Research paper

Seed Germination and Storage Behavior of Taiwan Incense-cedar (*Calocedrus macrolepis* Kurz var. *formosana* (Florin) Cheng & L. K. Fu)

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【Summary】

Taiwan incense-cedar (*Calocedrus macrolepis* var. *formosana*) is not only an endemic variety but also a valuable and vulnerable conifer native to Taiwan. The purpose of this study was to understand the germination characteristics of seeds of *C. macrolepis* var. *formosana* and determine its seed storage behavior. Optimal seed storage conditions and methods are also given for *ex situ* conservation. The respective germination percentages of 3 seedlots under fluctuating temperatures of 30/20℃ with 8 h of light for 8 wk were 68.0, 95.3, and 89.3%, and the mean germination times were 11.9, 10.9, and 10.9 d, respectively. All viable seeds of these 3 seedlots had completely germinated within 3 wk. Thus, seeds of *C. macrolepis* var. *formosana* exhibited no dormancy. In seedlot 1, with moisture contents (MCs) (on a fresh-weight basis) dried to 5.0~14.4%, the germination percentages of seeds with 2 yr of storage at -20℃ were 53.4~74.4%. In seedlot 2, when the MCs were controlled to 5.7~11.2%, germination rates after 2 yr of storage at -20℃ were 92.5~95.4%. In addition, germination rates of seedlot 3 dried to 8.2 and 11.3% MCs still remained as high as 80.8~89.8% after 3 yr of storage at -20 and -196℃. These results of maintaining good seed viability show that *C. macrolepis* var. *formosana* seeds seem to exhibit orthodox storage behavior. However, the germination percentage of seedlot 3 seeds decreased to about one-third of the original value when seeds were dried to about a 5% MC. Obviously, this characteristic of quickly losing seed viability shows the difference from small conifer tree seeds with orthodox storage behavior. Moreover, optimal MCs for maintaining seed viability were 8~11% rather than 5% when seeds from these 3 seedlots were stored at -196~15℃. Thus, we consider that seeds of *C. macrolepis* var. *formosana* are very likely to show intermediate seed storage behavior with some desiccation and sub-zero temperature tolerance, which differs from typical orthodox seeds. Sub-zero temperature storage was actually helpful for preserve Taiwan incense-cedar seeds. We recommend that fresh mature seeds of *C. macrolepis* var. *formosana* be quickly dried to 8~11% MCs and then hermetically sealed immediately before storage at -20℃. The reason why it is hard to preserve seeds of *C. macrolepis* var. *formosana* for long-term *ex situ* conservation is its probable intermediate storage behavior with a limited lifespan. Thus, we suggest that stored seeds of *C. macrolepis* var. *formosana* be renewed about every 10~15 yr.

Key words: Taiwan incense-cedar (*Calocedrus macrolepis* var. *formosana*), germination, seed storage behavior, intermediate, *ex situ* conservation.

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研究報告

臺灣肖楠種子的發芽與儲藏性質

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摘 要

臺灣肖楠為本島特有且為「易危」等級的珍貴針葉樹，本研究目的在明瞭其種子發芽特性與儲藏性質，並探究其最佳儲藏條件，希能提供精確的種子儲藏條件與方法以進行本種的區外保育。於2003年採於宜蘭縣大同鄉(第1批)、桃園市復興區(第2批)及台中市和平區(第3批)的三批種子，立即以30℃(8小時光照) /20℃(16小時黑暗)變溫發芽，經8週後之發芽率分別為68.0、95.3及89.3%，平均發芽日數分別是11.9、10.9與10.9天，各批種子幾均能在3週內發芽完畢，故臺灣肖楠種子不具休眠性。當第1批種子的含水率被控制在5.0~14.4% (鮮重)，於-20℃經2年儲藏後發芽率為53.3~74.4%；第2批種子的含水率被控制在5.7~11.2%，於-20℃經2年的儲藏後發芽率為92.5~95.4%；而第3批種子的含水率被降至8.2與11.3%，於-20及-196℃經3年的儲藏後，種子發芽率仍維持在80.8~89.8%，但第3批種子被乾燥到含水率約5%時，其發芽率迅速喪失約2/3，此特性與體型較小的針葉樹正儲型種子有所不同，且3批種子儲藏在-196~15℃時，各儲藏溫度均呈現出維持種子活力的最佳種子含水率是8~11%，而不是5%，因此，我們認為臺灣肖楠種子很可能是較耐乾旱且耐零下低溫的中間型種子。儲藏臺灣肖楠種子的適當溫度是零下低溫，建議應先將種子含水率控制在8~11%，然後立刻密封儲藏在-20℃的環境中。因臺灣肖楠種子很可能屬中間型，難以用儲存種子此方式來進行其長期區外保育，建議庫存種子應約每10~15年進行更新。

關鍵詞：臺灣肖楠、發芽、種子儲藏行為、中間型、區外保育。

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INTRODUCTION

According to the degree of desiccation tolerance of mature seeds, seed storage behaviors were initially classified into two categories: orthodox and recalcitrant (Roberts 1973). Orthodox seeds can tolerate desiccation and remain viable when the moisture content (MC) decreases to < 5% (on a fresh-weight basis; all MC values in this study are on a fresh-weight basis). As the MC and storage temperature decrease, the longevity

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of orthodox seeds is prolonged, and the relationships can be inferred from mathematical approaches (Roberts 1973).

Unlike orthodox seeds, recalcitrant seeds are particularly intolerant of desiccation. When they are dried to < 12~31% MCs, seed viability declines with concurrent prolongation of the drying duration (Roberts 1973). Furthermore, many recalcitrant seeds are extremely sensitive to temperature, and at temperatures of < 10~15℃, their viability often deteriorates, especially for tropical recalcitrant seeds (Bonner 1990). Hong and Ellis (1996), therefore, differentiated desiccation-intolerant seeds into temperate and tropical subtypes according to the level of temperature tolerance of recalcitrant seeds. Temperate-recalcitrant seeds are intolerant of dehydration but capable of being stored at temperatures close to 0℃ and MCs of 35~50%. Air circulation plays an important role in respiration in temperate-recalcitrant seeds during storage, i.e., seed longevity with storage at high MCs and appropriate air circulation is more likely to reach 1~3 yr. Temperate-recalcitrant seeds mainly include seeds of the Fagaceae (Lin 1995, Yang and Kuo 2018) and Lauraceae in Taiwan such as *Litsea acuminata* (Bl.) kurata (Lin and Wu 1991), *Machilus* spp. (Lin and Chen 1993, Lin et al. 1993), *Keteleeria davidiana* var. *formosana* (Yang et al. 2006a), and *Camellia brevistyla* (Yang and Kuo 2017). Different from temperate-recalcitrant seeds, tropical-recalcitrant seeds are intolerant of dehydration and low temperatures. Thus, they are almost unable to survive a temperature close to 0℃ and are even sensitive to 15~20℃. As tropical-recalcitrant seeds are prone to lose viability at low temperatures, the period for which they can be stored is short, even if they are stored at high MCs with good air circulation. That is to say, viable seeds begin to germinate shortly after storage at a high temperature. To prolong the storage duration, we employed a low-temperature approach to inhibit germination; however, the optimal storage conditions are difficult to determine, and seeds often lose their viability. In general, it is not easy for tropical-recalcitrant seeds to germinate after storage. Moreover, relative to the longevity of temperate-recalcitrant seeds, that of tropical-recalcitrant seeds is shorter. Take the Dipterocarpaceae for example. Among 79 species of these tropical-recalcitrant seeds, the maximum seed longevity is 1 yr, and the minimum is only 14 d (Tompsett 1987, 1989). These large, high-moisture seeds are almost all produced from large trees such as of the Dipterocarpaceae and Araucariaceae in tropical rainforests, which constitute the most economically important tropical trees, e.g., *Hevea brasiliensis*, *Theobroma cacao*, *Artocarpus heterophullus*, *Cocos nucifera, Persea americana*, *Dimocarpus longan*, *Mangifera indica*, *Durio zibethinus* (Chin 1988, Chin and Roberts 1980), *Litsea garciae*, *Diospyros philippensis*, and *Myristica ceylanica* var. *cagayanensis* (Yang et al. 2008a).

In addition to orthodox and recalcitrant seeds, Ellis et al. (1990a) found that seeds of *Coffea arabica* L. survived desiccation to 5~10% MCs but did not survive at a storage temperature of ≤ 10℃. They considered such seeds as "intermediate" which were moderately tolerant of desiccation but vulnerable to freezing temperatures. Subsequently, they also found that seeds of *Elaeis guineensis* (Ellis et al. 1991), *Citrus* spp. (Hong and Ellis 1995), *Acer* spp. (Yang and Lin 1999), *Zelkova serrata* (Yang et al. 2007), and *Litsea coreana* (Yang et al. 2008b) showed similar storage behaviors. Such findings imply the importance of intermediate seeds. According to Hong and Ellis (1996), most intermediate seeds survive desiccation to 10~12% MCs, but their viability declines with a concurrent decrease in MCs. The optimal storage temperature of intermediate seeds is mainly determined by the ecological environment of their native habitats. Therefore, some intermediate seeds can survive sub-zero temperatures while others cannot.

There are only 2 species in the genus of *Calocedrus* worldwide. One is *Calocedrus macrolepis* Kurz that grows in southwestern China and the other is pencil cedar (*C. decurrens* (Torr.) Florin) spanning North America. At present, Taiwan incense-cedar (abbreviated as Taiwan IC from here on) (*Calocedrus macrolepis* Kurz var. *formosana* (Florin) Cheng & L. K. Fu) is seen as a variety of *C. macrolepis* Kurz. Taiwan IC, a large evergreen conifer tree and an endemic varietas species in Taiwan, is distributed in the northern and central mountain areas of the island at elevations of 300~1900 m (Lin and Keng 1994). This species can reach 3 m in diameter, and tree height can be > 40 m. Taiwan IC often grows on steep, sunny slopes. Because of the good quality of its timber density, abundant essential oils, and greater erosion resistance, Taiwan IC produces large valuable timber and is a first-class softwood in Taiwan. No wonder that when scholars and experts re-evaluate the rank of valuable trees in Taiwan, Taiwan IC is always among the top five valuable coniferous trees. Due to its practical value, this species has become a top priority for afforestation of coniferous trees in Taiwan to 2021. Because populations of Taiwan IC occupy areas of less than 5000 km^2, the number of habitats is 5 or fewer, and they are completely separated. Furthermore, areas occupied by this species are increasingly being reduced such that the Council of Agriculture designated Taiwan IC as an endangered species (Lu and Lin 1996), but later Taiwan IC was estimated to be a vulnerable species by the Editorial Committee of the Red List of Taiwan Plants in 2017.

Ellipsoid-ovoid cones of Taiwan IC are about 1.5 cm long, and only 2 megasporophylls are capable of pollination and growth. Each ovuliferous scale produces 2 seeds, and usually only 1 or even neither of them can grow (Fig. 1). In general, each cone produces 1 or 2 seeds, and 3 or 4 seeds are rarely seen. The fruit-ripening stage is in October and November, but planted trees can possibly ripen early in September. When mature scales slip open, seeds are quickly dispersed by wind. The seeds have only a thin-coriaceous wing that is too tough to be removed. To keep fresh seeds from being damaged by excessive rubbing and kneading, we recommend that dewinging should be avoided when processing seeds of Taiwan IC. Dewinged seeds are about 4.2~5.0 mm long and about 2.2~2.5 mm wide.

Taiwan IC is worthy of reforestation and conservation, but only a few studies on the germination and seed storage behavior of this species have been published. Previous studies showed that the optimal germination performance was at a constant temperature of 20~25℃ or at fluctuating temperatures of 20~30℃ (Chung and Hu 1986a). However, seeds of Taiwan IC in this study with 10% MCs and 29% germination were stored at different storage temperatures (-20℃~room temperature), and the times when these seeds at different storage temperatures lost their viability were as follows: 7 yr (at -10℃), 5 yr (at -5℃), 2.5 yr (at 0℃), 2 yr (at 5℃), and 0.5 yr (at room temperature). In addition, seeds still retained about 10% germination after 8 yr of storage at -20℃. This result showed that lower storage temperatures were helpful in maintaining the viability of Taiwan IC seeds (Chung and Hu 1986b). From the above findings, it seemed that seeds of Taiwan IC are not like orthodox ones with good longevity;

Fig. 1. Mature cones and seeds of *Calocedrus macrolepis* var. *formosana*.

however, judging from the 30% germination of seeds at an MC of 10%, seeds of Taiwan IC with better desiccation tolerance are also quite different from recalcitrant ones. From nurserymen's experience, they generally believe that seeds of Taiwan IC too easily deteriorate when being stored, so in the past, seeds were immediately sown after being collected in autumn and winter. Based on all the above findings, we inferred that seed storage behavior of Taiwan IC is probably intermediate. In fact, it has been controversial whether long-term storage can be applied to seeds of Taiwan IC up to the present. In this study, statistical techniques were used to design our experiment, and a factorial combination of different MCs and storage temperatures was also used to investigate the storage behavior of Taiwan IC seeds and determine optimal storage conditions. Furthermore, the results are expected to offer useful information for nursery operations and *ex situ* conservation of this valuable and endangered species.

MATERIALS AND METHODS

Seed collection and processing

Table 1 gives detailed collection information of the 3 seedlots used in this study. At the time of collection, about 60 and 30% of brown cones of seedlots 1 and 2 were mature and dehiscent, respectively. In seedlot 3, cones were just mature and appeared brown at the beginning of collection. In this investigation, the collected cones of the 3 seedlots were all dried under indoor conditions until they naturally split open, and the seeds were manually extracted from the unopened fruits. Rates of larger filled seeds of the 3 seedlots were about 65, 45, and 50%, respectively. To present a clear picture of differences in seed deterioration with different treatments, the initial germination percentages of each seedlot were initially raised to the highest levels by seed selection. Larger filled seeds were manually selected, and small, undeveloped, and damaged seeds were discarded at the beginning of the study.

Determination of MCs

Seed MCs of the 3 seedlots were determined gravimetrically with 4 replicates. For each replicate, 10, 15, and 15 filled dewinged seeds from seedlots 1, 2, and 3 were randomly selected and cut into pieces of < 4 mm in length. Then, the minced seeds were dehydrated. MCs of the seeds were determined using a low-constant-temperature oven method (103±2℃ for 17±1 h) (International Seed Testing Association 1999). All MCs are presented on a percentage fresh-weight basis.

Germination assay

To avoid imbibition damage by rapid rehydration, seeds with different treatments were placed above water in a sealed container for 1 d before the germination test so that the seeds could take up water at ambient temper-

Table 1. Information on fruit collection dates and sources, seed characteristics, and germination of the 3 seedlots of fresh mature seeds of *Calocedrus macrolepis* var. *formosana*

Seedlot no.	Seedlot 1[1)]	Seedlot 2[1)]	Seedlot 3[1)]
Collection date	10 Sep. 2003	30 Sep. 2003	1 Nov. 2003
Collection location	Datong Township, Yilan County	Fuxing District, Taoyuan City	Heping District , Taichung City
Latitude, longitude	24°35'N, 121°31'E	24°40'N, 121°25'E	24°13'N, 121°07'E
Elevation (m)	150	1750	1350~1680
Moisture content (%, FW[2)] basis)	9.6±0.3	9.4±0.3	11.7±0.3
Number of seeds L^{-1}	18,838±727	34,438±721	36,438±1479
TSW[3)] (Thousand-seed-weight, g)	9.4±0.2	7.4±0.2	6.7±0.2
TSW of dewinged seeds (g)	8.8±0.2	7.1±0.1	6.1±0.2
Germination percentage[4)] (%)	68.0±8.6	95.3±0.5	89.3±2.6
Mean germination time[4)] (d)	11.9±0.5	10.9±0.2	12.5±2.1

1) Seeds of seedlot 1 were collected from several cultivated individuals, while seedlot 2 and 3 were from 2 and several wild individuals, respectively.

2) FW, fresh-weight.

3) Thousand-seed-weight was estimated at the moisture content shown.

4) Seeds were incubated at alternating night/day temperatures of 20/30 ℃ and 8 h of light for 8 wk.

ature (Ellis et al. 1990b). Then, the imbibed seeds were thoroughly mixed with clean sphagnum moss in sealable polyethylene (PE) bags (14 × 10 cm and 0.04 mm thick) with about 3/4 volume of adequate air inside for normal respiration. Excess water in the moss was squeezed out until a water content of about 450% by mass (on a dry-weight basis) was reached (Lin and Chen 1993). To estimate the germination capacity of fresh mature seeds and seeds for moist and dry storage, 25 seeds from seedlot 1, 80 seeds from seedlot 2, and 100 seeds from seedlot 3 were randomly sampled in 3, 3, and 4 replicates per treatment for the germination test at fluctuating temperatures of 30/20°C (day/night) with 8 h of light (50~80 μmol m^{-2} s^{-1}). During the 8-wk test period, the number of protruding seeds was counted once a week. Seeds with a radicle reaching 5 mm were counted as having germinated. Meanwhile, about 3~5 ml of water was added to the moss, and the air in the PE bags was renewed each week.

Germination speed

The equation for calculating the mean germination time (MGT) is: MGT = $\Sigma(n \times d) / N$, where n is the number of germinated seeds after each period of incubation in days (d), and N is the total number of emerged seeds recorded by the end of the test (Hartmann et al. 1989).

Moist storage treatment

The 4℃ moist storage durations of fresh seeds of the 3 seedlots are given in Table 2. These results were used to understand the effects of low-temperature stratification on seed germination and the impact of low-temperature storage on seed viability of Taiwan IC. Freshly collected seeds of each seedlot were thoroughly mixed with moist sphagnum moss in PE bags (14 × 10 cm, and 0.04 mm thick) and then placed at 4℃ for storage. In each bag, about 4/5 of the volume of air was left for seed respiration, and during storage, water was added and the air was refreshed monthly.

Temporary storage at room temperature

Formerly, nurseries considered seeds of Taiwan IC to be short-lived species with no potential for long-term storage. In fact, their perceived short lifespan may have had something to do with seed processing. To obtain a large harvest, cones were often collected in the early stage of maturity; however, that simultaneously caused the latter dehiscent duration to be prolonged. There were even many indehiscent cones left which needed to be manually opened to get to the seeds inside.

Table 2. Durations of stratification at 4℃ and dry storage durations at 4 moisture contents (MCs) stored at 3 or 4 temperatures of the 3 seedlots seeds of *Calocedrus macrolepis* var. *formosana* in this study

Seedlot no.	Seedlot 1	Seedlot 2	Seedlot 3
4℃ stratification duration (mo)	0, 1, 2, 3, 4, 6, 8, 10, 12, 15, 18, 21, 24	0, 1, 2, 3, 4, 6, 8, 10, 12, 15, 18, 21, 24	0, 1, 2, 3, 4, 5, 6, 8, 10, 12, 15, 18, 21, 24
MCs of dry storage (FW[1)] basis, %)	5.0±0.1, 7.9±0.4, 11.2±0.2, 14.4±0.4	5.7±0.1, 8.5±0.8, 11.2±0.6, 14.8±0.4	5.9±0.2, 8.2±0.3, 11.3±0.2, 14.9±0.6
Dry storage temperature (℃)	-20, 4, 15	-20, 4, 15	-196, -20, 4, 15
Dry storage duration (mo)	0, 1, 3, 6, 9, 12, 15, 18, 24	0, 1, 3, 6, 9, 12, 15, 18, 24	0, 1, 3, 6, 9, 12, 15, 18, 24, 36

[1)] FW, fresh-weight.

In addition, seed handling often took as long as 2~3 mo in years with a bumper cone crop. Generally, workers did not store seeds in a refrigerator during the handling period, which, we believe, was the main reason for the weak viability of Taiwan IC seeds. In other words, undergoing such seed handling techniques and temporary storage at normal atmospheric temperatures for a period of time may have led to a risk of seed ageing and decay. Starting from this point, we conducted a test to handle seeds of Taiwan IC under similar conditions: freshly collected seeds of seedlots 2 and 3 were stored in permeable cotton sacks and were hung at fluctuating relative humidities of 45~95% and ambient temperatures of 12~24℃ in the Seed Bank of Taiwan Forestry Research Institute. Finally, seed analyses of germination after 1, 2, 3, and 4 mo (from November 2003 to March 2004) were used to understand the effects of room-temperature storage on seed ageing of Taiwan IC.

Dry storage treatment and determination of moisture levels

Sub-seedlots exhibited different MCs, and the ranges were about 5~15% for the 3 seedlots. In this study, fresh mature seeds of the 3 seedlots were placed in hermetically sealed acrylic boxes with a small fan installed to circulate the air, and molecular sieves and pure water were used to respectively dry and moisten the seeds at temperatures of 15~20℃. When a sub-seedlot reached the desired MC during this controlled process, seeds were placed in an aluminum foil bag and temporarily stored at 4℃ for about 3~5 d to stabilize the water contents before the average equilibrium MC was determined. In seedlot 1, the MC of fresh mature seeds was 9.6±0.3% (Table 1). After dehydration or moisture treatments, 4 MC levels were controlled to 5.0±0.1% (15 d of desiccation), 7.9±0.4% (2 h of desiccation), 11.2±0.2% (1 h of humidification), and 14.4±0.4% (14 h of humidification). In seedlot 2, the MC of fresh mature seeds was 9.4±0.3%. The 4 MC levels were controlled to 5.7±0.1% (11 d of desiccation), 8.5±0.8% (2 h of desiccation), 11.2±0.6% (2 h of humidification), and 14.8±0.4% (13 h of humidification). In seedlot 3, the MC of fresh mature seeds was 11.7±0.3%. The 4 MC levels were controlled to 5.9±0.2% (36 d of desiccation), 8.2±0.3% (8 d of desiccation), 11.3±0.2% (2 h of desiccation), and 14.9±0.6% (17 h of humidification) after MC controlled treatments (Table 2). As soon as the desired MC of each sub-seedlot was achieved, seeds were sealed in double-layered aluminum foil bags before storage at different temperatures. Table 2 shows storage temperatures and durations of 4 MC levels of seeds of the 3 seedlots.

Data analysis

An analysis of variance (ANOVA) was used to analyze seed germination percentages to evaluate the effects of the stratification period on germination. Additionally, germination results of the combination of different storage temperatures, seed MCs, and storage periods were statistically analyzed by variables implemented in Tukey's test of the general linear model (GLM) procedure of R statistical software (The R Foundation).

RESULTS

Germination of fresh mature seeds

In seedlot 1, when fresh mature seeds were incubated at fluctuating temperatures of 30/20℃ for 8 wk, their germination percentage was 68.0% and the MGT was 11.9 d (Table 1). In seedlots 2 and 3, the germination percentages of fresh mature seeds under the same germination conditions as seedlot

1 were 95.3 and 89.3%, and the MGTs were 10.9 and 12.5 d, respectively (Table 1). Of the 3 seedlot seeds, seeds mainly emerged during 1~2 wk, 99% viable seeds had germinated within 3 wk, and no germination appeared after 5 wk (Fig. 2). Ungerminated seeds of the 3 seedlots had all rotted when cut open after the 8-wk germination period. The above findings show that seeds of Taiwan IC of the 3 seedlots exhibited no dormancy and had rapid germination speed.

Effects of stratification at 4℃ on germination

The germination percentage and germination speed were used to investigate the effects of low-temperature stratification on seed germination of Taiwan IC. In seedlot 1, seed germination percentages were 77.3±6.8% and 80.0±5.7% after stratification at 4℃ for 1 and 2 mo, respectively, which showed no significant differences (p = 0.3 and p = 0.18) compared to fresh seeds (68.0±8.6%) (Fig. 2). However, the MGTs of the seeds decreased to 7.2±0.2 and 7.3±0.3 d after stratification at 4℃ for the 1 and 2 mo, respectively, and significant differences in MGTs (p = 0.0002 and p = 0.0003) were found compared to fresh seeds (11.9 d) (Fig. 2). In addition, seeds of seedlot 1 began to germinate after stratification at 4℃ for 2 mo, and all viable seeds had germinated under dark, moist conditions within 2~4 mo (Fig. 2). Thus, during the design periods (from 0 to 24 mo) of 4℃ stratification, germination data were only obtained in the periods of 0~4 mo in seedlot 1.

In seedlot 2, the germination percentage and MGT of seeds were respectively 98.3±0.6% and 7.1±0.1 d after 1 mo of stratification at 4℃ (Fig. 2). There was no significant difference (p = 0.05) in germination, but a significant decrease in MGT (p = 0.00003) was found after 1 mo of stratification duration compared to fresh seeds (95.3% and 10.9 d). Moreover, seeds of seedlot 2 began to germinate under the same conditions after 1-mo stratification at 4℃, and viable seeds had completely germinated within 1~4 mo under dark, moist conditions (Fig. 2).

Like the seeds of seedlot 2, the germination percentage of seedlot 3 seeds were 85.8±1.8% after 1 mo of stratification at 4℃, and there was no significant difference (p = 0.1) in germination compared to fresh mature seeds (89.3%) (Fig. 2). Nevertheless, the MGT of fresh seeds of seedlot 3 after 1 mo of stratification at 4℃ significantly decreased from 10.9 to 7.1±0.1 d (p = 0.00005). In addition, seeds of seedlot 3 began to germinate at 4℃ under dark, moist conditions after 1 mo, and all viable seeds germinated during 1~3 mo (Fig. 2).

Effects of room temperature on seed ageing

Seed viability of seedlot 2 was still maintained within 2 mo of storage at fluctuating room temperatures. When the storage duration was extended to 3 and 4 mo, germination percentages of the seeds decreased to 83.0 and 85.3%, respectively; significant differences in germination (p = 0.007 and p = 0.02) were found compared to fresh seeds (95.3%) (Fig. 3). The MGT of the seedlot 2 seeds of storage at room temperature for 1 mo was 10.0 d, and there was no significant difference (p = 0.06) compared to fresh seeds (10.9 d). However, the MGTs of seeds stored at room temperature for 2, 3, and 4 mo significantly increased to 13.5, 14.5, and 14.6 d, respectively (p = 0.00007, p = 0.000006, and p = 0.00003) (Fig. 3). During 4 mo of storage without an airtight container at fluctuating room temperatures, the MCs of the seeds remained at 10.0~11.5%, and no significant difference (p > 0.05) was shown compared to fresh seeds (9.4%) (Fig. 3).

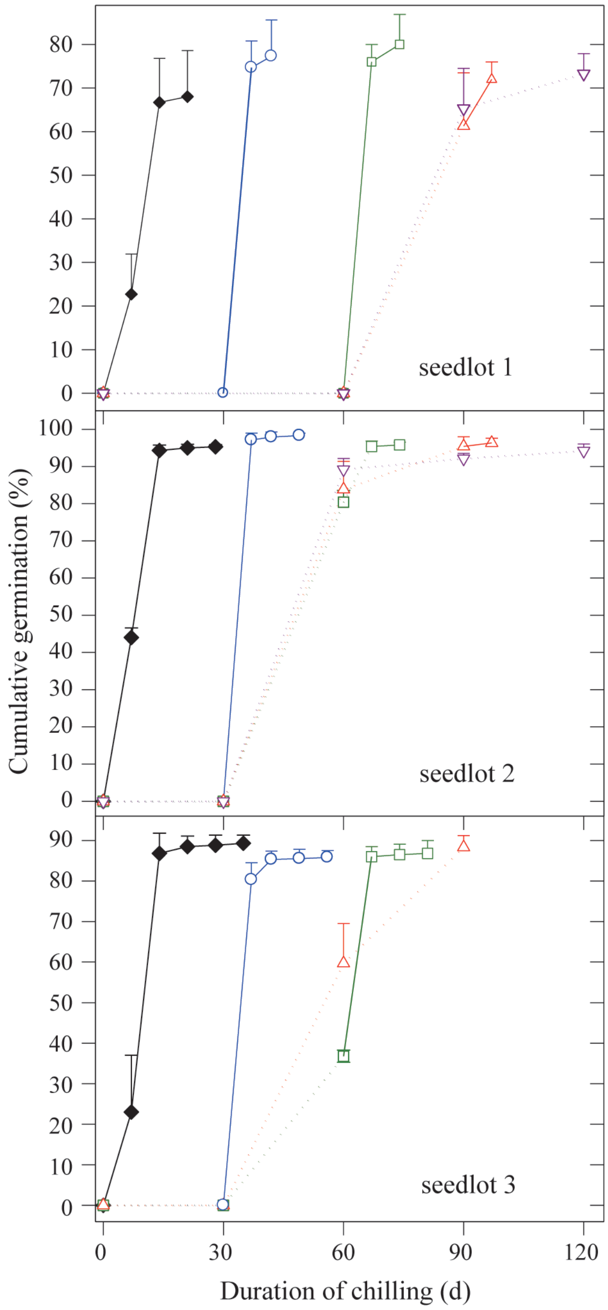

Fig. 2. Cumulative germination percentages of the 3 seedlots of *Calocedrus macrolepis* var. *formosana* at 4℃ moist stratification for 1~4 mo (○, 1 mo; □, 2 mo; △, 3 mo; ▽, 4 mo). Dotted lines (- - -) represent the cumulative germination percentages in the dark with 4℃ moist stratification, while solid lines (—) represent the cumulative germination percentages at fluctuating temperatures of 30/20℃ with 8 h of light after moist stratification. Filled diamonds (◆) represent the cumulative germination percentage of fresh mature seeds. Vertical bars represent the standard error of the mean.

In seedlot 3 seeds, germination percentages of storage at room temperature for 1 and 2 mo significantly decreased to 77.9 and 48.6% (p = 0.01 and p = 0.000002). After 3 and 4 mo of room-temperature storage, germination percentages declined to 39.5 and 21.4%, respectively (Fig. 3). The MGTs of seedlot 3 seeds of storage at room temperature for 1 and 2 mo were 10.7 and 10.1 d, respectively, and no significant difference (p = 0.59 and p = 0.08) was found compared to fresh seeds (10.9 d). However, MGTs of seedlot 3 seeds of room-temperature storage for 3 and 4 mo both significantly increased to 14.8 d (p = 0.00003) (Fig. 3). During 1~3 mo of room-temperature storage without an airtight container, the MCs of the seeds remained at 9.9~11.8%. There was no significant difference (p > 0.05) in MCs compared to fresh seeds (11.7%), but the MCs significantly increased to 13.7% after 4 mo (p = 0.002) (Fig. 3). From the above findings, seed ageing appeared after 2 mo when freshly harvested seeds of Taiwan IC were stored at fluctuating room temperatures.

Effects of MC, storage temperature, and storage duration on seed viability

Figures 4 and 5 show the effects of different MC levels and storage temperatures on germination percentages of Taiwan IC seeds of seedlots 1, 2, and 3 with dry storage for 0~24 or 0~36 mo, respectively. In seedlot 1, once the 4 desired MC levels were reached, seeds were immediately incubated under fluctuating temperatures of 30/20°C for 8 wk. Germination percentages of these seeds at MCs of 5.0, 7.9, 11.2, and 14.4% were 68.0±6.5%, 60.0±3.3%, 76.0±6.5%, and 58.7±5.0%, respectively. There was no significant difference (p > 0.5) in germination

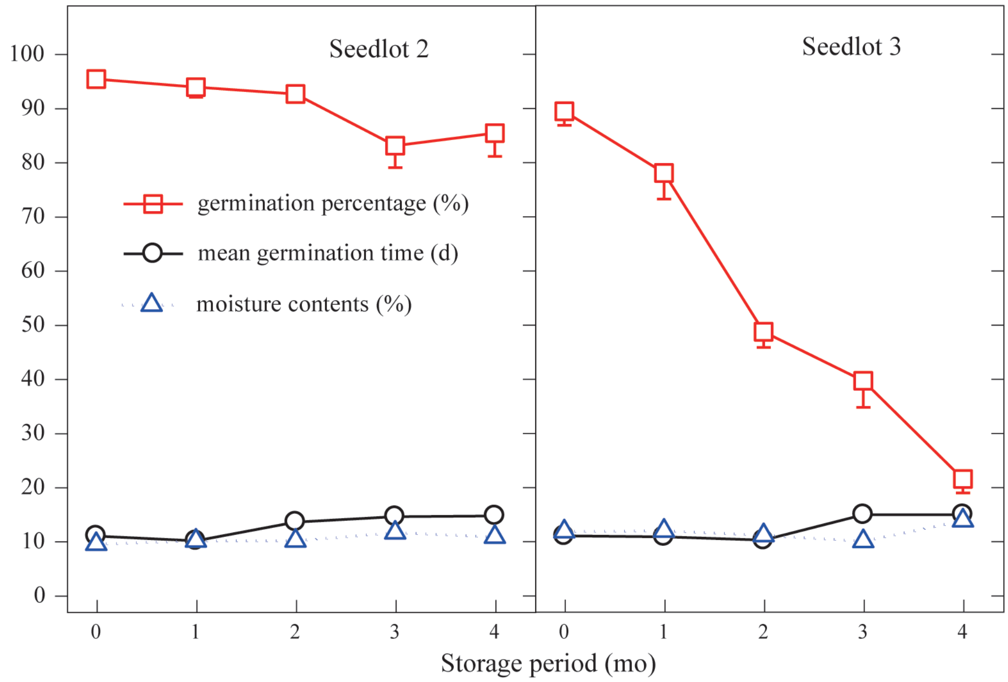

Fig. 3. Effects of ambient storage (12~24℃) for 0~4 mo on germination percentages (□), mean germination times (○), and seed moisture contents (△) of seedlots 2 and 3 of seeds of *Calocedrus macrolepis* var. *formosana*. Vertical bars represent the standard error of the mean.

compared to fresh mature seeds (68.0±8.6%). During storage at -20℃, seeds at MCs of 5.0, 7.9, 11.2, and 14.43% maintained germination percentages of 53.3~76.0%, 52.0~76.0%, 64.0~78.8%, and 56.0~73.3% within 24 mo, respectively. There was no significant decline in germination compared to fresh mature seeds after 24 mo of storage ($p > 0.1$) (Fig. 4). When stored at 4℃, seeds at MCs of 5.0, 7.9, and 14.43% had sharp declines in germination and significantly decreased to 6.7, 18.7, and 0% after 24 mo of storage ($p < 0.001$). In addition, germination percentages of seeds at an MC of 11.2% with 24 mo of storage decreased to 44.0±15.0%, but no significant difference ($p = 0.12$) in germination was found compared to fresh mature seeds (68.0%) (Fig. 4). When stored at 15℃, the germination result of seeds was similar to that at 4℃, but the viability of seeds at the 4 MCs decreased faster; they quickly deteriorated and almost all died after 24 mo (Fig. 4). Seed decay with different MC levels at 15℃ storage was faster than that of seeds stored at 4℃.

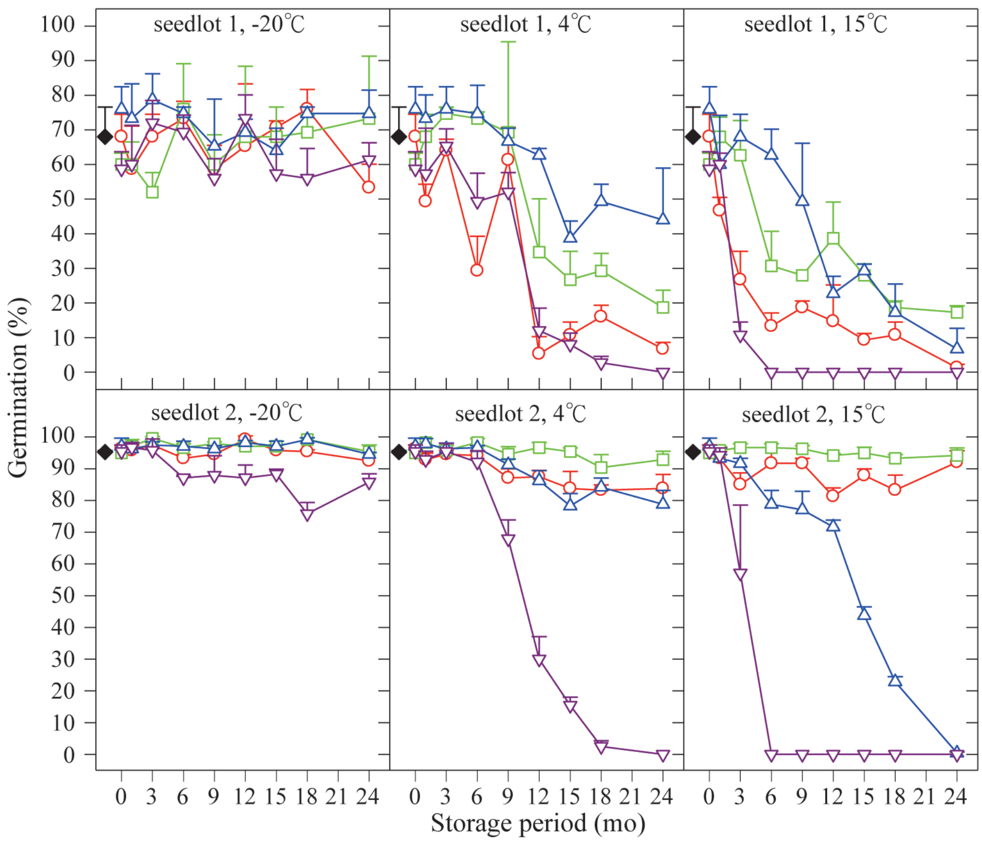

Fig. 4. Effects of storage temperatures (-20, 4, and 15℃) and moisture contents (MCs) (on a fresh-weight basis) on germination percentages of seedlots 1 and 2 seeds of *Calocedrus macrolepis* var. *formosana* stored for up to 24 mo. The initial germination percentages of fresh mature seeds of seedlots 1 and 2 were 68.0±10.6% and 95.3±0.6% (◆), respectively. MCs of seedlot 1 seeds: ○, 5.0±0.1%; □, 7.9±0.4%; △, 11.2±0.2%; ▽, 14.4±0.4%. MCs of seedlot 2 seeds: ○, 5.7±0.1%; □, 8.5±0.8%; △, 11.2±0.6%; ▽, 14.8±0.4%. Vertical bars represent the standard error of the mean.

In seedlot 2, after the drying process was completed, freshly dried seeds at 4 MC levels were immediately incubated under fluctuating temperatures of 30/20℃ for 8 wk. Germination percentages of seeds at MCs of 5.7, 8.5, 11.2, and 14.8% were 96.3±0.2%, 95.0±1.0%, 97.1±2.6%, and 95.4±2.1%, respectively. No significant difference ($p > 0.4$) in germination was found compared to fresh seeds (95.3±0.5%) (Fig. 4). After storage at -20℃ for 0~24 mo, seeds at 5.7, 8.5, and 11.2% MCs maintained high germination percentages (92.3~99.2%) and showed no significant difference ($p > 0.2$) compared to initial germination. However, seeds at an MC of 14.8% showed a slight decrease in germination after 6 mo of storage, and germination percentages (75.8~88.3%) with 6~24 mo of storage revealed significant decreases ($p < 0.03$) compared to the initial germination percentage (Fig. 4). During storage at 4℃, seeds at an MC of 14.8% had a sharp decline in germination, had significantly decreased to 67.9% after 9 mo of storage ($p = 0.003$), and almost all died after 18 mo of storage. In addition, germination percentages of seeds at MCs of 5.7 and 11.2% significantly decreased to 83.8 and 78.8% ($p = 0.02$ and $p = 0.006$) after 24 mo, respectively. However, there was no significant difference ($p = 0.26$) in germination of seeds at an MC of 8.5% compared to fresh seeds after 24 mo of storage, and the germination percentage was 92.9% (Fig. 4). When stored at 15℃, germination percentages of seeds at MCs of 14.8 and 11.2% rapidly dropped, and all seeds died after 6 and 24 mo of storage, respectively. Nevertheless, there was no significant difference ($p = 0.3$ and $p = 0.5$) in germination of seeds at the 2 other lower MCs compared to fresh seeds after 24 mo of storage, and their germination percentages at MCs of 5.7 and 8.5% were 92.1 and 94.2%, respectively (Fig. 4).

In seedlot 3, germination percentages of freshly dried seeds at the 4 MCs of 5.9, 8.2, 11.3, and 14.9% were 28.4, 85.5, 86.8, and 80.5%, respectively. Significant differences ($p = 0.000001$ and $p = 0.004$) in germination at MCs of 5.9 and 14.9% were found compared to fresh seeds (89.3%) (Fig. 5). When seeds were stored in a liquid nitrogen container (at -196℃), seeds at MCs of 8.2 and 11.3% retained high germination percentages of 80.0 and 83.2% after 36 mo of storage, respectively, and exhibited no significant difference ($p = 0.08$ and $p = 0.4$) compared to fresh seeds. Moreover, seeds at an MC of 14.9% exhibited an obvious drop in germination and had significantly decreased ($p < 0.001$) to 31.3~62.3% within 1~36 mo of storage. In addition, seed germination at an MC of 5.9% continued to decrease to 16.8% after 36 mo of storage. When stored at -20℃, germination percentages were 82.3 and 84.5% at MCs of 8.2 and 11.3% after 36 mo of storage, respectively. There was no significant difference in germination compared to fresh mature seeds ($p = 0.05$ and $p = 0.2$). However, the germination percentage of seeds at MCs of 5.9 and 14.9% significantly decreased to 16.0 and 55.0% after 36 mo of storage, respectively. During storage at 4℃, the rate of seed deterioration increased faster than those at -196 and -20℃. Germination percentages were 6.3, 48.0, 59.5, and 0% at MCs of 5.9, 8.2, 11.3, and 14.9% after 36 mo of storage, respectively. When stored at 15℃, seeds at MCs of 5.9, 11.3, and 14.9% had completely lost their viability after 36 mo of storage, and only the seeds at an MC of 8.2% had a germination percentage of 54.8% (Fig. 5).

DISCUSSION

Results of this study show that fresh mature seeds of Taiwan IC have no dormancy.

No pretreatment is needed to cause the seeds to germinate within 8 wk. This result is very different from that of pencil cedar (*C. decurrens*) seeds, whose innate dormancy caused by the embryo prevents them from germinating; so pencil cedar seeds showed higher germination percentages only when they were pretreated with 30~60 d of low-temperature stratification (Dirr and Heuser 1987, Young and Young 1992). In addition, stratification at 4℃ was only helpful to shorten the germination duration rather than raise the germination percentage of Taiwan IC seeds. Obviously, there is no economic efficiency in investing in equipment and labor for 1~2 mo of stratification operation to reduce the germination duration from 2 to 1 wk. In other words, it is useless to apply a low-temperature stratification strategy to improve Taiwan IC nursery seedlings. In addition, seeds of Taiwan IC are not suitable for wet storage at 4℃ because they would begin to germinate after 1 mo, and all viable seeds germinated under a dark condition within 1~4 mo (Fig. 2). Consequently, low-temperature moist storage is not appropriate for storing seeds of Taiwan IC.

The above results show that when Taiwan IC seeds are desiccated to about 5% MC in a short time, they did not lose viability and still maintained their original viability after 2 yr of storage at -20℃(Fig. 4). It seems that Taiwan IC seeds have orthodox storage behavior (Hong and Ellis 1996). However, the germination percentage of seedlot 3 seeds decreased to about one-third of the original value when seeds were dried to about 5% MC. Obviously, this characteristic of quickly losing seed viability in a period of 36 d of dehydration differs from small conifer tree seeds with orthodox storage behavior. Small conifer orthodox seeds usually can easily be dried to about 5% MC, and seeds with lower MCs do not rapidly lose viability when they are stored at 20~30℃ for 2 mo. Moreover, when these 3 seedlots seeds were stored at -196~15℃, every storage temperature indicated that optimal MCs for maintaining seed viability were 8~11% rather than 5% (Figs. 4, 5). Based on these findings, Taiwan IC seeds are not like orthodox seeds. Thus, we consider that Taiwan IC seeds are very likely to show intermediate seed storage behavior with some desiccation and sub-zero temperature tolerance, which differs from typical orthodox seeds. The above results show a clear relationship between

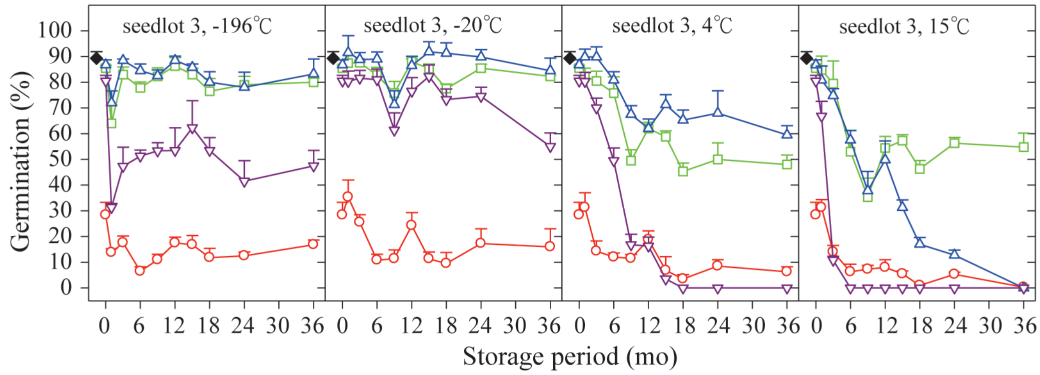

Fig. 5. Effects of storage temperatures (-196, -20, 4, and 15℃) and moisture contents (MCs) (on a fresh-weight basis) on germination percentages of seedlot 3 seeds of *Calocedrus macrolepis* var. *formosana* stored for up to 36 mo. The initial germination percentage of fresh mature seeds of seedlot 3 was 89.3±2.0% (◆). MCs of seeds: ○, 5.9±0.2%; □, 8.2±0.3%; △, 11.3±0.2%; ▽, 14.9±0.6%. Vertical bars represent the standard error of the mean.

viability and storage temperature of Taiwan IC seeds. During storage at different temperatures (4, 15, -20, and -196℃), the speed at which Taiwan IC seeds lost viability was 15 > 4 > -20 and -196℃. In other words, lower temperatures are actually helpful to preserve Taiwan IC seeds. We recommend that fresh mature seeds of Taiwan IC should be quickly dried to 8~11% MCs and then hermetically sealed immediately before storage at -20℃. The reason why it is hard to preserve Taiwan IC seeds for long-term *ex situ* conservation is probably their intermediate storage behavior with a limited lifespan. Thus, we suggest that stored seeds of Taiwan IC be renewed about every 10~15 yr. In addition, seeds of *C. decurrens* do not keep well in ordinary dry storage, but high viability can be maintained in a very cool and dry repository (Young and Young, 1992). One study indicated that *C. decurrens* showed intermediate seed storage behavior, and the recommended conditions for storage were 9~12% MCs and at < -5℃ (Gosling, 2007). Thus, Taiwan IC seeds demonstrate similar storage characteristics and optimal conditions as those of *C. decurrens* seeds.

In seedlot 3, the germination percentage of seeds at an MC of 5.9% sharply decreased to 28.4% when the drying process was completed, and that would be relevant to desiccation for long periods of time. In fact, seedlot 3 seeds were difficult to dehydrate. Despite using powerful desiccants such as molecular sieves (at about 1~3% RH), it still took 8 d to dry the seeds to about 8% MCs, but the other 2 seedlots only took about 2 h. Furthermore, seeds of seedlot 3 needed a longer period of time (about 36 d) to dehydrate fresh treated seeds from 12.5% to about 6% MCs, but the other 2 seedlots only took 15 and 11 d, respectively. From these results, we inferred that desiccation for a long period of time led some immature seeds of seedlot 3 to age. During the 36-d drying period, about 70% of seedlot 3 seeds deteriorated and died. To make a valid inference, the experiment on seedlot 3 seeds was carried out again under the same conditions the next year (in 2004). The findings showed that drying seeds to 5.6% MC at 20~26℃ took 48 d, and the germination percentage after desiccation decreased from 92.8 to 29.1%. The latter result was consistent with this study, which suggests that seeds of seedlot 3 actually showed weaker resistance to environmental stress and are indeed unlike orthodox seeds.

In this study, when the MC was about 10%, lower storage temperatures contributed to the maintenance of seed viability. This result is consistent with Chung and Hu (1986b)'s findings. However, some of their results are not totally the same as ours; for example, seed viability of their samples with 2 yr of storage at 5℃ had completely deteriorated, but the germination percentages of the 3 seedlots at an MC of about 11% all reached 70%, which was as high as the original germination percentage after 2 yr of storage at 4℃ in our study (Figs. 4, 5). Another example is that after 3 mo of storage at room temperature, the germination percentage of seeds decreased by 50%, and they had all died after 0.5 yr. This significant decrease in seed viability was similar to that of seedlot 3 of this study stored at room temperature but differed from that of seedlot 2 stored at room temperature (Fig. 3). The different results of seedlots 2 and 3 might be related to seed quality. Judging from the low initial germination (only 29%) of seeds selected by winnowing of Chung and Hu's study, we inferred that seed immaturity or improper drying treatment (from 12 to 10% MCs by heat at 35~40℃ for 4 h) caused seed damage, so that subsequently the seeds showed poor longevity and weak resistance to stress.

Seeds of Taiwan IC are immediately dispersed by wind when mature cones split open. To gather better seed crops, nurseries usually harvest cones of Taiwan IC when the color has just turned from green to yellowish-brown. Because the harvested cones still maintain high moisture, seed handling is not easy. Dehiscence of Taiwan IC cones usually takes a longer time, and manual work is also required to extract seeds from early indehiscent cones. In a mast year, it might take a period of about 2~3 mo to process abundant amounts of collected fruits; however, operators seldom temporarily store seeds in a refrigerator in Taiwan, and seed viability was influenced by high seed MC and ambient temperatures, which may be the main reason for seed decay. Thus, we simulated similar room storage conditions to seedlots 2 and 3, and seeds subjected to about 2 mo of storage at ambient temperature obviously displayed seed ageing (Fig. 3). In addition, the difference of seed ageing between these 2 seedlots might be correlated with the degree of cone maturity. Seeds with better maturity are more likely to offer strong resistance to environmental stresses (Schmidt 2000). This result was consistent with the cone collection data. Seeds of seedlot 3 were not fully mature because they had been collected too early, and their viability easily deteriorated in the room-temperature environment. The germination percentage of seedlot 2 seeds slightly decreased after 3 mo of storage at room temperature, but the MGT significantly increased after 2 mo of storage (Fig. 3). From these results, the seed maturity of seedlot 2 was fine, but seed ageing had already begun after 2 mo of storage, and for that reason, of the parameters used to estimate seed viability, MGT was much more sensitive than the germination percentage in this case. Therefore, seed ageing was often found when there was a significant increase in MGT, even if no significant decrease in the germination percentage was observed (Yang et al. 2006b). From the above findings, we inferred that seeds of Taiwan IC, even those with better maturity, began to be damaged by seed ageing after preliminary dehydration at an MC of about 11% and then stored at room temperature for about 2 mo. The solution for preventing seed ageing is to store treated seeds at 4℃ as soon as possible, which is helpful for maintaining viability for at least 0.5 yr (Figs. 4, 5).

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