Plant Biotechnol Rep (2011) 5:27–34
DOI 10.1007/s11816-010-0153-0

ORIGINAL ARTICLE

Overexpression of jasmonic acid carboxyl methyltransferase increases tuber yield and size in transgenic potato

Hwang Bae Sohn · Han Yong Lee · Ju Seok Seo · Choonkyun Jung · Jae Heung Jeon · Jeong-Han Kim · Yin Won Lee · Jong Seob Lee · Jong-Joo Cheong · Yang Do Choi

Received: 3 September 2010 / Accepted: 15 October 2010 / Published online: 10 November 2010

Abstract Jasmonates control diverse plant developmental processes, such as seed germination, flower, fruit and seed development, senescence and tuberization in potato. To understand the role of methyl jasmonate (MeJA) in potato tuberization, the *Arabidopsis JMT* gene encoding jasmonic acid carboxyl methyltransferase was constitutively overexpressed in transgenic potato plants. Increases in tuber yield and size as well as in vitro tuberization frequency were observed in transgenic plants. These were correlated with *JMT* mRNA level—the higher expression level, the higher the tuber yield and size. The levels of jasmonic acid (JA), MeJA and tuberonic acid (TA) were also higher than those in control plants. Transgenic plants also exhibited higher expression of jasmonate-responsive genes such as those for allene oxide cyclase (AOC) and proteinase inhibitor II (PINII). These results indicate that *JMT* overexpression induces jasmonate biosynthesis genes and thus JA and TA pools in transgenic potatoes. This results in enhanced tuber yield and size in transgenic potato plants.

Keywords Potato · Tuberization · Jasmonic acid carboxyl methyltransferase (JMT) · Jasmonic acid (JA) · Methyl jasmonate (MeJA) · Tuberonic acid (TA)

Introduction

The process of tuberization is affected by many factors, such as nitrogen levels, temperature, light, and hormones. Environmental factors change the levels of hormones related to the tuberization process. Several plant growth regulators, such as gibberellins (GAs), cytokinins, abscisic acid (ABA) and jasmonates, are involved in the regulation of potato tuberization (Xu et al. 1998; Jackson 1999; Abdala et al. 2002; Sarkar et al. 2006). Among these, jasmonates are well-known cellular regulators that are involved in diverse developmental processes, such as seed germination, root growth, fertility, and senescence (Creelman and Mullet 1997; Wasternack and Hause 2002; Cheong and Choi 2003). Also, jasmonates promote tuberization via cell expansion at the subapical region of the stolon (Koda 1999).

The importance of JA and MeJA in the tuberization process is well documented (Koda et al. 1991; Pelacho and Mingo-Castel 1991; Koda 1999). Treatment with low concentrations (10^{-6} M) of JA and MeJA promoted potato tuberization in vitro (Koda et al. 1991; Pelacho and Mingo-Castel 1991). Also, JA induced tuberization in yam plants (Koda et al. 1991; Koda 1999) and bulb formation in garlic plants (Ravnikar et al. 1994) in vitro. TA was not detected in yam plants; in this case, JA may largely

H. B. Sohn and H. Y. Lee contributed equally to this work.

H. B. Sohn · H. Y. Lee · J. S. Seo · C. Jung · J.-H. Kim · Y. W. Lee · J.-J. Cheong · Y. D. Choi (✉)
Department of Agricultural Biotechnology and Center for Agricultural Biomaterials, Seoul National University, Seoul 151-921, Korea
e-mail: choiyngd@snu.ac.kr

J. H. Jeon
Plant Cell Biotechnology Lab, Korea Research Institute of Bioscience and Biotechnology, Daejon 305-806, Korea

J. S. Lee
School of Biological Sciences, Seoul National University, Seoul 151-921, Korea

control tuberization. Takahashi et al. (1994) reported that JA and MeJA induced the swelling of potato tuber disks. It was reported that MeJA disrupted cortical microtubules in suspension cultures of tobacco BY-2 cells (Abe et al. 1990). Treatment with JA induced changes in the apical meristem morphology of potato stolons (Cenzano et al. 2003). These results showed that JA and MeJA seem to cause stop stolon elongation and induce the expansion of potato cells.

Substances that exhibit strong tuber-inducing activities have been isolated from potato leaves (*Solanum tuberosum* L.). Among them, tuberonic acid glucoside (TAG) has had its structure determined. TAG and its aglycone (tuberonic acid, TA), which were provided in growth medium, induced the tuberization of potato stolons cultured in vitro (Koda 1997). TAG and TA are structurally related to JA (Koda et al. 1988, 1991). Actually, it is known that the biosynthetic pathway of JA is correlated with that of TA. JA can be converted to TAG (Yoshihara et al. 1996). Treatment with JA and MeJA enhanced endogenous TA levels in *Arabidopsis* (Gidda et al. 2003) and in tobacco Bright Yellow-2 suspension culture (Swiatek et al. 2004). Moreover, the correlation between JA and TA is explained by increases in JA and TA in the whole potato plant during the onset of tuberization. For example, an increase in TA occurred right after a burst of JA during tuberization (Malkawi et al. 2007). Large amounts of JA, TA and TAG were also accumulated at low temperature, which induces tuberization (Nam et al. 2008).

We expected that altering the endogenous jasmonate level in potato through gene manipulation could affect its tuber-inducing activity and tuber yield. Recently, the JMT enzyme that is responsible for the formation of MeJA from JA has been identified in *Arabidopsis*. A transgenic *Arabidopsis* that overexpresses *JMT* exhibited elevated levels of endogenous MeJA and high expression of JA-responsive genes. Also, JA-related responses such as defense were observed (Seo et al. 2001). In this study, the *Arabidopsis JMT* gene was transformed into potato to overproduce MeJA. The resulting transgenic plants showed enhanced tuber yield and size compared to control plants.

Materials and methods

Plant materials and transformation

The potato tubers used in this study were *Solanum tuberosum* cv. *Jopung*. Virus-free potato tubers were kindly donated by the National Alpine Agricultural Experimental Station, Korea. Potato tuber discs were transformed as previously described (Sheerman and Bevan 1988), by co-cultivation with an *Agrobacterium tumefaciens* strain harboring a recombinant pBI111L vector (obtained from pBI121 in which the GUS gene had been removed) containing the full-length JMT cDNA in a sense orientation under the control of the cauliflower mosaic virus (CaMV) 35S promoter. Control plants were regenerated from a potato tuber disc with the empty vector pBI111L. Plant transformants were selected for resistance to 50 mg l^{-1} kanamycin and, after rooting, were transferred to soil and grown in the greenhouse. Selected transformed lines were propagated vegetatively in the greenhouse by sowing tubers.

Field experiment

Potato plants were grown in the experimental field of Seoul National University. The tubers were planted in August and harvested in November 2004 and 2006.

Blot analysis

For genomic Southern blot, 5 μg of genomic DNA were digested with *Eco*RI restriction enzyme, separated on 0.8% agarose gels, and transferred to nylon membranes. Northern blot analysis was performed with total RNA extracted from frozen, ground samples using the phenol–SDS–LiCl method (Carpenter and Simon 1998). Total RNA (4 μg) was separated on 1.3% agarose formaldehyde gels and transferred to GeneScreen Plus® hybridization transfer membranes (Perkin-Elmer). A radioactive JMT probe was labeled by random priming using [^{32}P]-dATP (Izotop). Equal loading of RNA samples in each lane was confirmed by visualizing the rRNA with ethidium bromide and UV light.

In vitro tuberization

Transgenic potato plants that contain the *JMT* gene were assayed for in vitro tuberization according to the protocol of Ahn and Zimmerman (2006), with minor modifications. Twelve nodal segments (5 mm in length, with one bud per node) taken from each 4-week-old line were placed in Magenta boxes containing a tuberization medium (MS medium supplemented with 6% sucrose). Nodal segments were grown for 2 weeks in the growth chamber and then transferred to SD (8 h light and 16 h dark cycle) conditions. Tuber formation was monitored for 4 weeks.

Quantification of jasmonates

After harvesting, the leaves were frozen immediately in liquid nitrogen and kept at −70°C until further processing.

Jasmonates were extracted from 1 g of leaf tissue ground into a fine powder. The jasmonates were quantified by GC/mass spectrometry (Koo et al. 2008). Tuberonic acid was quantified according to the procedure of Gidda et al. (2003). Standard TA was kindly provided by Professor T. Yoshihara.

Results

Overexpression of the *Arabidopsis JMT* gene in potato

To understand the role of JMT enzyme in tuber development, transgenic potato plants constitutively overexpressing *JMT* cDNA under the control of CaMV 35S promoter were generated. The pBI111L empty vector was also introduced into potato plants as a control.

Genomic Southern blot analysis confirmed that the *JMT* gene was stably integrated into the chromosomal DNA of potato plants, and the transgenic potato lines contained 2–5 copies of the transgene (Fig. 1a). The resulting transgenic lines were referred to as JMTox plants. Three independent transgenic lines, denoted JMTox 102, 227 and 605, were selected for further analyses.

JMTox 227 showed the highest levels of *JMT* expression, and JMTox 102 and JMTox 605 displayed intermediate levels (Fig. 1b). To demonstrate that the *Arabidopsis* JMT protein functions properly in a heterologous system, the levels of MeJA in the leaves of transgenic plants were analyzed by GC/MS. The results showed that the MeJA contents of transgenic plants were two- to fivefold greater than those in control plants (Fig. 1c). The levels of MeJA were correlated with the expression level of the transgene in the transgenic plants.

High-frequency tuberization in vitro of *JMT* overexpression lines

It has been reported that jasmonates are involved in potato tuberization (Koda et al. 1991, 1992; Koda 1999; Rodríguez-Falcón et al. 2006). It was therefore of interest to determine whether altering the level of MeJA could influence tuber formation.

Internode segments of transgenic plants were evaluated for tuber formation in vitro (Fig. 2). Transgenic plants started to form tubers within 3 weeks of transfer to inductive short-day conditions. At 3 weeks, 58–75% of the transgenic lines had tuberized, whereas 33% of the control plants had. At 4 weeks, the tuberization frequencies of the transgenic plants were 100% for JMTox 227 and 605, 83% for JMTox 102, but 42% for the control plants (Fig. 2a). At 3 and 4 weeks, all of the transgenic lines had produced

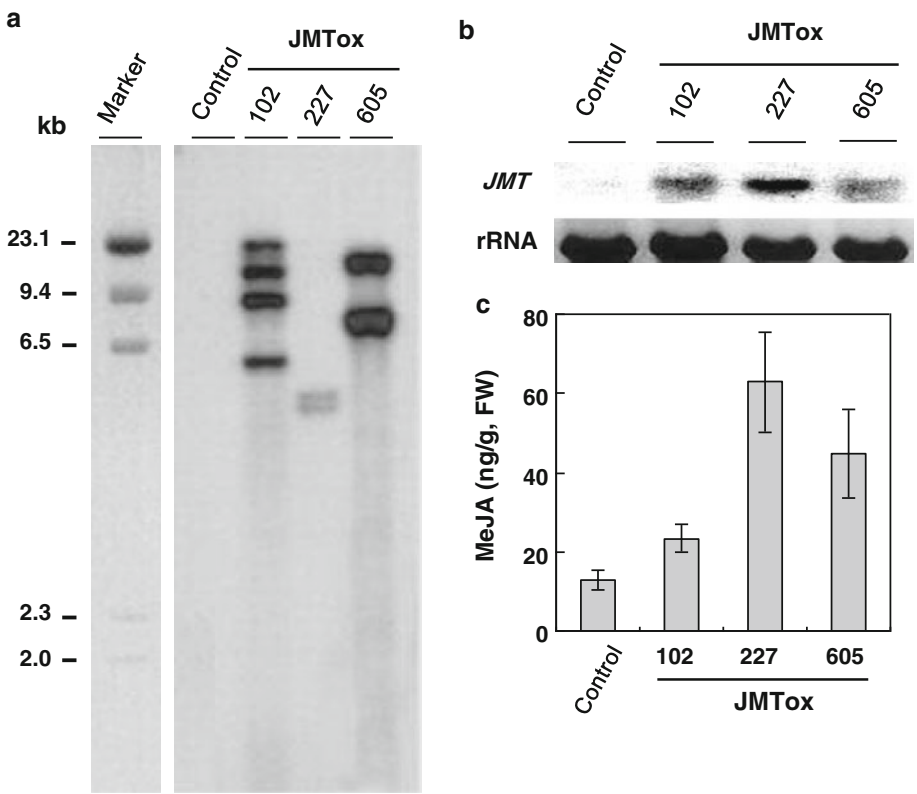

Fig. 1 *JMT* overexpression in potato. **a** Genomic Southern blot analysis of transgenic potato plant. Potato genomic DNAs were isolated from vector control and transgenic lines and digested with *Eco*RI. Samples were electrophoresed on 0.8% agarose gel and then hybridized with random-primed *JMT* DNA. *Numbers on the left side* of the gel are the sizes of the markers in kilobase pairs. **b** Northern blot analysis of *JMT* mRNA accumulation in transgenic potato plants. Total RNA (4 μg) from leaves of the vector control and the independent transgenic lines (JMT-ox 102, 227 and 605) were hybridized with the 32P-labeled probe. Transcript size was ~1.5 kb. **c** Quantification of MeJA in *JMT* overexpression lines

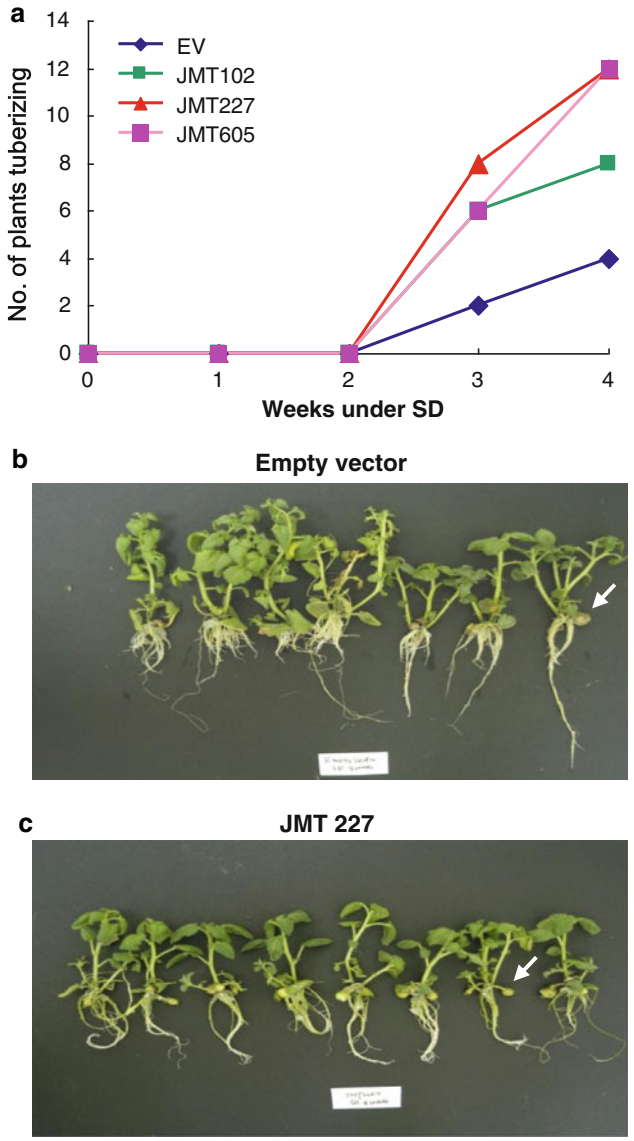

Fig. 2 In vitro tuberization of transgenic potato lines overexpressing the *JMT* gene. Micropropagated explants of the vector control and the three transgenic potato lines containing the *JMT* transgene (JMT 102, 605 and 227) were generated as described in the "Materials and methods" section. From these explants, nodal segments (5 mm in length) with one bud per node were taken from twelve individual potato plantlets per line. Twelve nodal segments per line were placed in three Magenta boxes containing the tuberization medium (MS medium and 6% sucrose) and incubated at 21°C under either an 8-h light/16-h dark (inductive) or a 16-h light/8-h dark (noninductive) photoperiod. **a** The number of transgenic plants that produced microtubers was counted weekly. The production of microtubers over the incubation period, expressed as the percentage of explants producing a microtuber, is plotted. The vector control (**b**) and JMT 227 lines (**c**) were grown for 2 weeks under LD and then for 4 weeks under SD

microtubers at frequencies that were two- to threefold higher than those of control plants (Fig. 2a). Tuberization frequencies were directly proportional to the levels of *JMT* expression and MeJA level.

Increased tuber size and yield in transgenic potato

The tuber yield was determined for transgenic plants grown in a field for two years (Fig. 3b, c). Similar to the enhanced in vitro tuberization frequency noted previously, increased tuber yields were observed in transgenic plants under field conditions. Even though the total number of tubers remained relatively constant, the total tuber weight or tuber yield increased with *JMT* gene expression in the different lines of transgenic plants (Fig. 3a). The yield increase was highest in JMTox 227. The tuber yield of the JMTox 227 line was approximately 1.5- to 2-fold higher, whereas the tuber yields of the JMTox 102 and 605 lines were only slightly higher than that of the control plants (Fig. 3b, c). In addition to higher tuber yields, larger tubers were harvested from the transgenic plants than the control plants. The number of small tubers was reduced, while the number of large tubers increased in the transgenic potatoes. In particular, in the JMTox 227 line, the tubers harvested in experiment II were threefold larger than those of the control plants (Fig. 3c). From the results obtained over the course of two years, we demonstrated that overexpression of the *JMT* gene reproducibly led to increases in tuber yield and size in direct proportion to the expression level of the *JMT* gene.

Quantification of JA, MeJA and TA in JMTox plants

An experiment to examine the time course of tuber formation in the field was performed. Total tuber weight increased from 10 weeks and reached its maximum at around 14 weeks (Fig. 4).

To test the effects of JA, MeJA and TA on tuberization, the fourth and fifth expanded leaves from field-grown transgenic plants were taken at 8 (before tuberization) and 10 (after tuberization) weeks, and the levels of JA, MeJA and TA were quantified by GC/MS analysis. Levels of MeJA were 3.4- to 5.1-fold higher in transgenic potatoes, as intended.

At 8 weeks, no tubers had formed in the transgenic and control plants. TA was not detected in the JMTox 227 and control plants, even though the levels of JA and MeJA in the leaves were much higher in the JMTox 227 than in the control plants (Fig. 5d).

At 10 weeks, the JMTox 227 plants produced larger and heavier tubers than the control plants (Fig. 5b, c). Even though the levels of total jasmonates including JA, MeJA and TA in the leaves increased abruptly in both transgenic and control plants, the relative concentrations were still about twofold higher in the transgenic plants. The levels of JA and MeJA were approximately 1.4- and 3.4-fold higher, respectively, in the leaves of the JMTox

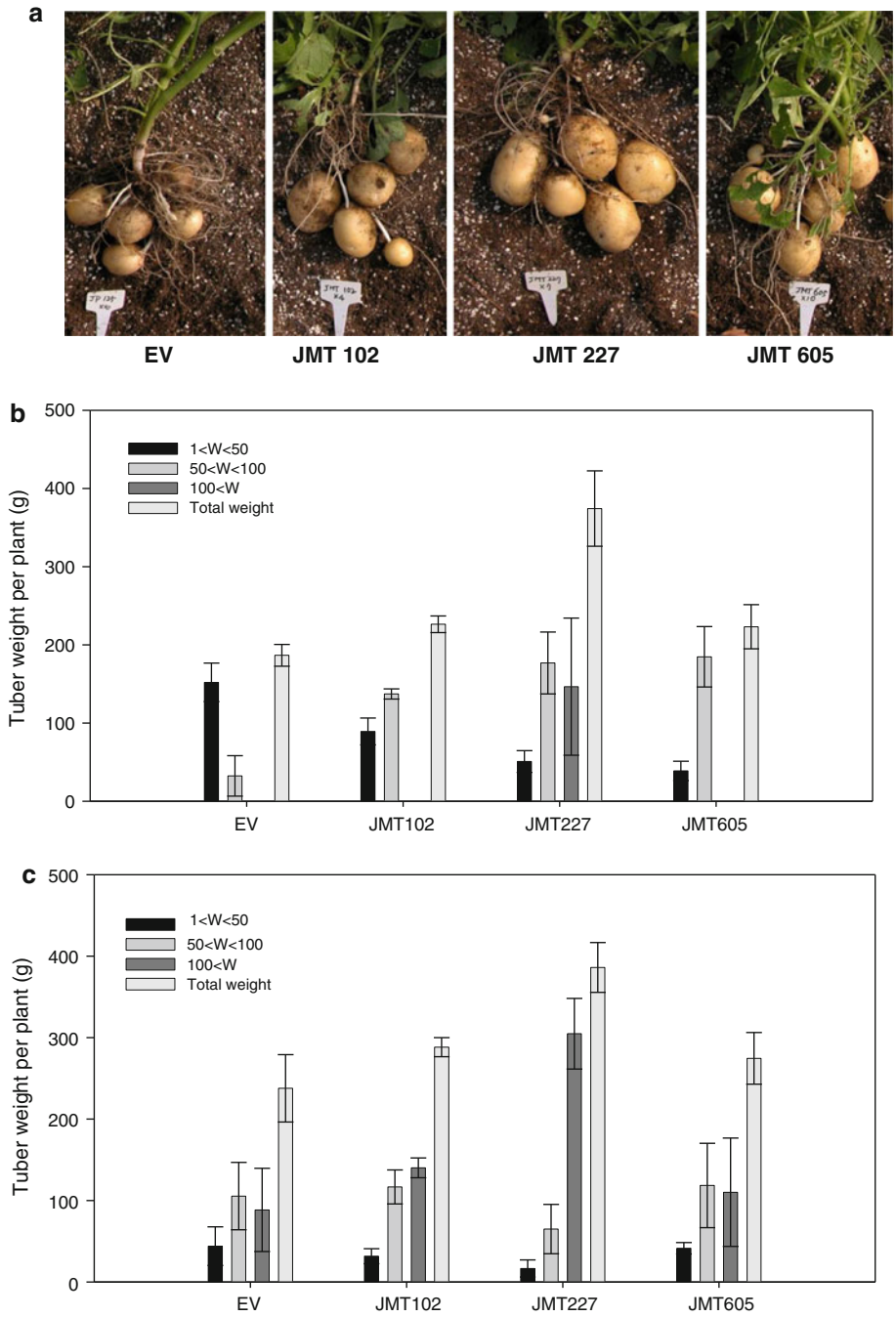

Fig. 3 Field test of *JMT* overexpression lines. **a** Yield per plant was determined by harvesting tubers from transgenic plants grown in the field 12 weeks after planting tubers into the soil. **b** In experiment 1, plants were grown under natural light conditions from August to November in 2004, and the data on tuber weight per plant shown in the plot are from seven vector control and independent *JMT* overexpression lines. **c** In experiment 2, plants were grown under natural light conditions from August to November in 2006. The data on tuber weight per plant shown in the plot are from seven replicate plants from each of the vector control and *JMT* overexpression lines. Vector controls were transgenic plants transformed with the empty binary vector pBI111L. SE values are shown for all data

227 compared to the control plants. The level of TA was also approximately 3.9-fold higher in the leaves of the JMTox 227 than those of the control plants. However, the levels of JA, MeJA and TA in tubers were much lower than those in leaves, and no differences were noted between the transgenic and control plants in this respect (Fig. 5d).

The expression levels of the JA-responsive genes *AOC* and *PINII* were also higher in the JMTox 227 plants (Fig. 5a). AOC is a key biosynthetic enzyme for JA (Cheong and Choi 2003). These results suggest that the increased MeJA levels in the *JMT*-overexpressing transgenic potatoes induce a biosynthetic enzyme for JA, which causes the increases in JA and TA.

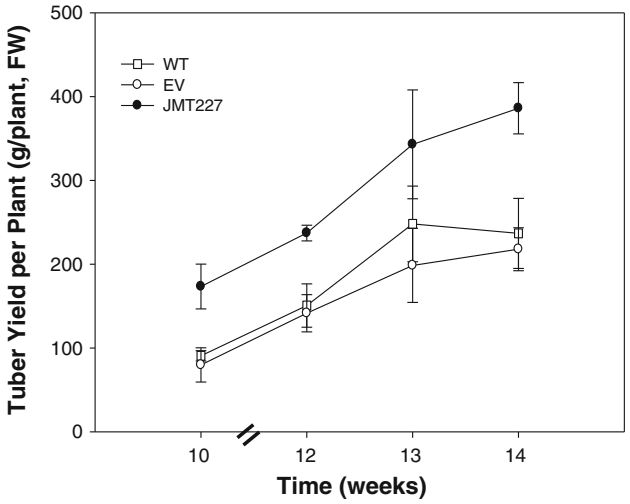

Fig. 4 Tuber yields in control and JMTox 227 plants. Mother tubers of the wild-type (*WT*), vector control (*EV*) and JMT-ox 227 lines containing the *JMT* transgene were planted as described in the "Materials and methods" section. After 10–14 weeks the tubers were harvested and the tuber yield per plant was measured for each line. Data for the vector control and *JMT* overexpression lines were obtained from seven replicate plants each. The vector controls were transgenic plants transformed with the empty binary vector pBI111L. SE values are shown for all data

Discussion

To understand the role of MeJA in tuber development in potato, we have overexpressed the *JMT* gene, which converts JA to MeJA, in this study. *JMT*-overexpressing plants exhibited much higher in vitro tuberization frequencies than control plants (Fig. 2). The transgenic plants also showed increased tuber yields and sizes under field conditions (Fig. 3). During tuberization, the levels of JA and MeJA in transgenic plants were approximately 1.4- and 3.4-fold higher, respectively, than those in the control plants, which led to an elevation of the TA level by about 3.9-fold. It is known that TA is synthesized from JA (Yoshihara et al. 1996; Gao et al. 2003; Swiatek et al. 2004; Miersch et al. 2004). When applied to potato plants, ^{14}C-labeled JA is converted to tuberonic acid glycoside (TAG) (Yoshihara et al. 1996). The increased level of TA may result from the higher level of JA in the transgenic plants. The increased concentrations of JA and MeJA can be attributed to the increased level of JA biosynthetic genes, such as *AOC* (Fig. 5). In our study, the degree of tuberization observed in the transgenic potatoes was correlated with the *JMT* overexpression level (Figs. 1, 2, 3).

Kolomiets et al. (2001) reported that mutants with reduced expression of *LOX1* showed a consequent reduction in tuber number and size. The application of theobroxide, which is a potato tuber-inducing compound, increased JA and TA levels. However, such increases were inhibited by salicylhydroxamic acid, which is a JA biosynthesis inhibitor (Gao et al. 2003, 2005). Treatment with JA and MeJA increased TA levels in a tobacco Bright Yellow-2 suspension culture (Swiatek et al. 2004). Moreover, Miersch et al. (2004) reported that JA and TA were increased in wounded leaves of a transgenic tomato overexpressing *AOS*, whereas they were not increased in wounded leaves of knockout biosynthetic mutants (35S::*AOC*antisense plants, *spr2* mutant, *acx1* mutant). These results demonstrate that the JA biosynthetic pathway is closely linked to the TA biosynthetic pathway in potato plants.

In transgenic *Arabidopsis*, overexpressing the *JMT* gene led to the overexpression of JA biosynthetic genes, including *LOXII* and *AOS*. It led to a higher level of MeJA and the induction of JA-responsive genes, including *JR2*, *VSP*, *DHS1*, and *PDF1.2* (Seo et al. 2001). In our study, transgenic potato plants showed increases in JA and MeJA and induction of JA-responsive genes such as *AOC* (Fig. 5). These observations in transgenic plants suggest that JMT can affect the JA biosynthetic pathway via the self-amplification, stimulation, or regulation of its own expression.

A favorable effect of JA on in vitro tuberization was reported by Koda et al. (1991, 1992) and Pelacho and Mingo-Castel (1991). Also, MeJA showed potato tuber-inducing activity in vitro (Koda et al. 1992). In our study, *JMT* overexpression in transgenic plants led to increased tuberization and tuber yield compared to control plants. Considering the reported tuber-inducing activities of JA and MeJA, these increases in tuberization and tuber yield were caused by enhanced levels of JA and MeJA in the transgenic potato plants (Figs. 2, 3, 5).

Koda et al. (1988) reported that levels of tuber-inducing substance(s), which were later found to contain TA, increased in a potato leaf under inducing conditions. TA showed strong tuber-inducing activity in vitro (Koda et al. 1991). In our study, enhanced levels of TA were observed in leaves of tuberized transgenic potatoes.

In transgenic potato plants, the elevated levels of JA and MeJA were correlated increased tuber size (Fig. 5). This result reinforces earlier reports that adding JA and MeJA to the growth medium affected potato tuberization via cell radial expansion (Matsuki et al. 1992; Takahashi et al. 1994).

In conclusion, overexpression of the *JMT* gene resulted in increases in the JA pool and TA levels in transgenic

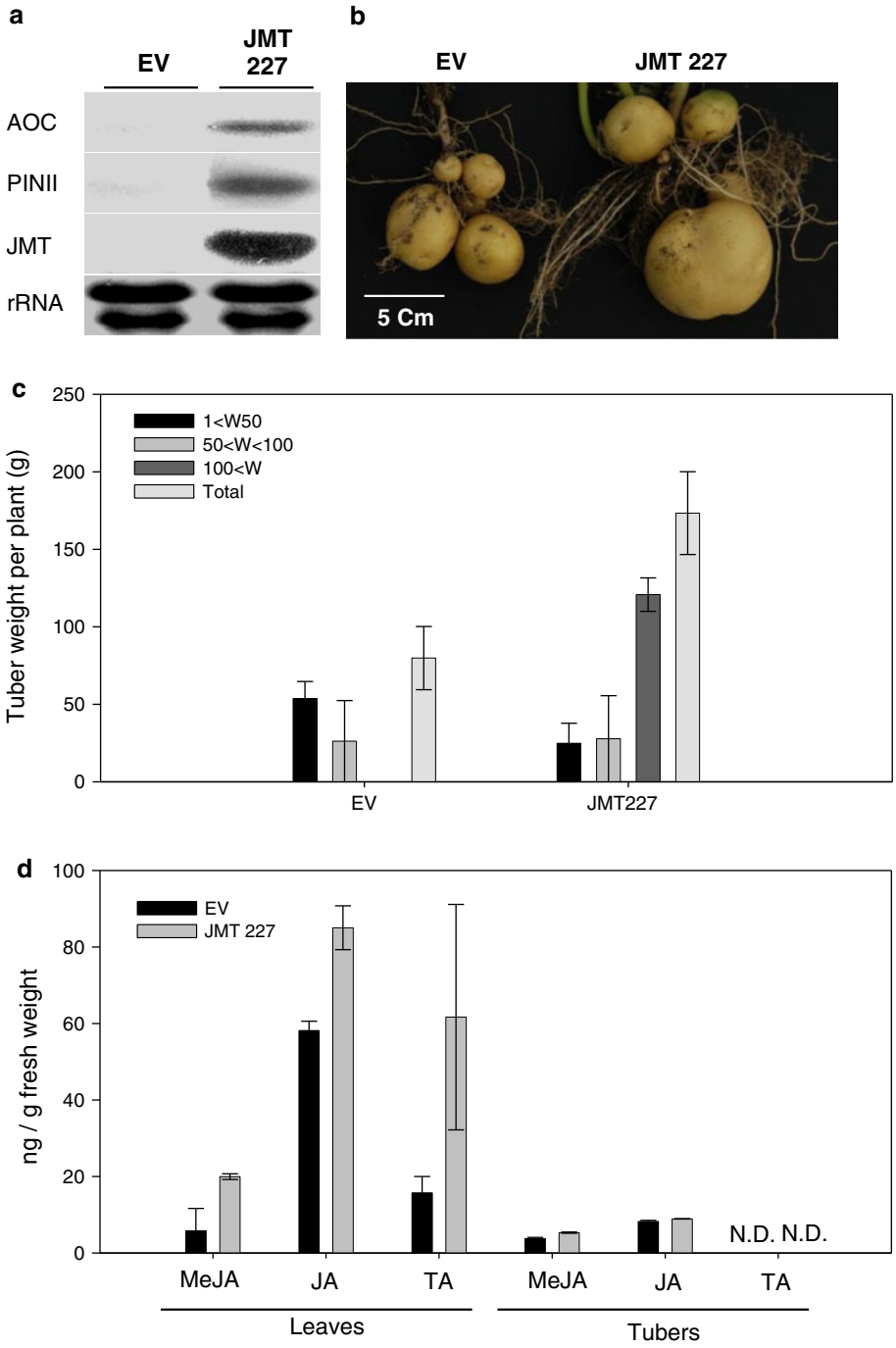

Fig. 5 Tuber yields and quantification of MeJA, JA and TA in transgenic lines. **a** Northern blot analysis in transgenic potato plants. RNA gel blot analysis was performed using 4 μg of total RNA and hybridized with 32P-labeled probes. Equal loading of RNA samples in each lane was confirmed by visualizing the RNA with ethidium bromide and UV light. **b** Tubers produced by the *JMT* overexpression lines are shown on the *right*. Overexpression lines were produced by introducing *JMT* cDNA under the control of the CaMV 35S promoter. Tubers were harvested from the transgenic plants after 10 weeks in the field. **c** Tuber yields of the vector control and the JMT 227 lines shown in **a**. Yields are given in grams as the average tuber fresh weight per plant ± SE. **d** Quantification of MeJA, JA and TA in the vector control and JMT 227 lines. Potato leaves and tubers were sampled from the transgenic plants after 10 weeks and processed for jasmonate quantification according to the method described in "Materials and methods." The values represent the results of an experiment in which two pools of three plants were analyzed

plants. The enhanced level of total jasmonates affected jasmonate-related responses such as tuberization. *JMT*-transgenic potato is a suitable system for studying the function of jasmonates in potato tuberization.

Acknowledgments Special thanks are extended to Professor T. Yoshihara for providing standard tuberonic acid. This work was supported by grants from the Crop Functional Genomics Center (CG2160 to YDC and CG2142 to J-JC) of MOEST and the Korea Research Foundation (KRF-2006-005-J04701 to Y.D.C.). Graduate Research Assistantships to HBS, HYL, JSS and CJ from the Brain Korea 21 project of the MOEST are also acknowledged.

References

Abe M, Shibaoka H, Yamane H, Takahashi N (1990) Cell cycle-dependent disruption of microtubules by methyl jasmonate in tobacco BY-2 cells. Protoplasma 156:1–8

Abdala G, Castro G, Miersch O, Pearce D (2002) Changes in jasmonate and gibberellin levels during development of potato plants (*Solanum tuberosum*). Plant Growth Regul 36:121–126

Ahn YJ, Zimmerman L (2006) Introduction of the carrot HSP17.7 into potato (*Solanum tuberosum* L.) enhances cellular membrane stability and tuberization in vitro. Plant Cell Environ 29:95–104

Carpenter CD, Simon AE (1998) Preparation of RNA. Methods Mol Biol 82:85–89

Cenzano A, Vigliocco A, Kraus T, Abdala G (2003) Exogenously applied jasmonic acid induces changes in apical meristem morphology of potato stolons. Ann Bot 91:915–919

Cheong J-J, Choi YD (2003) Methyl jasmonate as a vital substance in plants. Trend Genet 19:409–413

Creelman RA, Mullet JE (1997) Biosynthesis and actions of jasmonates in plants. Annu Rev Plant Physiol Plant Molec Biol 48:355–381

Gao X, Yang Q, Minami C, Matsuura H, Kimura A, Yoshihara T (2003) Inhibitory effect of salicylhydroxamic acid on theobroxide-induced potato tuber formation. Plant Sci 165:993–999

Gao X, Wang F, Yang Q, Matsuura H, Yoshihara T (2005) Theobroxide triggers jasmonic acid production to induce potato tuberization in vivo. Plant Growth Regul 47:39–45

Gidda SK, Miersch O, Levitin A, Schmit J, Wasternack C, Varin L (2003) Biochemical and molecular characterization of a hydroxyjasmonate sulfotransferase from *Arabidopsis thaliana*. J Biol Chem 278:17895–17900

Jackson SD (1999) Multiple signaling pathways control tuber induction in potato. Plant Physiol 119:1–8

Koda Y (1997) Possible involvement of jasmonates in various morphogenic events. Physiol Plant 100:639–646

Koda Y, Omer ESA, Yoshihara T, Shibata H, Sakamura S, Okazawa Y (1988) Isolation of a specific potato tuber-inducing substance from potato leaves. Plant Cell Physiol 29:1047–1051

Koda Y, Kikuta Y, Tazaki H, Tsujino Y, Sakamura S, Yoshihara T (1991) Potato tuber-inducing activities of jasmonic acid and related compounds. Phytochemistry 30:1435–1438

Koda Y, Kikuta Y, Kitahara T, Nishi T, Mori K (1992) Comparisons of various biological activities of stereoisomers of methyl jasmonate. Phytochemistry 31:1111–1114

Kolomiets MV, Hannapel DJ, Chen H, Tymeson M, Gladon RJ (2001) Lipoxygenase is involved in the control of potato tuber development. Plant Cell 13:613–626

Koo YJ, Yoon E, Song JT, Seo HS, Kim JH, Lee YW, Lee JS, Cheong JJ, Choi YD (2008) An advanced method for the determination of carboxyl methyl esterase activity using gas chromatography-chemical ionization-mass spectrometry. J Chromatogr B 863(1):80–87

Malkawi A, Jensen BL, Langille AR (2007) Plant hormones isolated from "Katahdin" potato plant tissues and the influence of photoperiod and temperature on their levels in relation to tuber induction. J Plant Growth Regul 26:308–317

Matsuki T, Tazaki H, Fujimori T, Hogetsu T (1992) The influences of jasmonic acid methyl ester on microtubules in potato cells and formation of potato tubers. Biosci Biotech Biochem 56:1329–1330

Miersch O, Weichert H, Stenzel I, Hause B, Maucher H, Feussner I, Wasternack C (2004) Constitutive overexpression of allene oxide cyclase in tomato (*Lycopersicon esculentum* cv. *Lukullus*) elevates levels of some jasmonates and octadecanoids in flower organs but not in leaves. Phytochemistry 65:847–856

Nam KH, Kong F, Matsuura H, Takahashi K, Nebeta K, Yoshihara T (2008) Temperature regulates tuber-inducing lipoxygenase-derived metabolites in potato (*Solanum tuberosum*). J Plant Physiol 165:233–238

Pelacho AM, Mingo-Castel AM (1991) Jasmonic acid induces tuberization of potato stolons cultured in vitro. Plant Physiol 97:1253–1255

Ravnikar M, Zel J, Plaper I, Spacapan A (1994) Jasmonic acid stimulates shoot and bulb formation of garlic in vitro. J Plant Growth Regul 12:73–77

Rodríguez-Falcón M, Bou J, Prat S (2006) Seasonal control of tuberization in potato: conserved elements with the flowering response. Annu Rev Plant Biol 57:151–180

Sarkar D, Pandey SK, Sharma S (2006) Cytokinins antagonize the jasmonates action on the regulation of potato (*Solanum tuberosum*) tuber formation in vitro. Plant Cell Tiss Organ Cult 87:285–295

Seo HS, Song JT, Cheong JJ, Lee YH, Lee YW, Hwang I, Lee JS, Choi YD (2001) Jasmonic acid carboxyl methyltransferase: a key enzyme for jasmonate-regulated plant responses. Proc Natl Acad Sci USA 98:4788–4793

Sheerman S, Bevan MW (1988) A rapid transformation method for *Solanum tuberosum* using binary *Agrobacterium tumefaciens* vector. Plant Cell Rep 7:13–16

Swiatek A, Dongen WV, Esmans EL, Onckelen HV (2004) Metabolic fate of jasmonates in tobacco bright yellow-2 cells. Plant Physiol 135:161–172

Takahashi K, Fujino K, Kikuta Y, Koda Y (1994) Expansion of potato cells in response to jasmonic acid. Plant Sci 100:3–8

Wasternack C, Hause B (2002) Jasmonates and octadecanoids-signals in plant stress response and development. In: Moldave K (ed) Progress in nucleic acid research and molecular biology. Academic, New York, pp 165–221

Xu X, van Lammeren AAM, Vermeer E, Vreugdenhil D (1998) The role of gibberellin, abscisic acid, and sucrose in the regulation of potato tuber formation in vitro. Plant Physiol 117:575–584

Yoshihara T, Amanuma M, Tsutsumi T, Okumura Y, Matsuura H, Ichihara A (1996) Metabolism and transport of [2–^{14}C](±) jasmonic acid in the potato plant. Plant Cell Physiol 37:586–590