	0.13 ns	1.37 ns

ns: Not sgnificant at 0.05 level.
*: Significant at 0.01-0.05 level.
**: Significant at 0.001-0.01 level.
***: Significant at <0.001 level.

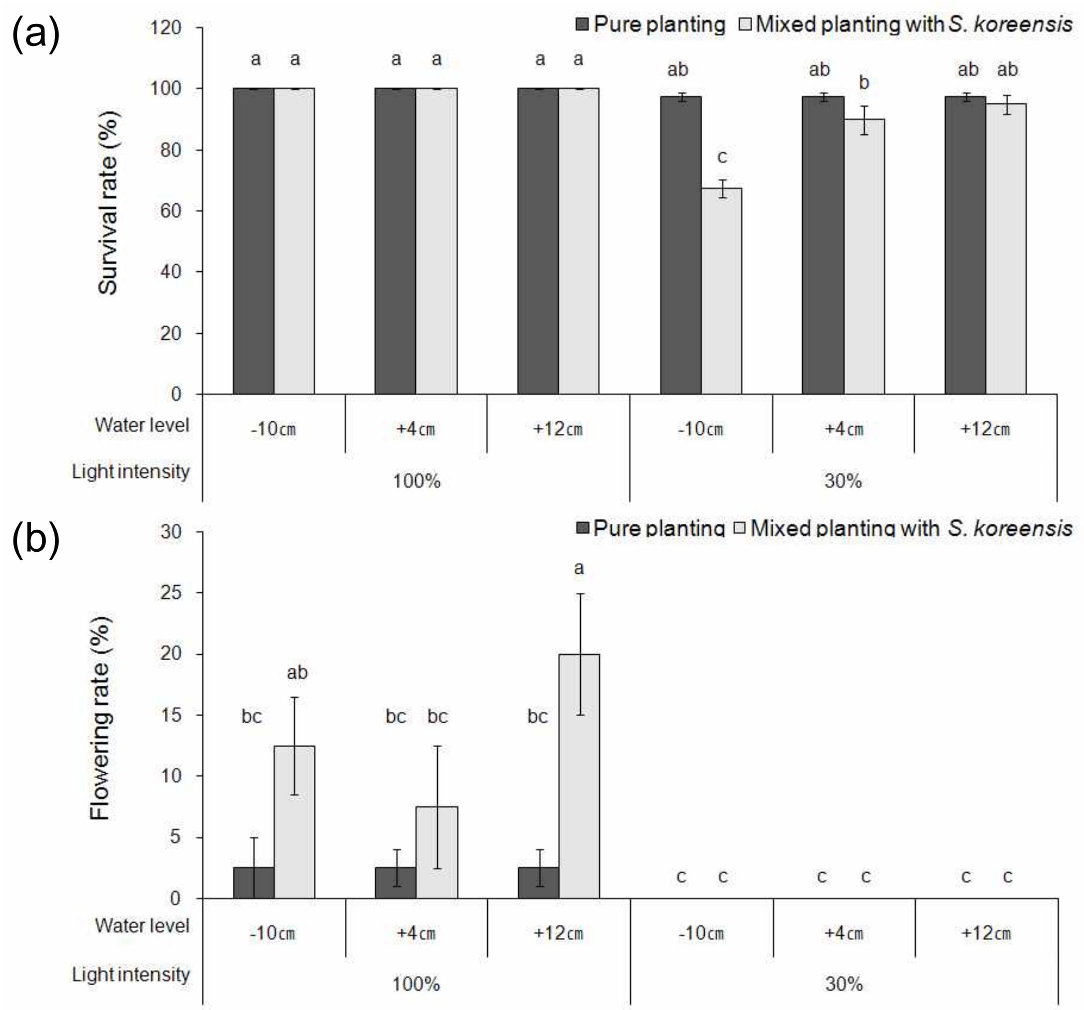


Figure 14. Final survival rate (a), flowering rate (b), height of the longest shoot (c), cumulative height (d), leaf number on the longest shoot (e), shoot number per genet (f), diameter of the thickest shoot (g), aboveground dry weight (h), belowground dry weight (i) and below : above -ground ratio (j) of 44-day-old *P. australis* seedlings (mean seedlings height: 63 ㎝) at different light intensity, water level and competition treatments at the end of the experiment (mean values ± SE, n = 5 for each treatment). 16 and 8 seedlings were used for each replicates of pure and mixed-planting treatment, respectively. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

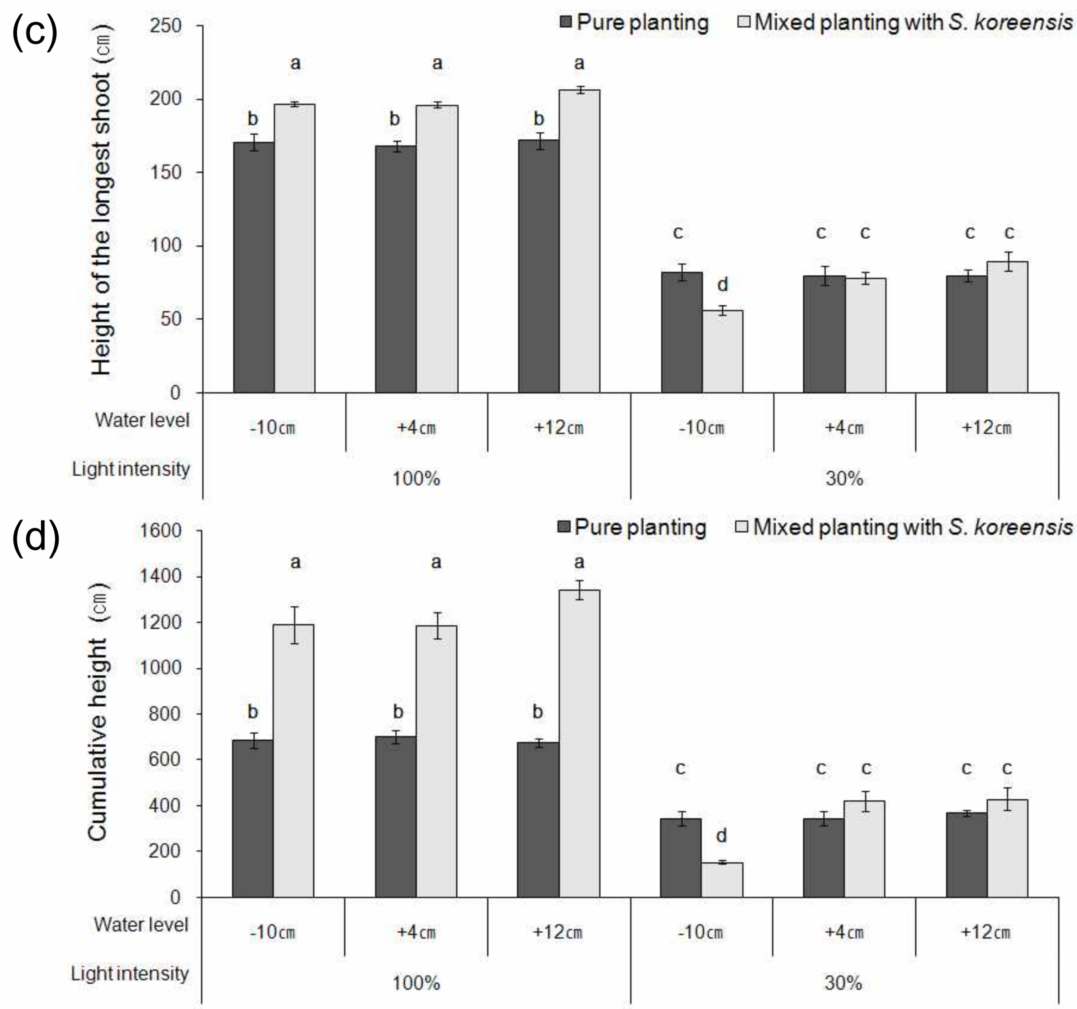


Figure 14. Continued (caption in page 52).

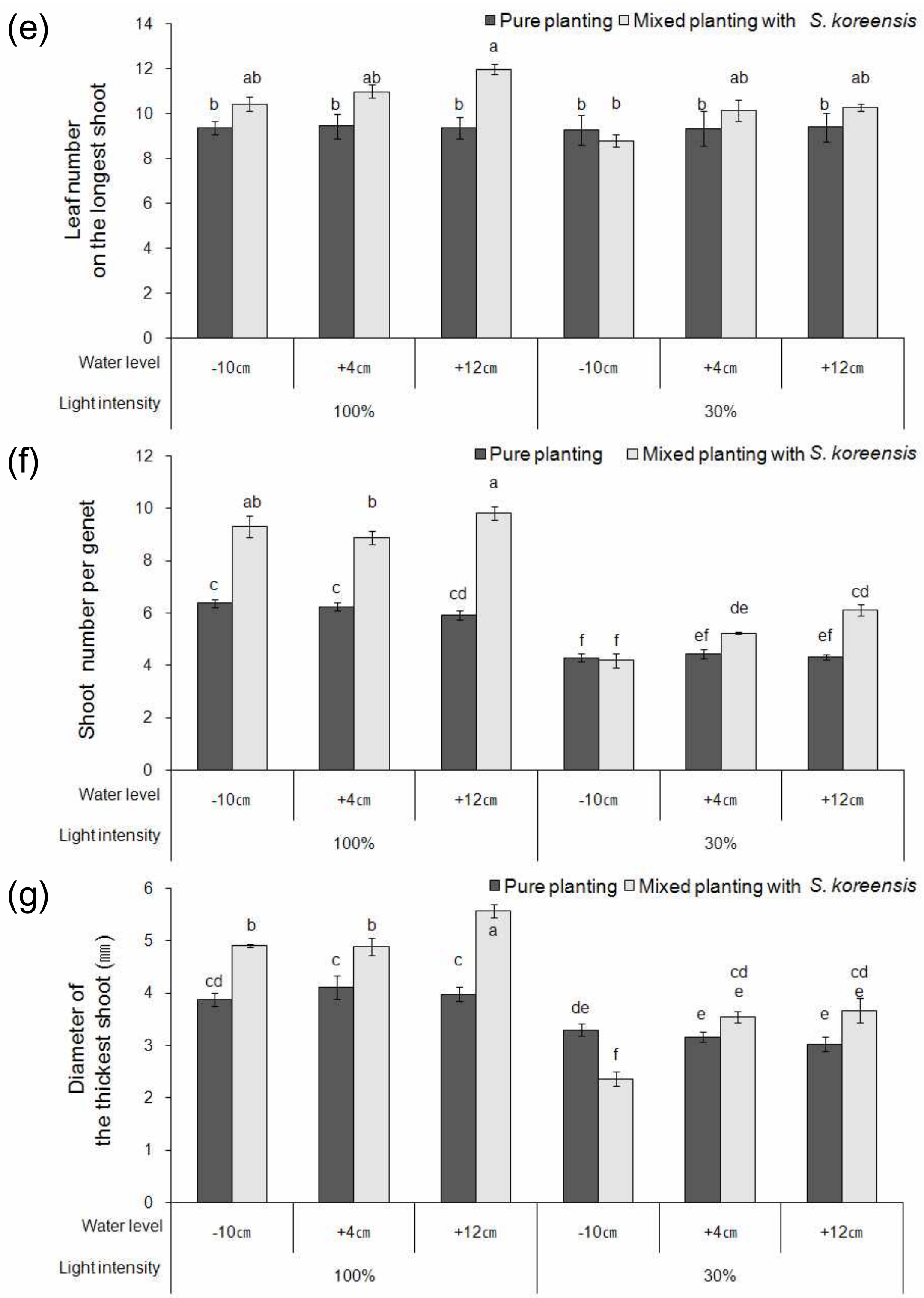


Figure 14. Continued (caption in page 52).

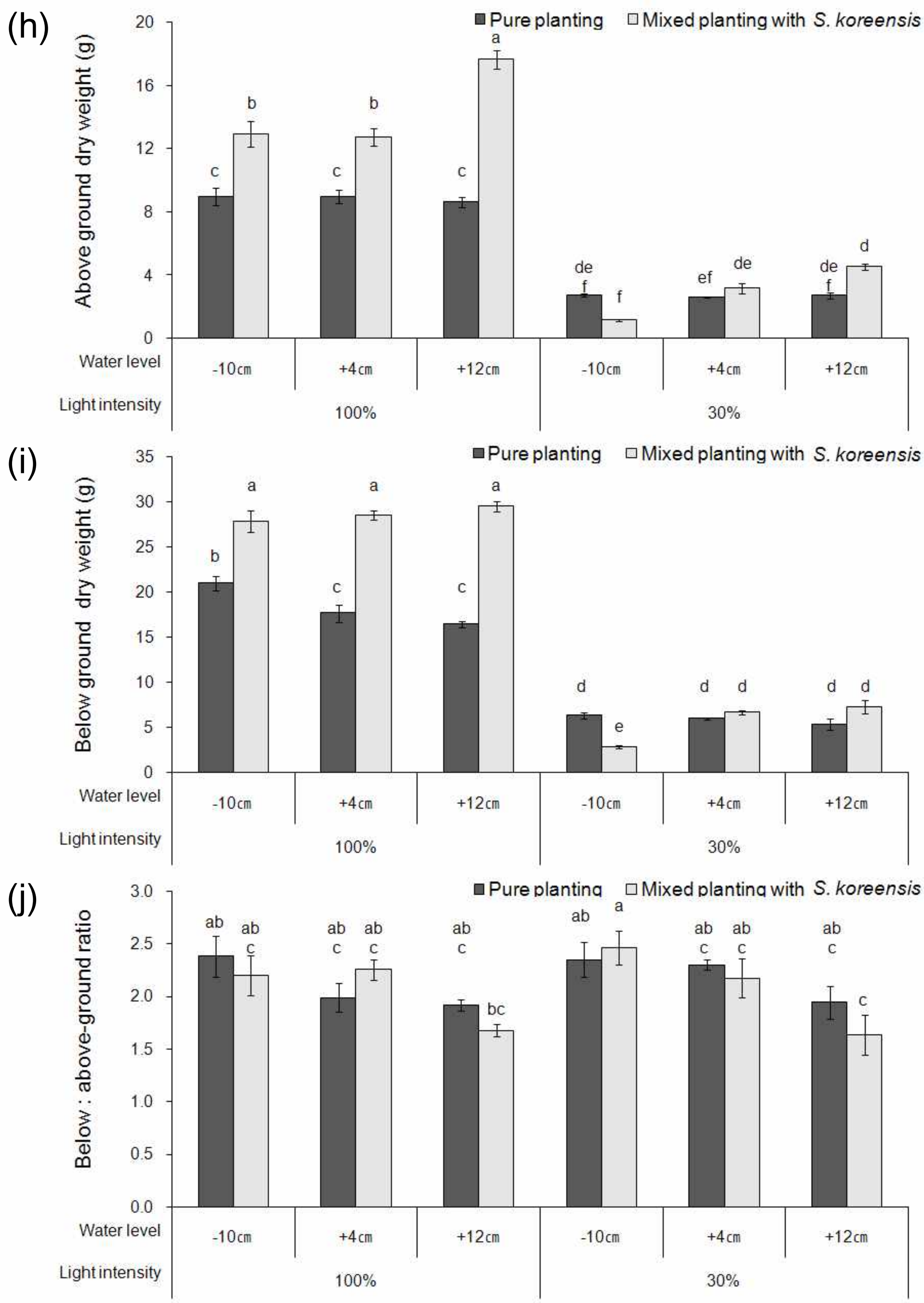


Figure 14. Continued (caption in page 52).

6.3. Response to interspecific competition

There were significant three-way interactive effect between light intensity, water level and species on mixed : pure-planting ratio (referred to hereafter as M/P ratio) in survival rate, height and biomass of the experiment of old seedling growth at harvest ($p<0.001$) (Table 8). Similar tendency of M/P ratio was seen according to treatments on all parameters (Figure 15). Only under 30%-light intensity × -10 ㎝-water level condition, the mean M/P ratios in height and biomass of *S. koreensis* were above 1, in contrast, those of *P. australis* were below 1 under only 30%-light intensity × -10 ㎝-water level condition (Figure 15).

As light intensity decreased, M/P ratios in all parameters of *S. koreensis* increased significantly within low water level condition (-10 ㎝ and +4 ㎝), not changed within high water level (+12 ㎝). On the other hand, as light intensity declined, those of *P. australis* tended to decrease on equal water level condition.

With increase of water level, M/P ratios in all parameters of *S. koreensis* decreased significantly within 30%-light intensity condition, not changed within 100%-light intensity except for survival rate. Within 100%-light intensity, M/P ratio in survival rate of *S. koreensis* was lower under +12 ㎝-water level than under -10 ㎝ and +4 ㎝. On the contrary to this, with increase of water level, M/P ratios in all parameters of *P. australis* increased significantly within 30%-light intensity. Within 100%-light intensity, those of *P. australis* slightly increased or not changed according to different water level.

Table 8. Analysis of variance for the effect of light intensity (100% and 30%), water level (-10 ㎝, +4 ㎝ and +12 ㎝) on mixed : pure-planting ratios of *S. koreensis* and *P. australis*.

Source of variation	d.f.	F-value: Mixed : pure -planting ratio in survival rate	Mixed : pure -planting ratio in height	Mixed : pure -planting ratio in aboveground dry weight	Mixed : pure -planting ratio in belowground dry weight	Mixed : pure -planting ratio in total dry weight
Light intensity	1, 48	0.00 ns	0.07 ns	0.90 ns	13.47 **	6.09 *
Water level	2, 48	14.04 ***	5.18 **	31.74 ***	8.97 ***	33.71 ***
Species	1, 48	55.01 ***	360.19 ***	1043.47 ***	1718.20 ***	1916.16 ***
Light intensity × Water level	2, 48	2.95 *	1.95 ns	13.02 ***	7.52 **	11.87 ***
Light intensity × Species	1, 48	74.45 ***	207.31 ***	358.29 ***	546.00 ***	746.02 ***
Water level × Species	2, 48	50.79 ***	70.89 ***	205.54 ***	252.28 ***	322.80 ***
Light intensity × Water level × Species	2, 48	14.14 ***	51.68 ***	63.43 ***	74.65 ***	100.50 ***

ns: Not sgnificant at 0.05 level.
*: Significant at 0.01-0.05 level.
**: Significant at 0.001-0.01 level.
***: Significant at <0.001 level.

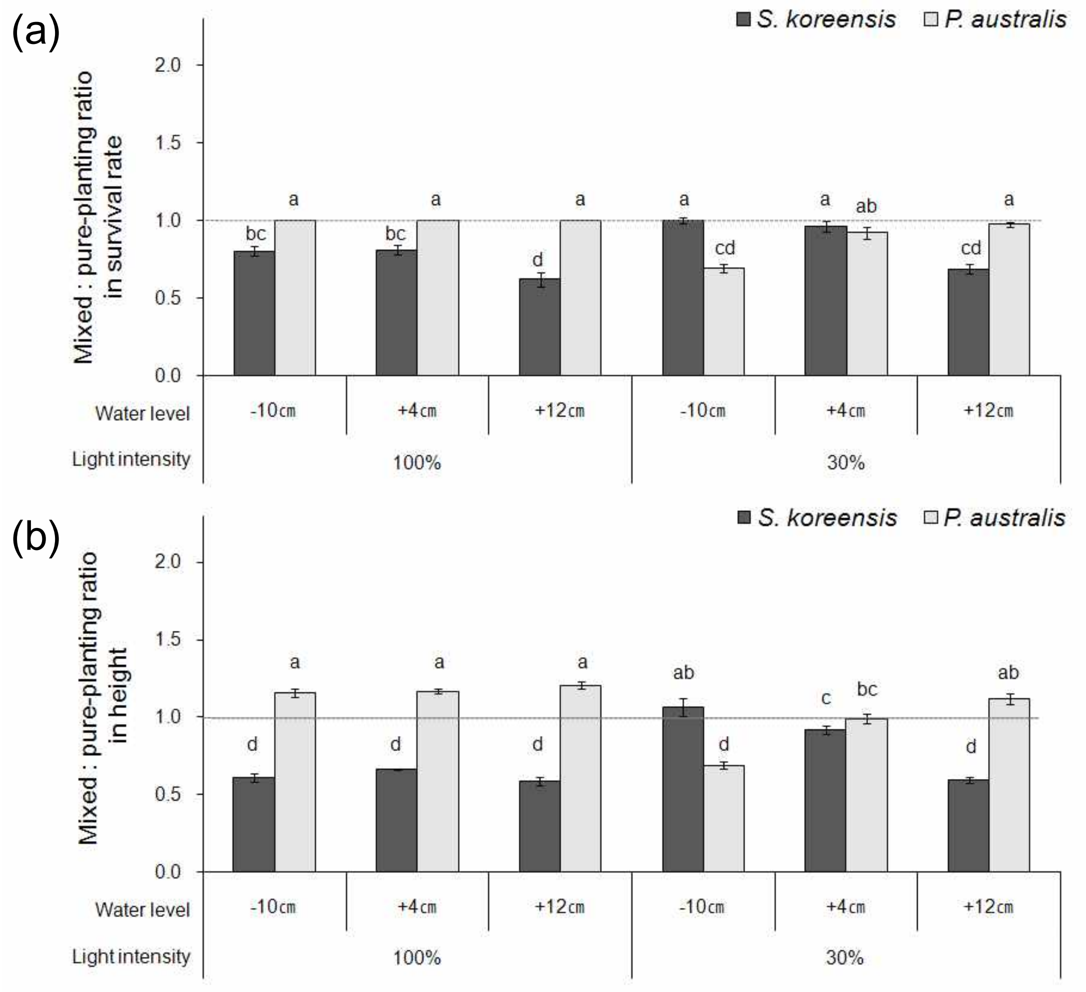


Figure 15. Mixed : pure-planting ratios in survival rate (a), height (b), aboveground dry weight (c), belowground dry weight (d) and total dry weight (e) of *S. koreensis* and *P. australis* seedlings at different light intensity and water level at the end of the experiment (mean values ± SE, n = 5 for each treatment). 16 and eight seedlings were used for each replicates of pure and mixed-planting treatment, respectively. Different letters over bar indicate significant differences (Tukey WSD Test at <0.05 level) between treatments.

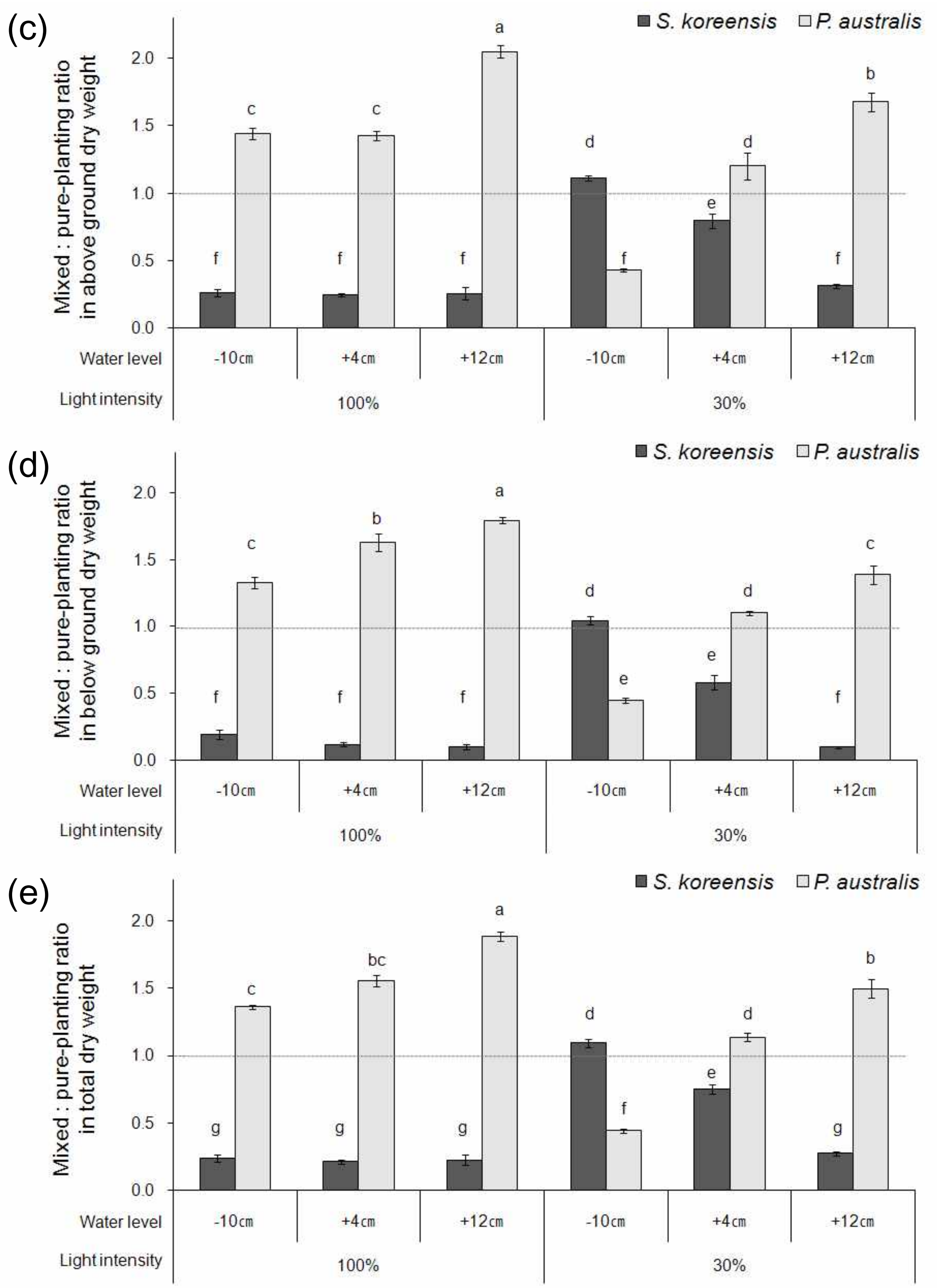


Figure 15. Continued (caption in page 58).

Discussion

1. Beginning interaction

304/㎡ of *P. australis* seedlings emerged in the seed bank collected at *S. koreensis* and *P. australis* community (Table 1). In contrast, any seedlings of *S. koreensis* did not emerge from the seed bank, and it agrees with Sacchi & Price (1992), who reported that no seed bank exists for *S. lasiolepis* because its seed longevity is too short. Even though any *Salix* seedlings could not be observed from the seed bank, I can assume that numerous seeds of *Salix* species would have scattered at period of seed dispersal because the coverage of *S. koreensis* (80%) is nearly three times more than that of *P. australis* (25%).

The germination period of two species was overlapped, the difference of date maximum germination occurred between two species was only two days (Figure 3). And Both species had grown until autumn consistently (Figure 1). If there are much differences in germination and growth periods between those species, it is hard to expect possible interactions between two species, or the species germinating quickly is much superior in competition. Actually, there are differences in germination period up to three months between certain wetland species (Fraser & Karnezis 2005; Kim & Ju 2005). Therefore, this results show that initial establishments from seed to 1-year-old seedling of those two species coincided each other temporally and spatially.

2. Germination

Although gemination rate of *S. koreensis* varied according to the light intensity, generally, it showed relatively high levels under most of treatments (ranged from 76.5% to 97.4%) (Figure 4). And the germination rate of *P. australis* was not influenced by light intensity and water level as well. (Figure 5). Many previous studies have reported that the germination rate of *P. australis* varies from several region (Gustafsson & Simak 1963; Haslam 1972; Ekstam, Johannesson & Milberg 1999; Shii & Kadono 2002). In the case of this experiment, the germination rate of *P. australis* ranged from 60.9% to 71.5% was relatively high like *S. koreensis*. The results suggest that shading and flooding were not limiting factors at germination stage of two species.

But seed viability of *S. koreensis* decreased within a few days, and any seeds cannot germinate 16 days after being released (Figure 6), and it is in accordance with previous studies (Densmore & Zasada 1983; Sacchi & Price 1992; Maroder et al. 2000). In addition, *S. koreensis* seedlings could not grow well even though seeds germinated if the seeds had begun to germinate long time after being released (Figure 8). Calculated by multiplication germination rate of seeds and survival rate of seedlings, the ratio of survivable individual to all dispersed seeds is only 3.2% when 8 days passed after seed dispersal, and all individual died when 10 days passed. In other words, environmental factor at the period of seed dispersal is very important for *S. koreensis*. On the other hand, 35.4% of *P. australis* seeds germinated after a year, so seed longevity of *P. australis* may be relatively longer than *S. koreensis*.

Under the place of enough wetness by appropriate water table, lots of seedlings of both species may emerge. But otherwise, there may be difference in seedling emergence between two species. If it does not rain at the period of seed dispersal, any *S. koreensis* seeds cannot survive under dry place, but *P. australis* seeds can wait for the proper environment.

3. Survival and growth of seedling

Both of flooding and shading are important factors determining vegetation establishment of plants (Lenssen, Menting & van der Putten 2003). From our results, we can say that both flooding and shading affect the seedling survival and growth of *S. koreensis* and *P. australis* (Figures 9, 10, 11 and 12). But flooding had relatively stronger influence on *S. koreensis* than *P. australis*, and shading was opposed to flooding. When there was no competition of two species, the interactive effect with flooding and shading was little, so it would suggest that those two factors have separate influence on survival and growth of seedlings. Lenssen, Menting & van der Putten (2003) reported that shading stress under flooding condition affect seedlings only if species have a tolerance to waterlogging. The result of little interactive effect of flooding and shading would mean that *S. koreensis* and *P. australis* are tolerant to flooding, and this is accepted generally (Cronk & Fennessy 2001; Mitsch & Gosselink 2007).

Flooding is very important factor particularly at germination and seedlings stages (Weiher & Keddy 1995; Fraser & Karnezis 2005). In this experiment, survival of too young *S. koreensis* seedlings (1 ㎝ in height and 20 days in age) was influenced by minor flooding, especially the flooding of twice as tall as its height (2 ㎝) killed all seedlings. In the case of 1-㎝-tall *P. australis* (eight days in age), 30% of seedlings overcame the flooding of twice level as its height, and grew continuously. The explanation could be given by previous study that *P. australis* seedlings could grow to 2-5 ㎝ high only from seed reserves (Haslam 1972). In the experiment of the relatively old seedlings (above 40 days in age), flooding level of 12 ㎝ above the soil surface reduced the survival and growth of *S. koreensis* seedlings (28 ㎝ in height), but did not influence on *P. australis* seedlings (63 ㎝ in height).

And shading of 70% affected survival and growth of both species irrespective of its age, but relatively more harmful to *P. australis* than *S. koreensis*. This agrees with previous study reported that seedling growth of *P. australis* is noticeably affected by light intensity (Haslam 1972). It was remarkable that some of very young *P. australis* seedlings (1 ㎝ in height) could overcome the flooding twice its height under full sunlight, but all seedlings could not under shading of 70%. It was thought that shading reduced resistance to flooding, and it was related to previous study found that more *P. australis* seedlings could not overcome the flooding over its height under dense algal presence than slight or not (Armstrong et al. 1999). Exceptionally there was no difference in leaf number on the longest shoot between 100% and 30% light intensity of 63 ㎝-tall *P. australis* seedlings, although height of seedlings were much different. It agrees with previous study that reported shading increased the weight ratio of leaf to stem of *P. australis* (Haslam 1972).

Above these, shading stress had an effect on reproduction of *P. australis*. Under full sunlight, *P. australis* seedlings made inflorescence in all pots for a year, to a greater or lesser degree, but under shading of 70% did not at all irrespective of water level. Haslam (1972) reported that inflorescence density of *P. australis* is decreased in unfavourable conditions, and it supports the result of this experiment.

Unlike under relatively small amplitude of water level (from -4 ㎝ to +4 ㎝), there was an obvious difference pattern in biomass allocation of both species under relatively large amplitude of water level (from -10 ㎝ to +12 ㎝). It is generally known that decreased allocation to root in response to flooding stress (Coops, van den Brink & van der Velde 1996; Edwards, Lee & Richards 2003; Kercher & Zedler 2004), but some previous studies of wetland plants reported that the allocation patterns did not change under slight intensity of flooding (Scanga 2011; Fraser & Karnezis 2005), and these agrees with the result of this experiment. And decreased allocation to roots versus shoots in response to shading has been reported by some previous studies (Kotowski et al. 2001; Scanga 2011), but this pattern was not observed in the experiment.

4. Growth rate of seedling

Seedlings growth rate of both species showed peak from mid June to mid August, and *P. australis* growed quickly and largely than *S. koreensis* (final height ratio of *S. koreensis* to *P. australis* without flooding and shading = 0.70) (Figure 1). The fast grow rate of wetland plants has advantage of overcoming the two stresses: flooding and shading.

First, wetland plants would avoid flooding stress by growing fast. Previous studies reported that the relative water level to seedling height is important for survival and growth of wetland plant seedlings (Mauchamp, Blanch & Grillas 2001; Kim 2012). In other words, it is important that not only its own tolerance to flooding, but also ability of increase in hight fast and period of flooding are important for seedlings to establish. In this study, *S. koreensis* seedlings have relatively weaker tolerance to flooding than *P. australis*, and growth rate in height of *S. koreensis* was also slower than *P. australis*. By the two components, *S. koreensis* seedlings could be more vulnerable to flooding than *P. australis*.

If the flooding of 2 ㎝ above the soil surface emerges and lasts long from mid May to early June, *S. koreensis* seedlings would be damaged seriously, but *P. australis* seedlings would not. And drastic flooding occurs by heavy rainfall from the end of June to August, and it is thought that flooding intensity and seedlings height during this period determine the seedlings establishment of many wetland plants. When flooding intensity in height is above *S. koreensis* seedlings and below *P. australis* seedlings, *P. australis* seedling is likely to establish at the place successfully, but *S. koreensis* is not (excluded other factors).

Second, by growing fast, wetland plants would have superiority at competition for light, so could avoid shading stress. Kotowski & Diggelen (2004) reported that either fast growth or large individual size are required for plants in fen to compete for light. In this experiment, *P. australis* seedlings growed quickly and highly than *S. koreensis*, and possessed large coverage by producing many shoots (about from 5 to 10 per genet). These would be related that *P. australis* seedlings is relatively weaker tolerant to shading than *S. koreensis*. If growth rate of *S. koreensis* is faster than that of *P. australis*, *P. australis* seedlings is hard to survive in the place *S. koreensis* seedlings grow.

5. Interspecific competition

The relative influence of flooding and shading on seedlings are opposite to each other according to two species. This inverse tendency caused the interactive effect of flooding and shading on competition of *S. koreensis* and *P. australis* (Figure 13, 14 and 15).

Under without two stresses, *S. koreensis* seedlings grew well at pure planting than mixed planting, and *P. australis* seedlings showed opposite tendency to *S. koreensis*. It means that *P. australis* can be dominant in competitive situation with *S. koreensis* when the planted number of those species was same. And under only flooding and out of shading, *P. australis* seedlings were more dominant than under without both two stresses. Under full sunlight and water level of 12 ㎝, survival rate of *S. koreensis* seedlings growing with *P. australis* seedlings was very low (50%), and height of those was also very short (about quarter of *P. australis*). Growth of *P. australis* seedlings was the highest of all treatments in the experiment, and flowering rate increased to 20% under the same condition. Under the opposite condition, only shading stress out of flooding, relative competitive ability of *S. koreensis* increases, and that of *P. australis* decreases. *S. koreensis* seedlings were taller than *P. australis*, and 35% of *P. australis* seedlings died under 30%-light intensity and -10 ㎝-water level. And the both two stresses were given, competition showed similar tendency as the case of without both two stresses.

The trends of result of competition were very similar between parameters, and were so clear, and showed distinct difference of response to environmental conditions between two species than planting separately. But this does not explain the direction of community formation completely. This study had performed for a year, but more work for several years is needed, because *S. koreensis* and *P. australis* are perennial. Aboveground of *P. australis* is dead, but that of *S. koreensis* remains survived in winter even. For the following year, *P. australis* grows in adverse condition for light, so competition between two species may be changed from the past.

It is also necessary to consider competition of belowground. The result showed that below : above-ground ratios of *S. koreensis* ranged between 0.1 and 0.5, but those of *P. australis* did between 1.6 and 2.4, and *P. australis* produced up to eight times belowground biomass of *S. koreensis* in some treatments. Previous studies have reported that rhizome system of *P. australis* was dense, and accumulated lots of reserve material, and was up to ten times as much biomass as aboveground (Haslam 1972; Fiala 1976).

6. Zonation

By understanding the factor to influence the seedlings establishment, plant distribution could be predicted (Seabloom, van der Valk & Moloney 1998). Menges & Waller (1983) explained the zonation of floodplain by plant strategies: species which have competitive ability to light dominated higher elevation areas, and species which have tolerance to flooding dominated lower elevation. According to this study, *S. kroeensis* may distribute higher elevation areas than *P. australis* (excluded other factors). But it's difficult to explain plant distribution in the fields because the range of water level fluctuation is highly variable, and not only seeds but also ramets start to form communities, and many species interact continuously.

In a small scale, actual vegetation also affect the plant distribution. Previous study reported that seedlings of *P. australis* were common only in open places, for example those without other macrophytes (Haslam 1972). Under the canopy of woody plants or dense adult macrophytes, *P. australis* seedlings are relatively difficult to establish than *S. koreensis* by shading stress (Kotowski & Diggelen 2004).

7. Management implications

Both of *Salix* species and *P. australis* are often classified into invasive alien plants (Henderson 1991; Cronk & Fennessy 2001; Mitsch & Gosselink 2007; Kettenring & Whigham 2009). Kim (2012) reported that understanding the ecological characteristics at the early stages of each plant is important for wetland management. And Fraser & Karnezis (2005) emphasized timing of flooding, and suggested that some invasive species could be controled by slight manipulation of water level at the early stages of seedlings.

This study also suggest information that invasion from seeds of both *S. koreensis* and *P. australis* could be suppressed even by slight flooding. For example, if water level maintains about 2 ㎝ in height for about three weeks, *S. koreensis* could not invade into managed region, and in the case of *P. australis*, 4 ㎝ of water level is needed from mid May to mid June. And based on the short seed longevity of *S. koreensis*, the way that state of soil surface is kept for seeds not to germinate could be considered at the period of seed dispersal.

The most important thing in controlling *Salix* species and *P. australis* is to carry out the management at the initial stage of growth: seed or young seedling. If seedlings once survive, both species grow so fast and then have larger size than other species. *P. australis* shoot from rhizome have relatively stronger tolerant to flooding than from seeds (Coops, van den Brink & van der Velde 1996; Fraser & Karnezis 2005), so controlling is more difficult after a year. Hammer (1997) also stated that early three years is very important in a newly restored or created wetland for restoration success. But flooding or desiccation has adverse effect on many other wetland plants seedlings (Fraser & Karnezis 2005), so more understanding about life history trait at different ages, especially gemrination and young seedlings, of each species inhabiting in management region is needed.

Both species are often used in restoring wetlands (Cronk & Fennessy 2001; Mitsch & Gosselink 2007). Especially, previous studies reported that some *Salix* species have positive effects on wetland ecology (McLeod, Reed & Nelson 2001; Lee et al. 2010), so usage of these species is worth in consideration. Lee et al. (2010) controled the invasive species, *Ambrosia trifida*, by introducing *S. koreensis* canopy. They focused on proper shading effect of *S. koreensis* canopy, and this decreased the dominance of invasive species and increased the species diversity. Pezeshki et al. (1998) reported that *S. nigra* showed maximum growth under ample soil moisture but not flooding condition, and it agrees with our results. Therefore, in order to introduce the *S. koreensis* by the form of seeds, maintenance of appropriate environmental condition should be guaranteed especially in the seed dispersal period.

Conclusion

This study shows that the competition of *S. koreensis* and *P. australis* in initial establishment process changes according to environmental conditions. Many seeds of both species could germinate irrespective of water level and light intensity. but *S. koreensis* could not establish from seed unless appropriate moisture condition for germination is formed in a few days (about eight days). Both flooding and shading has an adverse affect on survival and growth of seedlings of both species, but the relative influence of flooding and shading on seedlings are opposite to each other according to two species. Flooding is more harmful to *S. koreensis* than *P. australis,* especially right after germination. On the contrary, in shaded understory, seedling growth of *P. australis* is worse than that of *S. koreensis*.

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국문초록

버드나무(*Salix koreensis*)와 갈대(*Phragmites australis*)의 정착과 경쟁에 대한 실험적 연구

많은 습지에서 다년생 초본에서 목본으로의 식생변화가 관찰되었으며, 이러한 천이 과정을 이해하기 위해서는 각각의 식물 종에 대한 생활사적 특성과 환경 조건에 따른 종간 경쟁에 관해 아는 것이 중요하다. 본 연구의 목적은 국내 습지의 대표적 목본인 버드나무와 다년생 초본인 갈대의 종자로부터 유입되는 초기 정착과정을 환경에 따라 예측하는 것이다. 이를 위하여 수위, 광도, 종자산포 후 경과시간이 버드나무와 갈대의 종자발아, 유묘의 생존과 생장, 경쟁에 미치는 영향에 대한 실험을 수행하였다.

두 종의 정착과정은 공간적 시간적으로 동시에 일어났다. 두 가지 수위 조건(0㎝, +2㎝)과 세 가지 광도 조건(100%, 30%, 0%)을 조합한 실험결과, 버드나무의 발아율은 광도에 따라서 차이가 있었고, 갈대의 발아율은 두 가지 조건에 따른 차이가 없었다. 모든 조건 조합에서 두 종 모두 높은 발아율(버드나무: 76.5%-97.4%, 갈대: 60.9%-71.5%)을 보였기 때문에, 침수와 차광은 두 종의 발아에 제한요인이 되지 못했다. 종자분산 후 16일 만에 버드나무는 모든 종자가 활력을 잃어버렸으며, 또한 10일이 지난 후에 발아한 유묘는 모두 죽었다. 따라서 종자 분산 시기의 환경요인이 버드나무 유묘의 정착에 매우 중요한 것으로 생각된다. 반면에 갈대는 일 년이 지난 후에도 35.4%의 발아율을 보였다. 두 종의 유묘 모두 6월 중순과 8월 중순사이에 최대 생장률을 보였으며, 갈대가 버드나무보다 더 빠르고 크게 자랐다. 침수와 차광이 없는 환경에서 갈대의 초고에 대한 버드나무의 수고 비율은 0.70 이었다. 유묘의 높이가 1㎝일 때 네 가지 수위 조건(-4㎝, +1㎝, +2㎝, +4㎝)과 두 가지 광도 조건(100%, 30%)을 조합한 환경에서, 발아한 지 약 40일 지난 후에는 세 가지 수위 조건(-10㎝, +4㎝, +12㎝)과 두 가지 광도 조건(100%, 30%)을

조합한 환경에서 두 종 유묘의 생존율과 생장량을 관찰하였다. 침수는 갈대보다 버드나무의 유묘에 더 큰 영향을 미쳤다. 유묘의 높이가 1㎝인 경우에는, 모든 버드나무 유묘는 자신의 두 배에 해당하는 수위에서 죽었지만 갈대 유묘는 같은 수위에서 30%가 생존하고, 계속 자랐다. 발아한 지 약 40일 정도 지났을 경우에는, 버드나무 유묘는 수위가 증가하면서 생존율과 생장량이 감소하였지만 갈대 유묘는 영향받지 않았다. 차광은 두 종 모두의 유묘 생존율과 유묘 생장량을 감소시켰지만, 갈대에게 더 치명적이었다. 특별히 70%의 차광은 초고가 1㎝인 모든 갈대 유묘가 자신의 두 배에 해당하는 수위를 극복하지 못하게 하였다. 또한 70% 차광에서는 모든 갈대 유묘가 꽃을 피우지 못하였다. 두 종을 함께 심어서 관찰한 경쟁 실험 결과, 침수와 차광이 모두 모두 없는 환경에서는 갈대가 버드나무보다 상대적으로 우세하였다. 침수된 환경(+12㎝, +4㎝수위)에서는 갈대의 경쟁력이 증가하였고, 반대로 그늘진 환경(70% 차광)에서는 버드나무의 경쟁력이 증가하였다.

이 연구는 환경 조건에 따라 초기정착과정에서 두 종의 경쟁적인 우위가 다르게 나타날 수 있음을 보여준다. 종자 산포시기에 종자가 발아할 수 있는 습한 환경이 조성되지 않으면 버드나무는 정착할 수 없다. 침수는 두 종 모두의 유묘 생장과 생존에 부정적인 영향을 주지만, 버드나무가 갈대에 비해 침수에 더 취약하며, 특히 발아 직후의 수위가 중요하다. 반면에 다른 식물들로 인한 그늘 진 환경에서는 갈대가 버드나무보다 생육에 상대적으로 큰 지장을 받는다.

주요어 : 갈대(*Phragmites australis*), 경쟁,
버드나무(*Salix koreensis*), 정착, 차광, 침수

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