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Changes in the taste and textural attributes of apples in response to climate change

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The effects of climate change on the taste and textural attributes of foods remain largely unknown, despite much public interest. On the basis of 30–40 years of records, we provide evidence that the taste and textural attributes of apples have changed as a result of recent global warming. Decreases in both acid concentration, fruit firmness and watercore development were observed regardless of the maturity index used for harvest date (e.g., calendar date, number of days after full bloom, peel colour and starch concentration), whereas in some cases the soluble-solids concentration increased; all such changes may have resulted from earlier blooming and higher temperatures during the maturation period. These results suggest that the qualities of apples in the market are undergoing long-term changes.

Assessing the impacts of future climate change on fruit production allows researchers to predict changes in yield^{1,2} and in regions suitable^{3–5} for fruit production. Warming temperatures are already affecting phenology in many species of fruit trees. Many phenological time-course trends have been studied in fruit trees, including in Europe^{6–10}, North America¹¹, Asia^{12,13} and the Southern Hemisphere^{14,15}, and almost all of these trends are consistent with warming temperatures. In addition, agricultural changes related to regional climate change, such as alterations in cereal yield^{16–19} and wine rating²⁰, have been reported, but these studies have been limited to those in which data are readily available.

The apple (*Malus domestica* Borkh.) is an important and popular fruit, with a global production of about 60 million tonnes, ranking it third in worldwide fruit production²¹. Apples are commonly consumed as unprocessed fresh fruit, and fresh apples are available worldwide all year round. Good taste and texture in fresh apples are therefore important and well-established issues.

Previous studies have shown that long-term climate change has had a large impact on the alteration of phenology in apple cultivation. Flowering date has advanced by 2.2 days per decade in Germany²². Fujisawa and Kobayashi¹² indicated that the timings of bud break and flowering of apples were largely affected by the temperature in March and March–April, respectively, in Japan. In South Africa, Grab and Craparo¹⁵ reported that not only temperature but also rainfall during winter and early spring are important factors in the advance of the full bloom dates of apple.

The qualities of fresh apples are also influenced by air temperatures during the fruit growing season^{23–27}. Previous studies have speculated that fruit softening might be affected by the number of heating degree days²⁸. Hence, it is important to investigate whether recent warming has altered qualities such as the taste and textural attributes in fresh apples.

The effects of climate change are difficult to identify in aggregate agricultural statistics because of the influence of non-climate factors, especially technological improvements and breeding²⁹. As yet, there have been no reports of changes in the taste and textural attributes of foods—and especially fruits—as a result of climate change, although both of these qualities are important in maintaining high food quality and consumer interest.

Detecting long-term trends in these qualities requires data from apple orchards in which there have been no alterations in cultivars and management practices for extended periods. The establishment of high-precision measurement methods is also required. The objective of this study was to determine whether the attributes of taste and texture in apples have undergone changes as a result of recent climate change by conducting long-term (30–40 years) observations in two apple orchards in Japan.

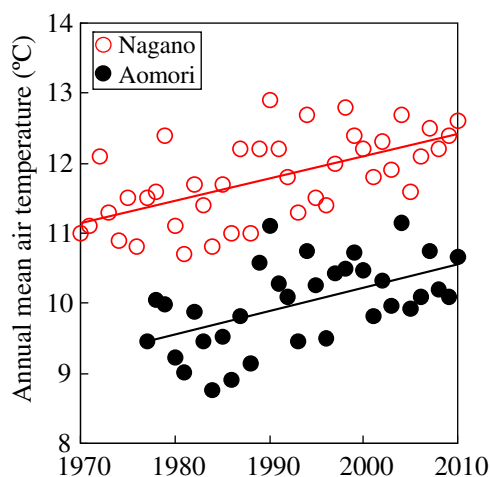


Figure 1 | Trends in meteorological values. The time series of annual air temperature in Nagano (1970–2010) and Aomori (1977–2010) with linear regression lines.

Results

Trends in climate and phenology. We carried out cultivation trials in Japan for the ‘Fuji’ apple in Nagano Prefecture (between 1970 and 2010) and Aomori Prefecture (between 1975 and 2010), and for the ‘Tsugaru’ apple in Nagano (between 1980 and 2010). ‘Fuji’ is currently the leading apple cultivar in the world³⁰. ‘Tsugaru’ is the second most common apple in Japan, but it ripens about 2 months earlier than ‘Fuji’. Nagano and Aomori Prefectures are Japan’s top two apple-producing regions, accounting for more than 70% of total apple production³¹.

During the 40-year period of apple cultivation, there were significant correlations between time and annual mean air temperatures (Fig. 1; Supplementary Table S1). The annual mean air temperature rose by 0.31°C and 0.34°C per decade in Nagano and Aomori, respectively, but no significant correlations with time were found for annual precipitation, sunshine duration and solar radiation.

Supplementary Table S1 also shows the temporal trends for the respective periods closely related to bud break (March) and blooming (March–April). Trends for precipitation from winter to spring, which positively correlated with flowering date¹⁵, were also examined. The mean air temperature exhibited a significant increasing trend ($P < 0.05$) except in March–April in Aomori ($P < 0.1$). In general there were no significant long-term trends in precipitation or sunshine duration (solar radiation), but the precipitation in March

and in December–April and the sunshine duration in March–April exhibited a significant increase in Nagano.

Supplementary Table S2 shows the temporal trends of mean air temperature, precipitation and sunshine duration (solar radiation) during the fruit maturation periods, assuming that the maturation periods corresponded to the last 70 days before harvest of ‘Fuji’ (100–170 days after full bloom in Nagano, 110–180 days in Aomori) and the 30 days before harvest of ‘Tsugaru’ (90–120 days after full bloom). There were increasing temporal trends in mean air temperature during the maturation periods of ‘Fuji’ ($P < 0.05$) and of ‘Tsugaru’ ($P < 0.1$).

The bud break and full bloom dates of apples advanced earlier in both cultivars in both areas (Fig. 2; Supplementary Table S3). The temporal trends were significant ($P < 0.05$) for the bud break dates of ‘Fuji’ and ‘Tsugaru’ and for the full bloom dates of ‘Fuji’ (in Nagano). Phenological dates advanced by 1.0–2.3 days per decade.

Temporal trends in taste and textural attributes. The usual harvest season of ‘Fuji’ starts on 1 November in both Nagano and Aomori; the acid concentration, firmness and watercore rating of ‘Fuji’ were recorded on this date throughout the study period. Decreases were observed in all three attributes in both areas (Fig. 3; Table 1). Conversely, there was a progressive increase in the soluble-solids concentration, by which the sugar concentration is commonly elevated. Testing was conducted in ‘Tsugaru’ on 1 September, which is the usual date when harvest starts for this cultivar in Nagano, and similar trends were observed. Overall, for both cultivars, decreasing temporal trends were recorded in the acid concentration (0.16–0.20 g L⁻¹ per decade), firmness (0.04–0.33 kg) and watercore rating (0.17–0.38), whereas the soluble-solids concentration increased by 0.20–0.28°Brix per decade. Although the magnitude of the changes in both cultivars was not high, most of the changes were significant. These results suggest that the taste and textural attributes of both cultivars changed during the study period.

The choice of which maturity index to use for harvest can be influenced by the marketing strategy of the apple producer. Indexes such as calendar date, number of days after full bloom, fruit peel colour and the disappearance of starch are commonly used to determine the harvest dates of ‘Fuji’³² and ‘Tsugaru’ apples. To assess changes in the taste and textural attributes of apples in the actual circulation market, the ratings of taste and textural attributes, as judged by these indexes, were calculated.

Calendar date is used when apples are shipped on a predetermined date each year by contract with vendors. Furthermore, calendar date is useful in very late maturing cultivars such as ‘Fuji’ to avoid frost

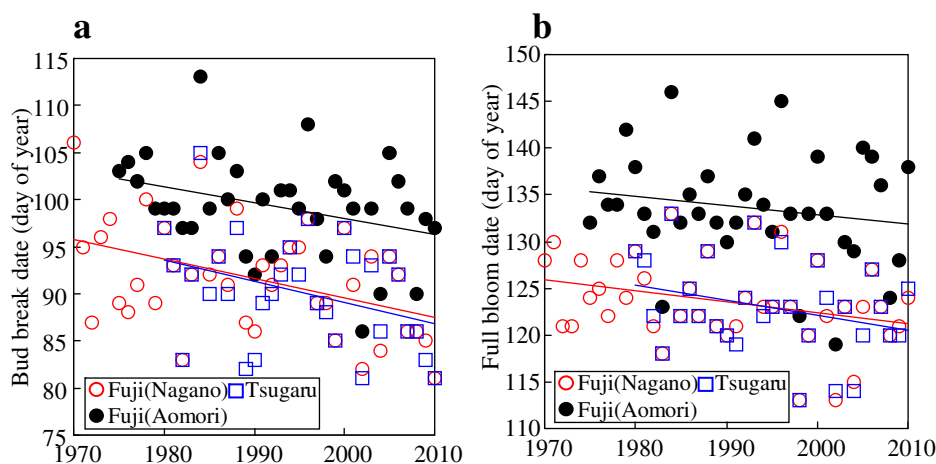


Figure 2 | Trends in phenological changes. Time series of (a) bud break date and (b) full bloom date. Lines represent linear regressions.

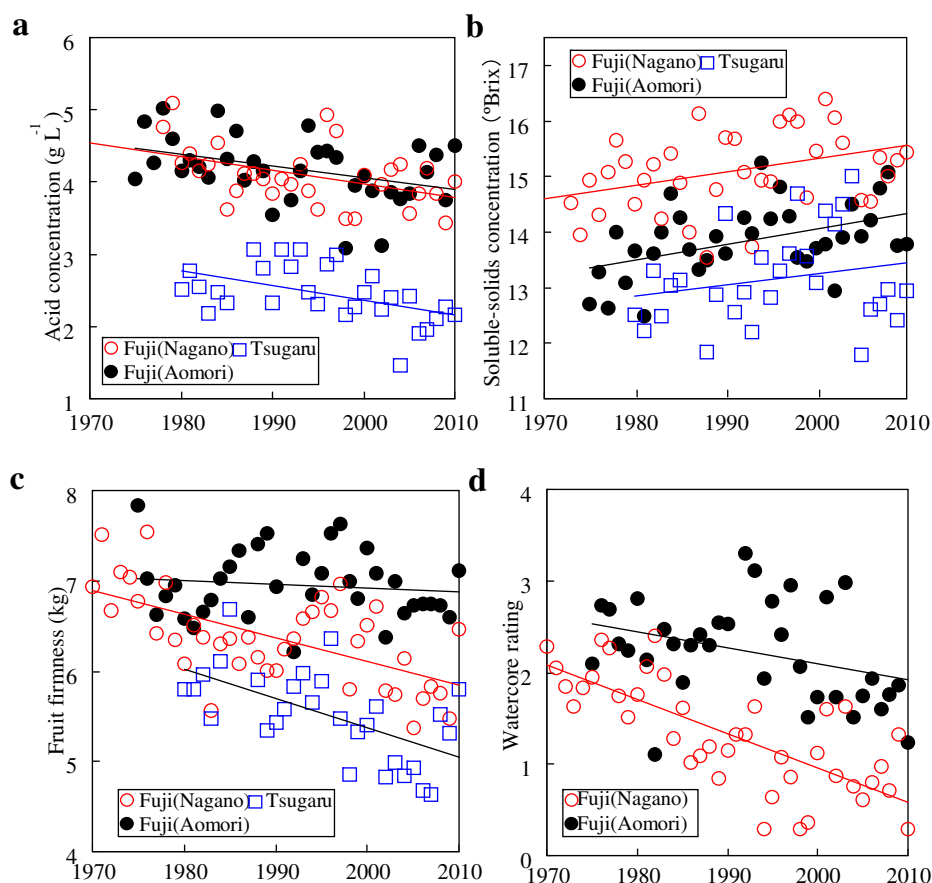


Figure 3 | Trends in taste and textural attributes of apples. Time series of (a) acid concentration, (b) soluble-solids concentration, (c) fruit firmness and (d) watercore rating recorded on 1 November (‘Fuji’) or 1 September (‘Tsugaru’). Lines represent linear regressions.

injury, irrespective of the ripening status. However, because flesh maturity depends on blooming date and air temperature, the flesh maturity level of fruits harvested according to calendar date varies from year to year.

The number of days after full bloom and the peel ground colour are closely related to flesh maturity. The former index is associated with the regional climate, with fewer days being required in cooler areas than in warmer areas³³. ‘Fuji’ can be harvested at approximately 180 days after full bloom in Nagano and 170 days after full bloom in Aomori, whereas ‘Tsugaru’ apples are usually harvested 120 days after full bloom in Nagano. The recommended ground colour rating (the base peel colour before an apple turns red) for harvest of ‘Fuji’ and ‘Tsugaru’ is 3 in all areas. Measuring starch concentration is particularly useful for harvesting apples for storage because of the need for accurate maturity assessment. The recommended starch concentration rating for harvest is 2. The blush indicates the redness of the fruit peel, which is an important quality attribute in competitive apple markets; a rating level of 3 is recommended for harvest. All of the rating methods are described in more detail in the Methods section.

The correlation coefficients between the date when these maturity indexes reached the recommended values and time are shown in Supplementary Table S4. The trends in these indexes were unclear, whereas the trend in the case of number of days after full bloom in Nagano was clear; this index displayed axiomatic earlier trends in parallel with the earlier full bloom dates (Supplementary Table S3).

The trends in the taste and textural attributes of the fruit harvested according to each maturity index are shown in Table 1. Decreases were observed in acid concentration, firmness and watercore ratings on the benchmark days after full bloom. The correlation coefficients

were significant, with the exception of that for the firmness of ‘Fuji’ in Aomori. The observed changes showed a trend similar to those observed from the calendar date basis.

Irrespective of significance, the changes in acid concentration, fruit firmness and watercore rating, as assessed by the benchmark ratings for blush, ground colour and starch concentration, also showed similar tendencies: namely, they did not vary regardless of the maturity index used. Soluble-solids concentration assessed by using any of the maturity indexes exhibited increasing trends; however the trends were not significant, with the exception of ‘Fuji’ assessed by using calendar date, ground colour and starch concentration.

The average change rates per decade in the taste and textural attributes of both cultivars, as assessed by using the five maturity indexes, including calendar date, were -0.16 g L^{-1} for acid concentration, 0.21°Brix for soluble-solids concentration, -0.18 kg for firmness and -0.28 for watercore rating (Table 1).

Discussion

The analysis showed advances in the bud break and full bloom dates for both apple cultivars. Fujisawa and Kobayashi¹² found negative correlations between bud break date and mean air temperature in March as well as between flowering date and mean air temperature in March–April in the main apple-producing district in Japan. By comparing the phenological response to the long-term trend in air temperatures with the response to year-to-year fluctuations in air temperatures, they revealed that long-term changes in the phenology of apples are attributable to long-term changes in temperature.

In our study, the mean air temperatures in March and in March–April increased (Supplementary Table S1). Strong negative correlations



Table 1 | Summary of mean and temporal changes in taste and textural attributes of apples assessed by using five maturity indexes (calendar date, number of days after full bloom, blush rating, ground colour rating and starch concentration rating) in ‘Fuji’ in Nagano and Aomori and in ‘Tsugaru’ in Nagano

Maturity index	Cultivar	Location	Mean (unit)	<i>r</i>	<i>P</i>	Trend (unit)	SE	<i>n</i>
			(g L ⁻¹)			(g L ⁻¹ year ⁻¹)		
Acid concentration								
CD (1 Nov.)	Fuji	Nagano	4.1	-0.450	0.010	-0.019	0.007	32
CD (1 Nov.)	Fuji	Aomori	4.2	-0.384	0.023	-0.016	0.007	35
CD (1 Sep.)	Tsugaru	Nagano	2.5	-0.472	0.010	-0.020	0.007	29
DAFB (180)	Fuji	Nagano	4.1	-0.415	0.018	-0.016	0.006	32
DAFB (170)	Fuji	Aomori	4.2	-0.393	0.020	-0.014	0.006	35
DAFB (120)	Tsugaru	Nagano	2.5	-0.411	0.027	-0.014	0.006	29
GC (3)	Fuji	Nagano	4.2	-0.386	0.029	-0.016	0.007	32
BL (3)	Fuji	Nagano	4.1	-0.316	0.078	-0.015	0.008	32
BL (3)	Fuji	Aomori	4.2	-0.191	0.360	-0.012	0.013	25
SC (2)	Fuji	Aomori	4.2	-0.435	0.009	-0.017	0.006	35
						Average	-0.016	
Soluble-solids concentration			(°Brix)			(°Brix year ⁻¹)		
CD (1 Nov.)	Fuji	Nagano	15.1	0.364	0.025	0.024	0.010	38
CD (1 Nov.)	Fuji	Aomori	13.8	0.459	0.006	0.028	0.009	35
CD (1 Sep.)	Tsugaru	Nagano	13.2	0.219	0.254	0.020	0.017	29
DAFB (180)	Fuji	Nagano	15.0	0.294	0.074	0.018	0.010	38
DAFB (170)	Fuji	Aomori	13.8	0.329	0.054	0.024	0.013	35
DAFB (120)	Tsugaru	Nagano	13.0	0.076	0.694	0.006	0.015	29
GC (3)	Fuji	Nagano	14.8	0.346	0.033	0.024	0.011	38
BL (3)	Fuji	Nagano	15.0	0.226	0.171	0.016	0.011	38
BL (3)	Fuji	Aomori	13.5	0.189	0.364	0.016	0.017	25
SC (2)	Fuji	Aomori	13.9	0.440	0.008	0.036	0.013	35
						Average	0.021	
Fruit firmness			(kg)			(kg year ⁻¹)		
CD (1 Nov.)	Fuji	Nagano	6.4	-0.610	0.000	-0.026	0.005	41
CD (1 Nov.)	Fuji	Aomori	7.0	-0.119	0.496	-0.004	0.006	35
CD (1 Sep.)	Tsugaru	Nagano	5.5	-0.595	0.001	-0.033	0.009	29
DAFB (180)	Fuji	Nagano	6.4	-0.587	0.000	-0.023	0.005	41
DAFB (170)	Fuji	Aomori	7.0	-0.040	0.820	-0.001	0.006	35
DAFB (120)	Tsugaru	Nagano	5.6	-0.467	0.011	-0.022	0.008	29
GC (3)	Fuji	Nagano	6.5	-0.577	0.000	-0.027	0.006	40
BL (3)	Fuji	Nagano	6.4	-0.537	0.000	-0.024	0.006	41
BL (3)	Fuji	Aomori	7.2	-0.404	0.045	-0.019	0.009	25
SC (2)	Fuji	Aomori	6.9	-0.204	0.240	-0.007	0.006	35
						Average	-0.019	
Watercore rating						(year ⁻¹)		
CD (1 Nov.)	Fuji	Nagano	1.1	-0.56	0.001	-0.034	0.005	30
CD (1 Nov.)	Fuji	Aomori	2.2	-0.34	0.043	-0.017	0.008	35
DAFB (180)	Fuji	Nagano	1.0	-0.60	0.000	-0.039	0.010	30
DAFB (170)	Fuji	Aomori	2.1	-0.34	0.044	-0.023	0.012	35
GC (3)	Fuji	Nagano	1.9	-0.543	0.002	-0.032	0.009	30
BL (3)	Fuji	Nagano	1.9	-0.730	0.000	-0.046	0.008	30
BL (3)	Fuji	Aomori	1.6	-0.258	0.213	-0.020	0.016	25
SC (2)	Fuji	Aomori	2.3	-0.206	0.235	-0.012	0.010	35
						Average	-0.028	

Pearson correlation coefficient between each quality value and time (*r*), *P* value of *r* (*P*), slope of linear regression (Trend), standard error of the Trend (SE) and number of observation years (*n*). Maturity index column denotes calendar date (CD), number of days after full bloom (DAFB), ground colour rating (GC), blush rating (BL), and starch concentration rating (SC). Benchmark value is given in parenthesis in the maturity index column. Significant *P* values are in bold (*P* < 0.05).

(*P* < 0.001) were found between temperature and the phenological events (Fig. 4; Supplementary Table S5). These results were similar to the findings by Fujisawa and Kobayashi¹², suggesting that the phenological advances in our study were caused by recent warming in the experimental orchard.

The precipitation in March and in December–April and the sunshine duration in March–April exhibited a significant increase in Nagano (Supplementary Table S1), but a significant correlation with phenological dates was recorded only in precipitation in December–April (Supplementary Table S5). Total rainfall in winter–early-spring, as opposed to temperature, is positively correlated with full

bloom dates of apple trees in South Africa¹⁵. In our study, total precipitation in December–April exhibited a significant increase in Nagano (Supplementary Table S1), and the full bloom date was negatively correlated with rainfall; this finding was not consistent with the results in South Africa. The relationship between precipitation and blooming may not be simple in heavy-snow regions such as Nagano.

Our results showed that the taste and textural attributes of apples harvested on 1 November (‘Fuji’) or on 1 September (‘Tsugaru’) changed during the long-term observation period (Fig. 3; Table 1). The acid concentration, firmness and watercore rating all decreased,

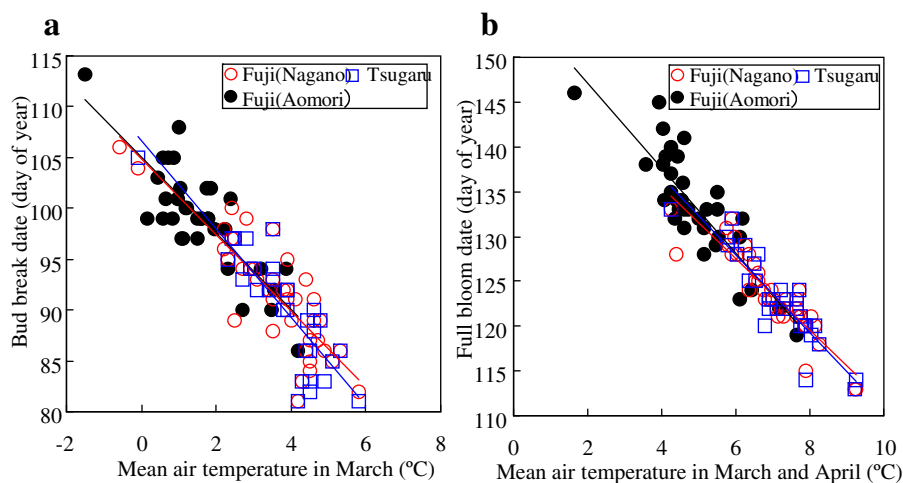


Figure 4 | Phenological responses to temperature. Relationship between (a) bud break date and mean air temperature in March and (b) full bloom date and mean air temperature in March–April. Lines represent linear regressions.

whereas the soluble-solids concentration increased. Here, it should be noted that the acid concentration of fruit is strongly correlated with the sensorial perception of sourness³⁴, and that watercore rating is linked to storage stability³⁵. The correlations between firmness and hardness³⁶ and between soluble-solids concentration and sweetness³⁴ are weaker than that between acid concentration and sourness; nevertheless, firmness and soluble-solids concentration have generally been used as the respective indicators of hardness and sweetness. Because the soluble-solids concentration increased and the acid concentration decreased, the soluble-solids to acid ratio, another indicator of sweetness³⁴, significantly increased (‘Fuji’ in Nagano, $P = 0.001$; ‘Fuji’ in Aomori, $P = 0.000$; ‘Tsugaru’, $P = 0.017$).

With advancing maturity, apples show gradual decreases in acid concentration and firmness and increases in soluble-solids concentration. The observed trends in fruit taste and textural attributes on the benchmark calendar date seemed to be partly ascribable to the earlier fruit maturity derived from the earlier blooming dates, except in the case of watercore rating, because apples grown under high temperatures seldom exhibit watercore disorder³⁷. Instead, Yamada et al.²⁵ demonstrated that low temperature directly causes watercore disorder in apples without influencing the level of fruit maturity.

The mean air temperatures during the maturation periods of ‘Fuji’, exhibited a significantly increasing trend ($P < 0.05$), and that for ‘Tsugaru’ showed an increasing trend ($P < 0.1$, Supplementary Table S2). Previous studies using temperature-controlled chambers have indicated that high temperatures during the maturation (pre-harvest) period can reduce the acid content^{24,25}, firmness²⁴ and watercore rating^{25,26}. Therefore, the increase in temperatures during the maturation period is probably another reason for the observed decrease in the acid concentration, firmness and watercore rating of fruits harvested on the benchmark calendar date. In contrast, previous studies have shown that the soluble-solids concentration is unaffected by temperature^{24,25,27}.

Because determination of harvest date on the basis of the number of days after full bloom may cancel out the effect of the advancement of fruit maturity by earlier blooming, the effects of air temperature during the maturation periods on the taste and textural attributes of fruit judged by the number of days after full bloom can be detected more clearly than those judged by calendar date. Both acid concentration and watercore rating in fruit, as judged by the number of days after full bloom, showed significant decreasing temporal trends, and firmness also exhibited a significant decreasing trend for the two cultivars in Nagano (Table 1). The relationship between these attributes and air temperature during the maturation period is shown in Figure 5 and Supplementary Table S6. Acid concentration, fruit

firmness of ‘Fuji’ in Nagano and watercore rating were significantly negatively correlated with mean temperature during the maturation period. These relationships were in agreement with those shown in previous experiments in temperature-controlled chambers^{24,26}. Therefore, the temporal trends of these attributes assessed by the number of days after full bloom (Table 1) were probably a result of increasing air temperature during the maturation period (Supplementary Table S2).

The residual errors of the regression formulas shown in Figure 5 were further analyzed by separately comparing those from before 1990 with those after 1991. No significant differences between the mean values of the residual errors from before 1990 and after 1991 were found in any parameters of fruit quality (Supplementary Table S6). This result suggests that factors other than air temperature have little effect on the long-term trends.

A strong correlation ($P < 0.001$) between watercore rating and temperature during the maturation period was found (Fig. 5, Supplementary Table S6). Watercore is characterized by water-soaked and translucent flesh tissues and is prevalent in cultivars such as ‘Fuji’ but absent in ‘Tsugaru’. To avoid the development of watercore, which causes internal browning during storage³⁵, ‘Fuji’ apples for storage must be harvested before being fully ripe. If the harvest time of ‘Fuji’ could be delayed because of decreased watercore development by warming, this could contribute to a decrease in the acid concentration and an increase in the soluble-solids concentration of stored apples.

Our findings suggested that harvest date, as judged by four (blush, ground colour, starch concentration and calendar date) of the five maturity indices, did not show significant temporal trends (Supplementary Table S4). These results support the findings of a study conducted in the Mediterranean region⁸, which reported an advance in the unfolding time of apple leaves but no significant change in fruiting date.

It is well known that anthocyanin levels, which are responsible for the redness in apple peel blush, are inversely related to field temperature³⁸; anthocyanin accumulation in ‘Fuji’ decreases at temperatures greater than 25°C³⁹. Starch degradation is also inhibited by high temperatures during maturation²⁵. Our results were in accordance with these findings; temperatures during maturation were positively correlated with number of days from full bloom to the dates when the blush or starch concentration ratings reached the benchmark values (Supplementary Table S7).

However, no significant temporal trends were found in the blush ratings or starch concentration (Supplementary Table S4). This may be because a slower advance toward the benchmark maturity index

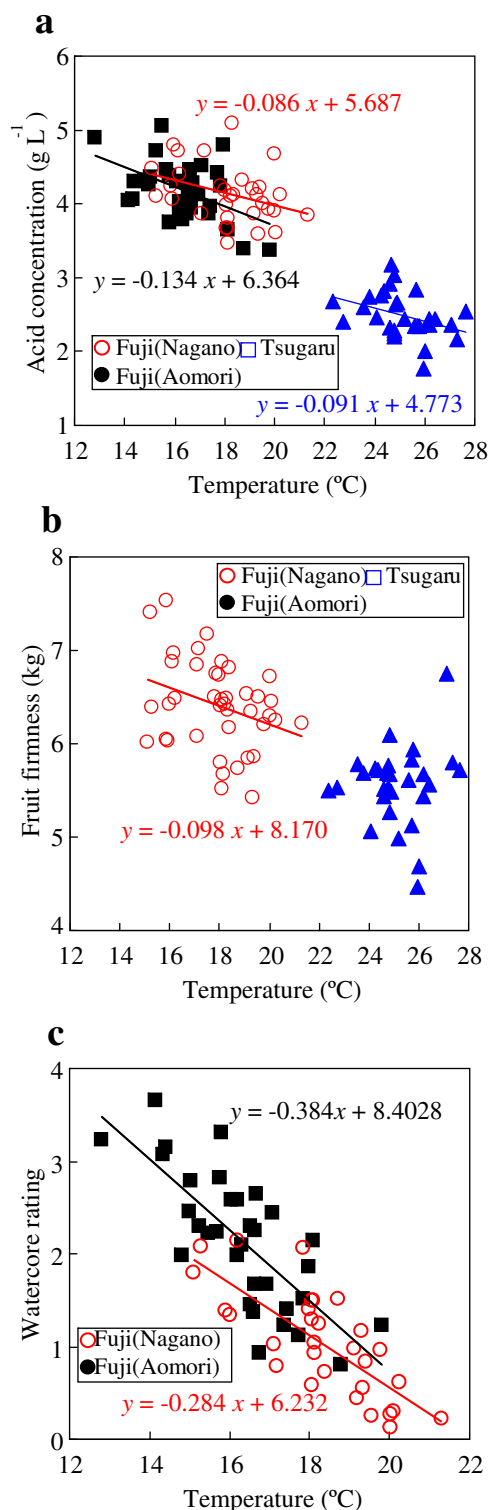


Figure 5 | Responses of taste and textural attributes or maturity indexes in apples to mean temperatures during the maturation period, which is 110–180 (‘Fuji’ in Nagano), 100–170 (‘Fuji’ in Aomori) or 90–120 (‘Tsugaru’) days after full bloom. Relationships between mean temperature during the maturation period and (a) acid concentration, (b) firmness in Nagano and (c) watercore rating of fruit on 180 (‘Fuji’ in Nagano), 170 (‘Fuji’ in Aomori) and 120 (‘Tsugaru’) days after full bloom, all of which showed significant temporal trends (Table 1). Lines represent linear regressions with regression formulae.

values caused by warming offset the advance in fruit maturity induced by the earlier blooming. Menzel⁶ previously reported that higher spring temperatures advanced leaf colouring as a result of earlier leafing, whereas warmer temperatures in autumn could delay it. This may be true for the apple peel as well: high temperatures during spring could advance the peel blush rating as a result of earlier blooming, but warmer temperatures in autumn could have the opposite effect. The long-term trends in taste and textural attributes, as judged by peel colour rating and starch concentration, were similar to those derived from calendar date (Table 1). This may be because there was little change in the dates upon which the peel colour ratings and starch concentration reached the benchmark values over the study period.

In conclusion, we identified changes in attributes of the taste and textural attributes of apples in response to recent climate warming. These changing quality attributes are likely to be caused by earlier blooming and higher temperatures during the maturation period. Regardless of the maturity index used to determine harvest date, reductions in acid concentration, fruit firmness and watercore development were observed, whereas the soluble-solids concentration increased in some cases. These results suggest that the taste and textural attributes of apples in the market are undergoing change from a long-term perspective, even though consumers might not perceive these subtle changes. If global warming continues to progress, the changes in the taste and textural attributes of apples could be more striking as blooming dates become even earlier and temperatures increase during the fruit maturation period.

Methods

Location of the orchards and planting material. Data related to fruit taste and textural attributes (see below in detail) of the ‘Fuji’ apple (*Malus domestica* Borkh.) were collected at experimental orchards located in Nagano Prefecture (36.6°N, 138.3°E; 360 m a.s.l.; brown lowland soil) from 1970 to 2010 and in Aomori Prefecture (40.6°N, 140.6°E; 70 m a.s.l.; ando soil) from 1975 to 2010; data for the ‘Tsugaru’ apple were taken from the experimental orchard in Nagano Prefecture from 1980 to 2010. Nagano Prefecture is regarded as a warmer climate region and Aomori as a colder climate region in terms of apple production areas in Japan¹². We used the collected data to analyze the long-term effects of climate change on fruit quality. Apple trees were grown in the same orchards at the experimental stations within each prefecture during the study period. In all of the experimental orchards, the apple trees were consistently managed according to the prefecture-recommended management system, which included soil management, pruning, hand-pollination, fruit thinning and other related factors. Using the management system helped to avoid the problem of pronounced alternate bearing.

‘Fuji’ and ‘Tsugaru’ are dominantly sweet cultivars with a low acid content. Collectively, both cultivars account for 67% of all apple production in Japan³¹. ‘Fuji’ accounts for about one-half of the apple production in East Asia with China producing 14 million tonnes a year³⁰.

Measurement of taste, texture, maturity indexes and phenology. About 20 fruits of each cultivar were picked at random from experimental orchards every 5–10 days during the maturation period to measure the acid concentration, soluble-solids concentration, fruit firmness and watercore rating (only for ‘Fuji’), as well as the peel blush rating (only for ‘Fuji’), peel ground colour rating (only for ‘Fuji’ in Nagano) and starch concentration rating (only for ‘Fuji’ in Aomori) as maturity indexes. We selected apples from trees that were at least 10 years old for this study so that the data on fruit quality would be free from any potential anomalies associated with the use of younger trees.

Acid concentration was measured in juice by titration with 0.1 N NaOH and expressed as a percentage of malic acid. Soluble-solids concentration was measured by refraction (°Brix) with a hand-held refractometer. Fruit firmness was assessed on opposite sides of the fruit with a firmness tester with an 11 mm plunger. The extent of watercore (0 = none to 4 = severe) in each ‘Fuji’ was determined visually after the fruits had been cut transversely. The blush (1 = delicate red to 6 = dark red) and ground colour (1 = green to 8 = deep yellow) of the fruit peel were assessed visually by comparing apples with the standardized colour chart for Fuji⁴⁰. For starch degradation of ‘Fuji’ in Aomori, a transverse fruit section was dipped into a solution of 1% iodine and 5% potassium iodide, and the colour was compared with those on a stained starch pattern chart (0 = completely white to 5 = completely black).

The bud break date was defined as the date when green leaf tips had appeared from about 10% of all apical buds. Similarly, the full bloom date was defined as the date when more than 70% of all king flowers were fully expanded.

Data on ‘Fuji’ apples in Nagano were obtained between the following dates: 1978–2000/2002–2010 (acid concentration), 1973–2010 (soluble solids), 1981–2010 (watercore), 1971–2010 (acid colour) and 1970–2010 (other data). Data on ‘Fuji’



apples in Aomori were obtained between the following dates: 1975–2010 (phenology), 1985–1990/1992–2010 (blush) and 1975–1990/1992–2010 (other data). Data on ‘Tsugaru’ apples were obtained between the following dates: 1980–2010 (phenology) and 1980–1985/1988–2010 (other data). No measurements were taken during the interim years.

Comparison of inter-annual fruit data. The dates of measurement of fruit qualities varied from year to year. Therefore, to detect inter-annual data variability, the taste (acid or soluble-solids concentration) and texture (firmness or watercore rating) values on a given date were determined by using a linear regression formula from the line of the recorded dates and the measured values in each year. An example of the procedure is shown in Supplementary Figure S1a for the soluble-solids concentration of ‘Fuji’ in Nagano for 5 years (1980–1984). The dates upon which the maturity indexes (peel colour rating or starch concentration rating) reached a given value each year were also calculated by using a linear regression formula (Supplementary Fig. S1b).

Climate data. We used climate data (daily temperature, precipitation and sunshine duration) recorded at the Japan Meteorological Agency observatories closest to the apple cultivation sites. The data from 1970 to 2010 in Nagano were obtained from the Nagano Local Meteorological Observatory (Nagano City; 36.7°N, 138.2°E; 412 m a.s.l.) located 11.4 km from the cultivation sites. The temperature and precipitation data in Aomori were obtained from the observatory of the Automated Meteorological Data Acquisition System (Kuroishi City; 40.7°N, 140.6°E; 30 m a.s.l.; 4.1 km from the cultivation sites), which has run since 1977. Because of continuity breaks in the sunshine duration data as a result of equipment change in 1986 at that observatory, solar radiation data observed at Aomori Local Meteorological Observatory (Aomori City; 40.8°N, 140.8°E; 3 m a.s.l.; distance of 23.4 km) were used as a substitute for sunshine duration for the entire period.

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Author contributions

T.S. and T.M. analyzed the relationship between field data and temperature and wrote the paper. H.O. and N.F. collected field data and analyzed trends in each area.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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