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In vitro proliferative capacity of satellite cells derived from Brown Vietnamese cattle (*Bos indicus*)

*Minh Thai Nguyen[1,2], Chung Chinh Doan[1,2], Son Nghia Hoang[1,2], Thi Anh Linh Dinh[2], Han Thai Minh Nguyen[3,4], Nhung Thi Nguyen[5], Hanh Van Nguyen[6], Loan Thi Tung Dang[7], Nhan Lu Chinh Phan[2], Long Thanh Le[1,2], Chi Nguyen Quynh Ho[1,2]**

[1]*Biotechnology Department, Graduate University of Science and Technology, Vietnam Academy of Science and Technology, Hanoi, Vietnam*
[2]*Animal Biotechnology Department, Institute of Life Sciences, Vietnam Academy of Science and Technology, Ho Chi Minh, Vietnam*
[3]*Center for Biotechnology and Genomic Medicine, Medical College of Georgia, Augusta University, Augusta, GA, USA*
[4]*Life Science Department, University of New Hampshire at Manchester, Manchester, NH, USA*
[5]*Department of Animal Biotechnology, Institute of Biology, Vietnam Academy of Science and Technology, Hanoi, Vietnam*
[6]*VNU University of Engineering and Technology, Hanoi, Vietnam*
[7]*Faculty of Biology and Biotechnology, University of Science, Vietnam National University, Ho Chi Minh, Vietnam*

**Corresponding author: hnqchi@ils.vast.vn*

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Abstract: Finding suitable animal cell sources for cultured meat production remains a major challenge and continues to attract significant scientific interest, particularly in the development of bovine cultured meat. These cells must demonstrate robust proliferative capacity and the ability to maintain stemness. In this study, we aimed to evaluate the proliferation capacity and morphological alterations of bovine satellite cells (bSCs) derived from the Brown Vietnamese cattle during long-term *in vitro* expansion. The results showed that bSCs possessed a high proliferative potential, sustaining over 20 passages. These cells retained the expression of Pax7 and Pax3, specific markers for bovine satellite cells, in both early and late passages. Accumulation of bSCs in the G0/G1 phase at late passages indicated cell cycle arrest and reduced proliferation during prolonged culture. Morphological features of cellular senescence were also identified in late passage bSCs, including cytoplasmic enlargement, increased cell and nuclear size, and a decreased nucleocytoplasmic ratio. These findings suggest that bSCs from the Brown Vietnamese cattle represent a promising cell source for cultured meat research, demonstrating initial proliferative capacity and maintenance of cell identity, although proliferation potential declines under extended *in vitro* conditions due to cellular senescence.

Keywords: bovine satellite cells; cultured meat production; *in vitro* expansion; myogenic markers; replicative senescence

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In recent years, the field of cultured meat has emerged as a pioneering research direction, aiming to support sustainable meat production by reducing the environmental impacts associated with conventional livestock farming, particularly greenhouse gas emissions, while decreasing the reliance on large-scale animal slaughter and improving animal welfare (Floor and Manlosa-Kirk 2025; Moss 2025; Tavan et al. 2025). One of the key factors in this technology is the ability to successfully isolate and culture satellite cells – a type of skeletal muscle stem cell that plays an important role in the regeneration and development of muscle tissue (Stout et al. 2022; Han et al. 2023a; Yun et al. 2023). Like many other tissues, skeletal muscle depends on resident stem cell populations for homeostatic maintenance and repair throughout life (Relaix et al. 2021). These functions are primarily mediated by satellite cells, whose proliferation, self-renewal, differentiation, and population composition must be tightly regulated to maintain an appropriate balance among quiescent, activated, and differentiating cell states within the stem cell niche (Yin et al. 2013; Tierney and Sacco 2016). Disruption of this balance may impair muscle regeneration, promote progressive tissue degeneration, or contribute to tumorigenesis (Tierney and Sacco 2016). Therefore, understanding single-cell behaviour is essential for elucidating the functional heterogeneity and regulatory dynamics of the satellite cell compartment at the population level.

Satellite cells possess the capacity for self-renewal and differentiation into mature muscle fibres, forming the cellular foundation for *in vitro* cultured meat production (Pawlikowski et al. 2015; Murach et al. 2021). The previous studies of satellite cell heterogeneity have determined various sub-populations exhibiting unique properties according to their location, states of quiescence, multipotency, cell cycle, or profiles of gene expression (Rodriguez-Outeirino et al. 2021; Guilhot et al. 2024).

In Vietnam, Brown Vietnamese cattle are a valuable domestic breed with the ability to adapt well to tropical climates and produce high-quality meat with a distinctive flavor (Quach et al. 2023). However, to date, very few studies have been conducted to evaluate the biological potential of satellite cells isolated from this breed of cattle under *in vitro* culture conditions. This study aims to evaluate the proliferation ability of satellite cells isolated from skeletal muscle of Vietnamese Brown cattle, thereby providing basic data for potential applications in the fields of meat culture and regenerative biology. At the same time, research on stem cells from indigenous cattle breeds also contributes to the preservation and development of Vietnam's valuable genetic resources in the context of integration and development of modern biotechnology.

MATERIAL AND METHODS

Cell isolation and culture. Bovine neck muscle tissues were sourced at slaughterhouses and promptly transported to the laboratory within a maximum of 3 h post-harvest. The tissue was disinfected with 2% cetyltrimethylammonium bromide (CTAB, RM4867-100G; HiMedia Laboratories Pvt. Ltd., Mumbai, India) and subsequently washed with phosphate-buffered saline (PBS, D411-500ML; Diagnovum, Greifswald, Germany) containing 1% Penicillin-Streptomycin (D910-100ML; Diagnovum, Greifswald, Germany). The tissue was dissected into small pieces (approximately 0.5 × 0.5 cm) and washed with PBS. These tissue fragments were transferred into 6-well culture plates and maintained in DMEM/Ham's F-12 medium (D812-500ML; Diagnovum, Greifswald, Germany) supplemented with 15% fetal bovine serum (FBS, D204-500ML; Diagnovum, Greifswald, Germany), 1% Penicillin-Streptomycin, and human fibroblast growth factor (hFGF, 15 ng/ml, 10018B100UG; Thermo Fisher Scientific, Waltham, MA, USA). Cells were cultured at 37 °C in a humidified atmosphere containing 5% CO_2. Cells were passaged at a 1 : 3 split ratio upon reaching 90% confluence. All experiments were performed using satellite cells isolated from a single donor of Brown Vietnamese cattle (biological replicate, $n = 1$), and each experimental condition was conducted in triplicate (technical replicates, $n = 3$).

Cell density analysis. Cell density was assessed by seeding 1×10^3 cells per well in 96-well plates (701001; NEST Biotechnology Co., Ltd., Wuxi, China). After 2 days of culture, cell density was determined by nuclear staining and automated nucleus counting. Cells were fixed with 4% paraformaldehyde (TCL119; HiMedia Laboratories Pvt. Ltd., Mumbai, India) for 30 min and permeabilised using 0.1% Triton X-100 at 4 °C overnight (1086031000; Merck, Darmstadt, Germany). Cells were incubated with 4',6-diamidino-2-phenylindole (DAPI, G1012-

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10ML; Servicebio Technology Co., Ltd., Wuhan, P.R. China) at a final concentration of 2 µg/ml for 30 min at room temperature in the dark. Cells were rinsed three times using PBS to remove excess dye. Fluorescent imaging and quantification of nuclei were evaluated using the Cytell Cell Imaging System (GE Healthcare Life Sciences, Marlborough, MA, USA). The Cytell Cell Cycle App was used for nucleus counting and assessment of nuclear features, including intensity, shape, and area. For accurate detection of cell nuclei, the software's nuclear area threshold was set to 150 μm^2 and sensitivity to 50%.

WST-1 assay. Bovine satellite cells were seeded into 96-well plates at a density of 2×10^3 cells per well. After 2 days of culture, cell viability and proliferation were measured using the WST-1 assay kit (ab65473; Abcam plc, Cambridge, UK). 10 µl of WST-1 reagent was added to each well and incubated for 3.5 hours. Absorbance was read at 450 nm using the GloMax® Explorer Microplate Reader (Promega Corporation, Madison, WI, USA).

Apoptosis detection. Cells were cultured in T-25 flasks (707003; NEST Biotechnology Co., Ltd., Wuxi, P.R. China) at a density of 1×10^5 cells/flask. After 2 days of culture, cells were harvested by trypsinisation using 0.25% Trypsin-EDTA (D705-100ML; Diagnovum, Greifswald, Germany) and centrifuged at 1 500 rpm for 5 minutes. Apoptosis was assessed using the FITC Annexin V Apoptosis Detection Kit I (556547; BD Biosciences, San Jose, CA, USA). After two washes with cold PBS, cells were resuspended in 100 µl of 1X Binding Buffer and incubated with 5 µl of FITC Annexin V and 5 µl of propidium iodide (PI) for 15 min at room temperature in the dark. Subsequently, 400 µl of 1X Binding Buffer was added, and samples were analysed within 1 h using a BD Accuri C6 Plus flow cytometer (BD Biosciences, San Jose, CA, USA). Fluorescence signals were acquired in the FITC (fluorescein isothiocyanate) and PE (phycoerythrin) channels, and the data were analysed using the BD Accuri C6 Plus software.

Cell cycle analysis. Cells were cultured in T-25 flasks at a density of 1×10^5 cells/flask. After 2 days of culture, cells were harvested by trypsinisation using 0.25% Trypsin-EDTA and centrifuged at 1 500 rpm for 5 minutes. Following PBS washes, cells were fixed with cold 70% ethanol at 4 °C for 30 minutes. After fixation, cells were treated with RNase A (100 µg/ml), then add 100 µl RNase A and incubate at 37 °C for 30 minutes. Cells were washed again and stained with 5 µl PI solution (50 µg/ml) (556547; BD Biosciences, San Jose, CA, USA), following that the cells were incubated for 15 min, at RT. Cell cycle phases were analysed using the BD Accuri C6 Plus flow cytometer.

Immunostaining. Cells were cultured in 96-well plates at a density of 1×10^3 cells/well. After 2 days of culture, cells were fixed with 4% paraformaldehyde for 30 min and permeabilised using 0.1% Triton X-100 at 4 °C overnight. Cells were incubated with primary antibodies against Pax7 (100516-T32; Sino Biological Inc., Beijing, P.R. China) and Pax3 (100423-T32, Sino Biological Inc., Beijing, P.R. China). After washing, cells were incubated with Alexa Fluor® 488-conjugated Goat Anti-Rabbit antibody (GB25303; Servicebio Technology Co., Ltd., Wuhan, P.R. China) for 1 h at room temperature. Nuclear counterstaining was performed with DAPI for 30 minutes. The cells were washed 3 times with PBS for 10 min each. The expressions of Pax7 and Pax3 were visualised under a fluorescence microscope.

Statistical analysis. Data are presented as mean ± standard deviation (SD) from at least three independent experiments. Statistical analyses were performed using SigmaPlot v11.0 (Systat Software Inc., San Jose, CA, USA). Differences among groups were analysed by one-way ANOVA followed by Tukey's post hoc test. Statistical significance was set at $P < 0.05$.

RESULTS

Cell proliferation assay. After a three-week culture, bSCs expanded from bovine muscle tissue. These bSCs were used for sub-culturing and assessing the *in vitro* proliferative capacity by determining the *in vitro* expansion, changes in cell density, and cell viability. As shown in Figure 1, bovine satellite cells (bSCs) exhibited fibroblast-like morphology during *in vitro* expansion, characterised by large, flat, and spindle-shaped cells. An increase in cell density was observed from passage 1 to passage 21 (Figure 2). Cell viability was assessed using the WST-1 assay, based on optical density (OD) measurements. bSCs at passage 4 demonstrated a higher OD value (1.43 ± 0.04) compared to those at passage 1 (0.95 ± 0.01), indicating increased viability. However, from passage 7 (1.03± 0.01) onward, the OD values progressively declined,

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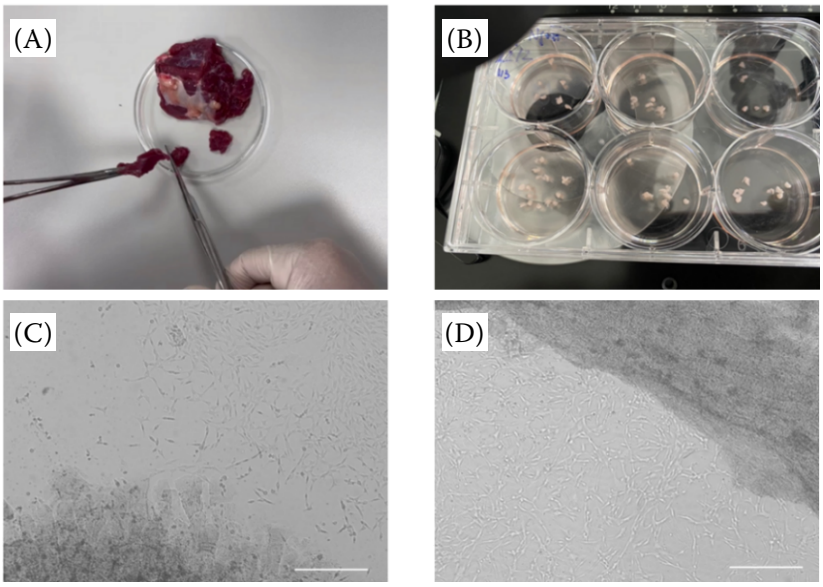

Figure 1. Primary bovine satellite cells (bSCs) culture
(A,B) Bovine muscle tissues were prepared for cell culture. (C,D) Cells expanded from tissue. The cells exhibited fibroblast-like morphology such as large, flat, elongated shapes. Scale bar = 223.64 μm

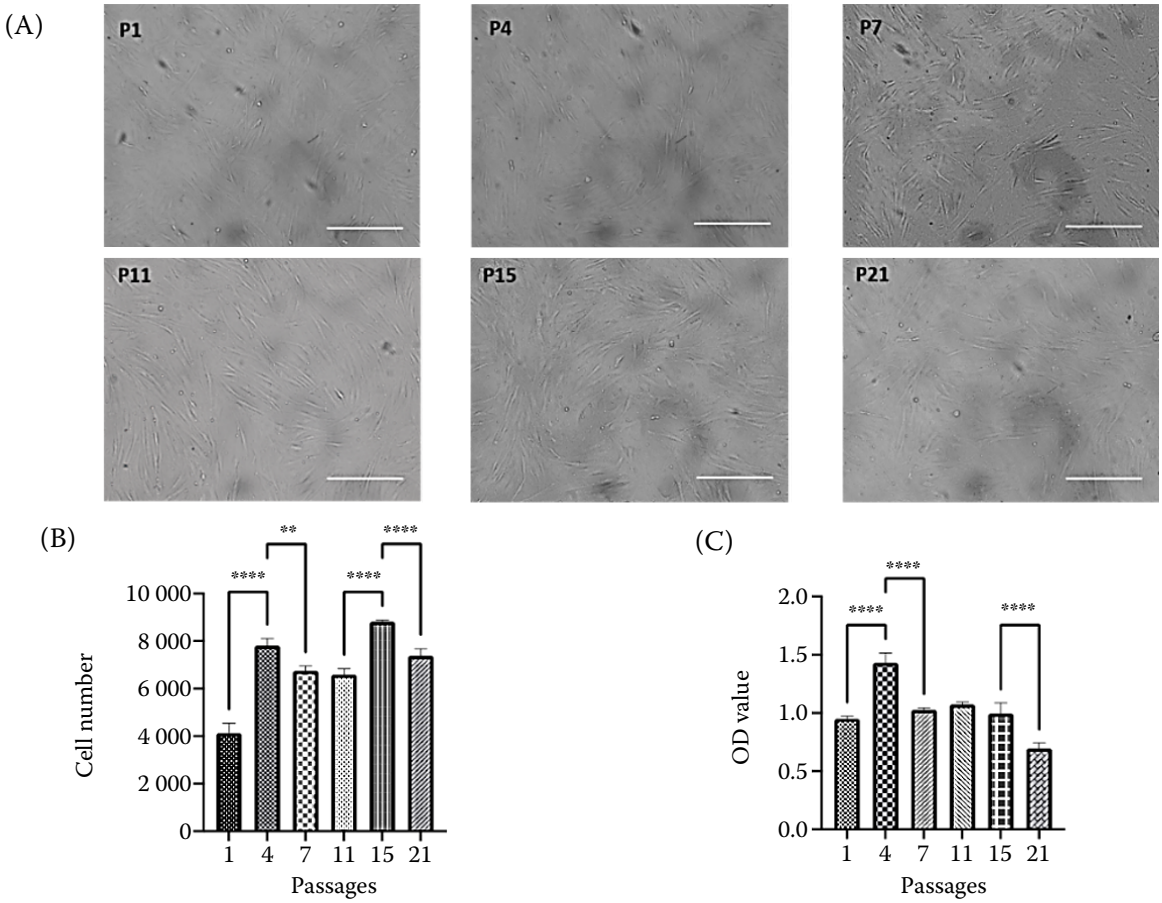

Figure 2. Changes in bovine satellite cells (bSCs) proliferation during *in vitro* expansion
(A) Microscopic images of cells from passage 1 to passage 21. (B) Cell density analysis using the Cell Cycle App. of Cytell microscope. (C) Cell viability assessed by WST-1 assay through optical density (OD) measurement
Significant at $^{**}P < 0.01$, $^{****}P < 0.000\ 1$; scale bar = 223.64 μm

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reaching 0.70 ± 0.05 at passage 21. These results suggest a gradual reduction in the proliferative capacity of bSCs during extended *in vitro* culture.

Cell viability and apoptosis analysis. Flow cytometry was applied to estimate cell viability and apoptosis. In early passages, bSCs maintained high viability, reaching 95.93% at passage 1 and 94.24% at passage 7 (Figure 3). This viable ratio was decreased in bSCs from the late passages. This reduction suggested that bSC viability is adversely affected by prolonged *in vitro* culture. On the other hand, the ratio of apoptotic cells was increased in bSC population under long-term *in vitro* expansion, demonstrated by giving rise from the apoptotic proportion of 4.07% in passage 1 to 14.83% in passage 21.

Cell cycle analysis. The changes in cell cycle progression of bSCs were evaluated by flow cytometry (Figure 4). During *in vitro* expansion, bSCs showed the increase of proportion of cells in the G0/G1 phase from passage 4 (73.03 ± 5.51%), passage 7 (81.36 ± 2.59%), and passage 11 (82.97 ± 1.23%), compared to cells from passage 1 (62.91 ± 5.44%). This increased ratio was continuously observed in bSCs from passage 15 (86.45 ± 0.37%) and passage 21 (88.29 ± 1.06%). In contrast, the proportion of cells in the G2/M phase was reduced from passage 1 (28.95 ± 4.28%) to passage 21 (3.30 ± 0.32 %). These results suggested that bSCs were induced to enter cell cycle arrest phase for long-term *in vitro* expansion.

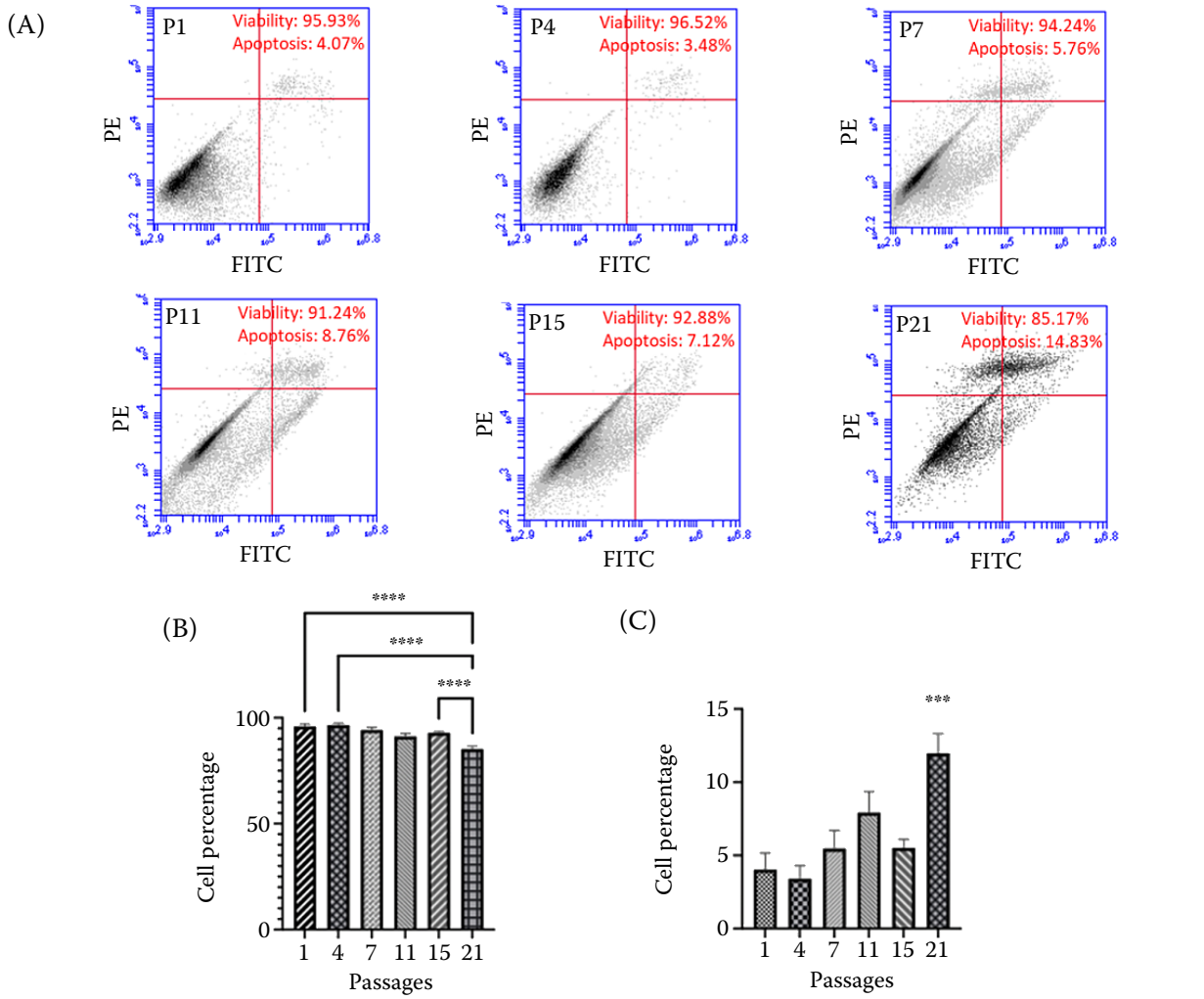

Figure 3. Flow cytometry analysis

(A) Cell viability and apoptosis distributions in flow cytometry panels. (B) The viability proportion. (C) The apoptotic proportion

Significant at ***$P < 0.001$, ****$P < 0.000\ 1$

FITC = fluorescein isothiocyanate channels; PE = phycoerythrin channels

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Cellular morphology evaluation. The morphology of bSCs was assessed by changes in forward scatter (FSC) value, cell area, nuclear area, and nucleo-cytoplasmic ratio. Figure 5A illustrates

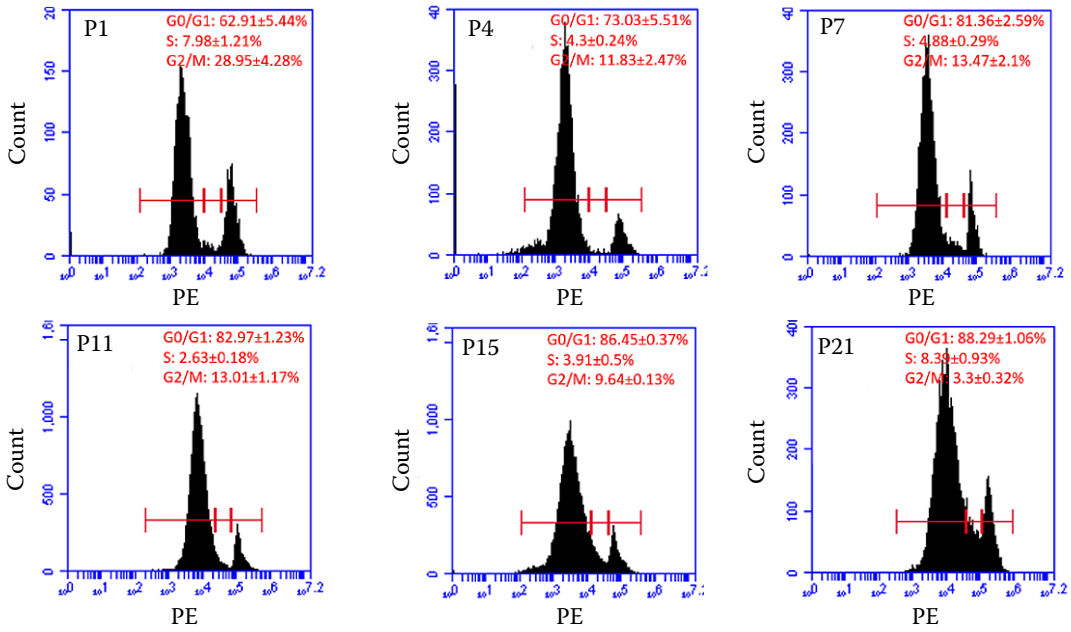

Figure 4. Cell cycle progression analysis
Cycle distributions of cells from passage 1 to passage 21
PE = phycoerythrin channels

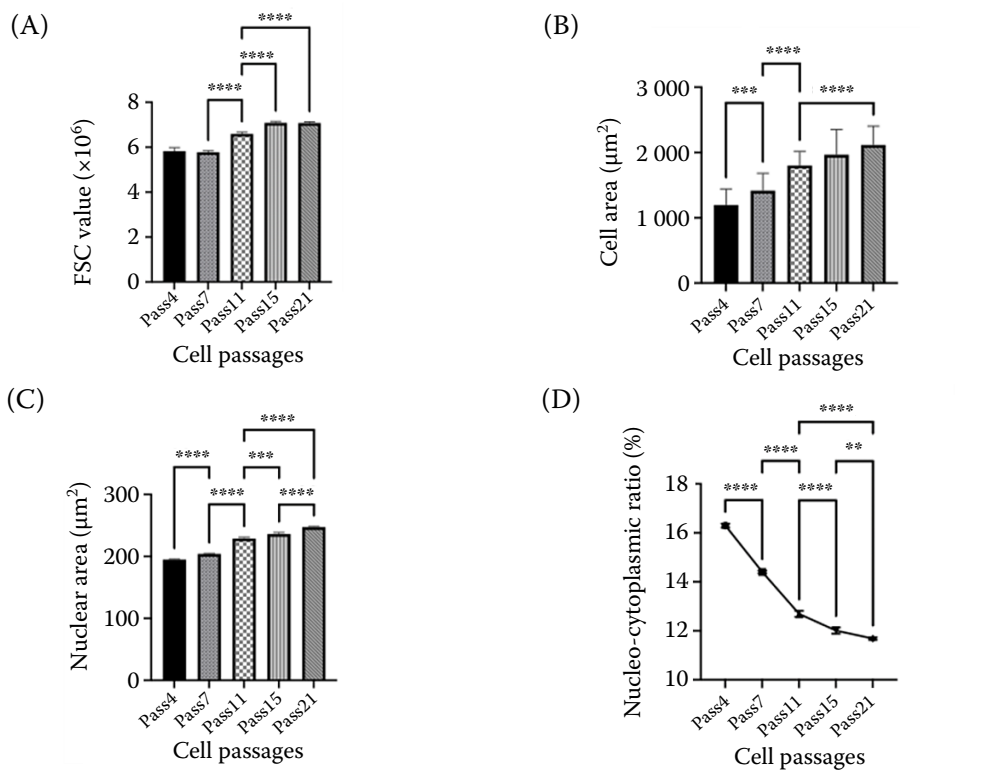

Figure 5. The area changes of cell and nuclei during *in vitro* expansion from passage 4, passage 7, passage 11, passage 15 and passage 21
(A) Forward scatter (FSC) value. (B) Cell area. (C) Nuclear area. (D) Nucleocytoplasmic ratio
Significant at $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.000\ 1$

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an increase in FSC values of bSCs during prolonged *in vitro* expansion. This result was supported by the enlargement of bSCs from passage 4 (1 195.123 ± 35.4 μm^2) to passage 21 (2 116.67 ± 47.82 μm^2) (Figure 5B), which causes an increase in cell area. Moreover, bSCs exhibited the expansion of nuclei from passage 4 (194.75 ± 0.48 μm^2) to passage 21 (247.352 5 ± 0.55 μm^2) (Figure 5C). The alteration in cellular and nuclear morphology led to a reduction in the nucleo-cytoplasmic ratio, which reflects the proportion of nuclear to cytoplasmic area (Figure 5D). Changes in nuclear morphology of bSCs were also observed in Figure 6, where nuclei areas in late passages (15 and 21) were larger than those in early passages (4 and 7). These findings suggest that cytoplasmic expansion surpasses nuclei growth over time, a feature commonly associated with cellular senescence.

The expression of Pax7 and Pax3 proteins, which are specific markers for quiescent and activated satellite cells, respectively, were also evaluated through immunostaining analysis. As illustrated in Figure 7, positive signals for both Pax7 and Pax3 were observed in bSCs at both early (passage 1) and

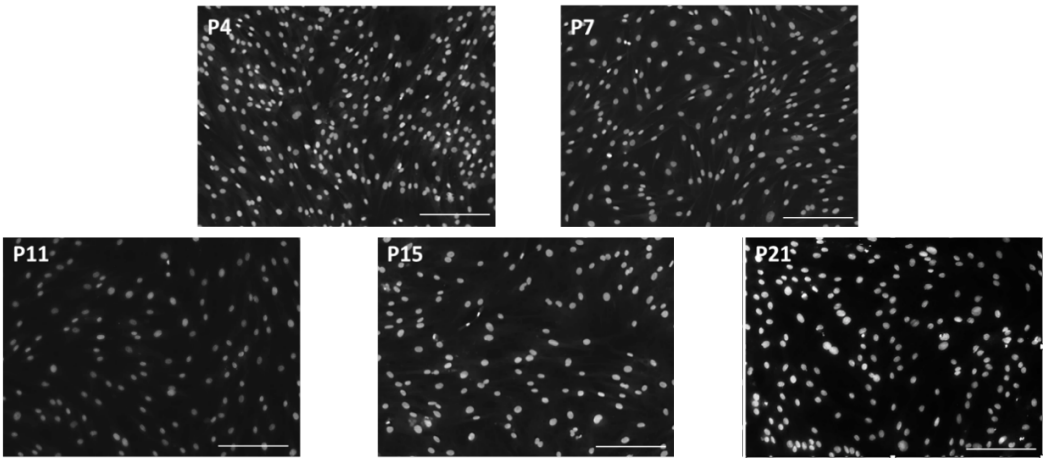

Figure 6. Alterations in nuclear morphology of bovine satellite cells (bSCs) during passaging (P4–P21)
Nuclei were counterstained with DAPI. Scale bar = 223.64 μm

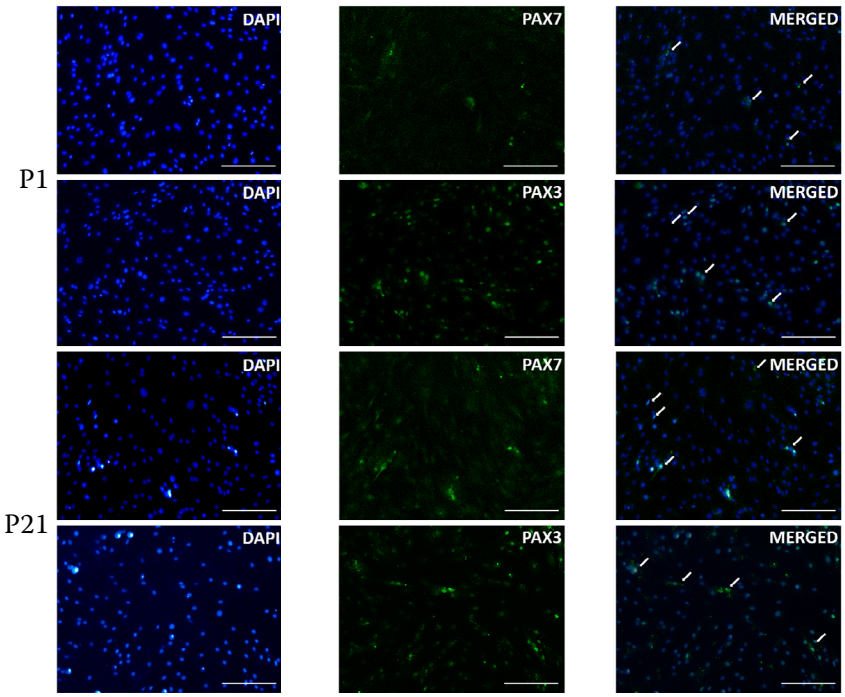

Figure 7. The expression of PAX7 and PAX3 in bovine satellite cells (bSCs) was examined by immunostaining
Nuclei were counterstained with DAPI. The white arrows indicate PAX3 and PAX7 expressions. Scale bar = 223.64 μm

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late (passage 21) stages of culture. These findings suggest that despite prolonged *in vitro* expansion, the cell population retained a subset of satellite cells in both quiescent and activated states, indicating the persistence of myogenic potential over successive passages.

DISCUSSION

In the skeletal muscle development and regeneration, satellite cell proliferation is a crucial biological process (Kaczmarek et al. 2021; Careccia et al. 2023). It describes the activation and division of satellite cells, which are stem cells found in muscles, into myogenic precursor cells, or myoblasts. These cells are capable of self-renewing to maintain the stem cell pool or of undergoing proliferation and differentiation into muscle fibres (Yin et al. 2013; Su et al. 2020). In this study, we found that bSCs exhibited a high proliferative capacity, sustaining expansion for more than 20 passages, indicating their ability to self-renew during *in vitro* culture. This is an important characteristic of bSCs for studies on cultured meat production (Park et al. 2023; Kim et al. 2024).

In healthy animal tissues, the balance of terminal differentiation and cell loss determines the proliferation of progenitor cells. Cells can endure replicative senescence in response to improper growth signals or after undergoing numerous cell divisions (Kang et al. 2024). Senescent cells accumulate in mammalian tissues throughout aging and age-related illnesses, most likely causing the unavoidable loss of tissue function with aging (Sorrenti et al. 2023). Under *in vitro* conditions, cytoplasmic enlargement, increased nuclei size, and elevated cell cycle arrest are key indicators of cellular senescence (Campisi 1997; Son et al. 2019). The present work found that the number of apoptotic cells increases in late passages. bSC proliferation was reduced, which occurred due to an increased ratio of cells in the G0/G1 phase, leading to an induction of cells entry into the arrest phase in the cell cycle progression. These changes were considered as the replicative senescent properties in bSCs (Pizzul et al. 2023).

Previous studies have shown that satellite cells derived from different animal species exhibit limited proliferative capacity during prolonged *in vitro* culture. Satellite cells isolated from cattle breeds such as Jeju black cattle, Hanwoo, and Holstein were maintained up to passage 12; however, their proliferative activity progressively declined, as evidenced by the inability to achieve confluency at day 6 of passage 12 and the marked reduction in nuclear number during serial passaging (Park et al. 2023; Kim et al. 2024). Similarly, porcine satellite cells were reported to sustain proliferation for only up to seven passages under long-term culture conditions (Han et al. 2023b; Ren et al. 2024). Human satellite cells demonstrated the ability to expand beyond 10 passages, although their proliferation rate remained lower than that observed in mouse satellite cells (Benedetti et al. 2021). These findings indicate that limited passage number and reduced proliferative capacity are major constraints in the development of large-scale cultured meat production systems. These studies indicate that satellite cells derived from different animal species exhibit distinct proliferative capacities during *in vitro* culture. In the present study, although bSCs isolated from Brown Vietnamese cattle displayed certain senescence-associated characteristics during serial passaging, they maintained substantial proliferative potential *in vitro*. These findings suggest that bSCs from Brown Vietnamese cattle may represent a promising cell source for bovine cultured meat research and production.

The adult skeletal muscle stem cells known as satellite cells are functionally heterogeneous, which means that they are a diverse population with a range of characteristics and the ability to regenerate. The recent data showed that their origin, gene expression profiles, cell cycle behaviour, stemness, and capacity for self-renewal or differentiation are all associated with this heterogeneity (Yin et al. 2013). In adult skeletal muscle, the expression of the paired domain transcription factors Pax7 and Pax3 were found in most satellite cells (Mousavi and Jasmin 2006; Yin et al. 2013; Ulrich et al. 2025). Pax7 plays a major role in maintaining the undifferentiated state of satellite cells and expresses exclusively in all quiescent and proliferating satellite cells in a variety of species, including zebrafish, salamanders, frogs, mice, pigs, chicks, and humans (Al Tanoury et al. 2020), while Pax3 is necessary for maintaining the migration of these cells in the somite and their migration to the myogenic sites (Wang et al. 2021). In this investigation, the expression of Pax7 and Pax3 proteins was detected in bSCs from the early

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passage and the late passage. This result demonstrated that a population of Pax3/Pax7-expressing progenitor cells was maintained in bSCs during long-term *in vitro* expansion. These cells could be considered as a source of myogenic cells that are crucial for the creation of skeletal muscle or cultured meat production (Relaix et al. 2005; Hicks et al. 2023).

CONCLUSION

In this study, bSCs isolated from the muscle tissue of Brown Vietnamese cattle exhibited high proliferative capacity under *in vitro* culture conditions. The maintenance of progenitor cells within the bSC population was confirmed by the continued expression of specific markers, including Pax7 and Pax3. However, the emergence of cells displaying senescent features poses a limitation to the expansion of bSCs. Future studies should focus on optimising culture conditions to enhance bSC proliferation and facilitate large-scale cell production for bovine cultured meat research.

Conflict of interest

The authors declare no conflict of interest.

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