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Impacts of soil carbon on hydrological responses – a sensitivity study of scenarios across diverse climatic zones in South Africa

Soil organic carbon (SOC) content and the water holding capacity of soils are two properties which link the carbon and hydrological cycles. Hydrological model inputs seldom include soil carbon as a parameter even though soil carbon content is known to influence soil water retention capacities. This study is a sensitivity analysis of changes in hydrological responses when the model inputs include different soil carbon percentages for the topsoil horizon. Sensitivities of hydrological responses such as transpiration, runoff volumes, the stormflow component of runoff and extreme runoff events to SOC content were quantified under various climatic conditions in South Africa. The soil water holding capacities at the drained upper limit (i.e. field capacity), permanent wilting point and saturation were calculated for the topsoil horizon, using SOC dependent pedo (soil)-transfer functions for different soil carbon scenarios and locations in South Africa. These variables, together with other pre-determined soil- and location-related inputs, as well as 50 years of daily climate, were then used as inputs in a process-based hydrological model. Overall, it was found that increased SOC content in the topsoil horizon leads to an increase in transpiration, a reduction in runoff, especially in its stormflow component, and a reduction of extreme runoff events. However, these changes are relatively small compared to the influence of climate, particularly of rainfall amount and distribution.

Significance:

- Organic carbon content of the soil and the water holding capacity of soils link the carbon and hydrological cycles.
- Management interventions that increase SOC lead to win-win situations because, in addition to climate change mitigation, plant water availability improves, and overall surface runoff 'flashiness' becomes more regulated.
- While rainfall amount and distribution over space and time remain the most critical determinants of hydrological responses, increased SOC in the topsoil horizon leads to increases in transpiration and thus plant growth, and to a reduction in runoff, especially in its stormflow component, and hence to a small reduction of severe flooding events.

Introduction

The amount of soil organic carbon (SOC), and more broadly soil organic matter, is directly linked to the chemical, physical and biological properties of soil. Soil texture, rather than SOC, is the main determinant of soil water holding capacity, i.e. the volume of water that can be held by the soil. However, SOC also plays a role, thereby linking the carbon and hydrological cycles.¹⁻³ Mechanisms of general soil water absorption and retention are explained in soil science textbooks.⁴ SOC itself has a water retention effect through affecting soil structure and adsorption properties⁵, as well as through soil aggregation and associated pore space distribution⁶.

The SOC impact on soil water retention depends on the type of soil, on soil carbon content and on the amount of water in the soil at a given point in time.⁵⁻¹¹ A positive correlation of SOC with water retention and/or selected water potentials is extensively reported in the literature⁸⁻¹³, with limited exceptions¹³⁻¹⁵. The importance of SOC in estimating water retention is affected by textural composition^{5,16}, with this effect being of higher importance in coarse-textured soils than in fine-textured soils^{5,8,16}. A US database analysis linked an increase of 1% (of soil weight) in SOC content to a 2% to >5% increase in plant available water content.¹⁷ Soil water is a key controller of metabolic processes in the soil and of plant growth and productivity.¹⁸ Changes in soil water retention with SOC additions affect the timing and duration of plant water availability, and are especially valuable in low carbon soils.⁹

The quantification of the relationship between SOC content and soil water retention has been reported as part of selected pedo (soil)-transfer functions which are empirical relationships between parameters of soil characteristics and more readily obtainable data on soil properties.^{19,20} Soil water retention is commonly measured at suctions of 33 kPa and 1500 kPa. It is assumed that these water holding volumes are indicators of that particular soil's hydrological variables of drained upper limit (DUL) and permanent wilting point (WP), respectively, while plant available water is the water held between DUL and WP²¹ Rawls et al.⁵ and Saxton and Rawls¹⁶ developed equations for water retention at suctions of 33 kPa and 1500 kPa which included clay, sand and silt content, as well as SOC, based on US soil databases, with the equations of Rawls et al.⁵ being the more robust.²² Soil porosity equations were also developed by Rawls et al.⁷

Soil organic carbon in South Africa is generally low and spatially highly variable.²³ With hydrological responses expected to change in South Africa in the next 50 years due to climate and land use change, there has to date

been no baseline study to illustrate how soil carbon content impacts hydrological responses. This study focuses on the sensitivity of hydrological processes – e.g. stormflow and plant physiological responses, specifically transpiration rate – to varying amounts of soil carbon. The aim of this study was to use a process-based daily time-step hydrological model to explicitly include soil carbon contents across seven hydroclimatic zones using SOC-dependent pedo-transfer functions for different soil carbon scenarios and locations in South Africa. The results of this study would then indicate the SOC threshold at which hydrological processes are impacted upon and where these soils are located in South Africa.

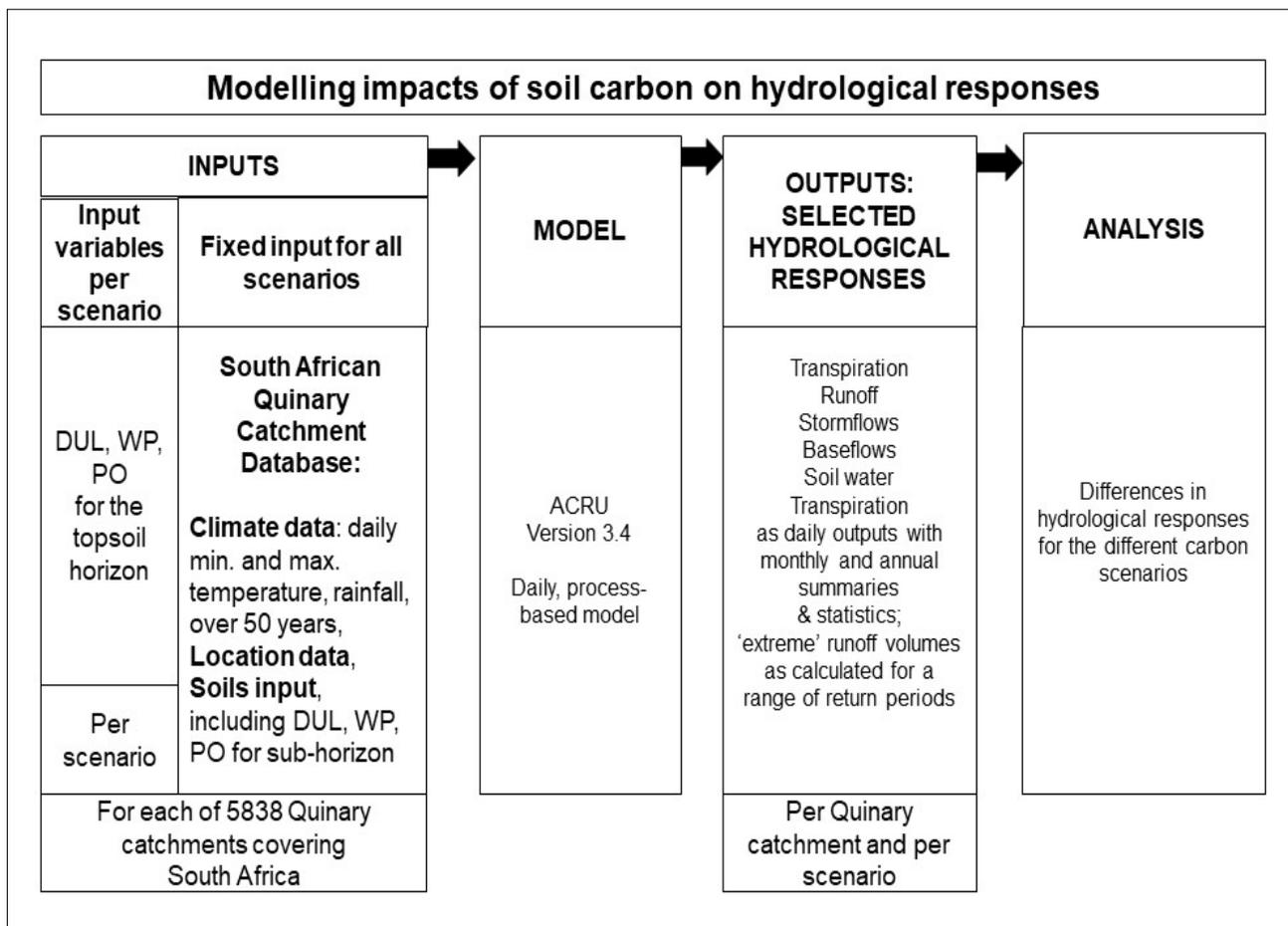
Methodology

Six scenarios with varying carbon content were defined. One scenario was based on the actual SOC contents in the topsoil horizon, as derived from the soil carbon database^{24,25}, with an average SOC of 1.2% and a range between 0 and 12%. To be able to calculate sensitivities to changes in SOC content, hypothetical doubling and halving of the actual SOC amount were undertaken, with the three carbon scenarios being termed 'C_{actual}', 'C_{half}' and 'C_{double}'. The half scenario was included because land-use change mostly results in a reduction of SOC; however, conservation agriculture, irrigation and afforestation could result in an increase – hence the double scenario. In addition to the above scenarios, unrelated to actual SOC contents, assumptions of hypothetical SOC contents of 1%, 2% and 4% were made, with these three carbon scenarios being termed 'C₁', 'C₂' and 'C₄'. This approach was used to exclude the impact of the spatial variability of actual SOC in order to determine the sensitivity of the modelled hydrological responses. While a change of SOC from 1% to 4% is perhaps unrealistic, this was chosen to show more extreme changes. While hydrological modelling includes the

soil profile properties, and therefore properties of the top- and subsoil horizons, we focused only on changes of SOC in the topsoil horizon, where substantial changes are more likely.

The soil-dependent hydrological soil water variables of DUL, WP and porosity (PO) for the topsoil horizon were calculated for each carbon scenario using the pedo-transfer functions by Rawls et al.⁵, but corrected as per Nemes et al.²² to read SOC rather than soil organic matter. First, soil textural contents of clay and sand, as well as SOC, were obtained from the Soil Profile Database.²⁶ The conversion from point values to area values has been explained in detail in Schütte et al.²⁴

A schematic on the more detailed methodology of modelling impacts of soil carbon on hydrological responses is shown in Figure 1. To model hydrological responses in southern Africa, the Quinary Catchments Database²⁷ is frequently used. In the Quinary Catchments Database, South Africa, Lesotho and Eswatini (formerly known as Swaziland) were delineated into 5838 hydrologically relatively homogeneous response units, the so-called Quinary catchments, which are hydrologically interlinked with each linked to a 50-year data set of daily climate as well as location (e.g. altitude and slope), natural vegetation and soil properties. This existing database was used in this study to model hydrological responses, but with the DUL, WP and PO values of the topsoil horizon in the Quinary Catchments Database replaced with the newly calculated values. By using this approach to model the various scenarios, per-scenario results of hydrological responses can be obtained on a Quinary catchment spatial resolution across southern Africa, with the responses including transpiration, runoff, and its components of stormflow and baseflow, all for a statistically median year, for the 1:10 dry year, the 1:10 wet year, as well as for design 1-day, 2-day and 3-day runoff events calculated for a range of return periods by volumes.



DUL, drained upper limit; WP, wilting point; PO, porosity

Figure 1: Schematic describing modelling impacts of soil carbon on hydrological responses.

Table 1: Selected stations, their locations, their representative Quinary catchment and characteristics, monthly means of daily maximum temperature (°C), monthly rainfall (mm) and of A-Pan equivalent evaporation totals (mm) for the period 1950–1999 for the seven hydroclimatic zones, after Hughes²⁹

Station Quinary name Quinary number	Latitude Longitude Elevation (masl)	Acocks ³² Vegetation type & Dominant soil texture	Monthly mean of climatic variable (°C or mm)	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Ann
Mount Edgecombe U20M3 Quinary 4707	29°42'S; 31°02'E 82.9 m	Coastal Forest and Thornveld (#01) Loam	Daily maximum temperature	24	25	26	27	27	27	25	24	23	22	23	23	25
			Rainfall	96	96	118	124	117	102	61	38	17	22	38	61	888
			A-Pan evaporation	92	99	127	111	97	100	81	73	63	66	76	82	1068
Mara A71D3 Quinary 327	23°09'S; 29°33'E 918.8 m	Arid Sweet Bushveld (#14) Loamy Sand	Daily maximum temperature	28	28	29	29	28	27	26	24	22	22	24	26	26
			Rainfall	25	57	78	76	55	34	24	8	4	1	3	9	375
			A-Pan evaporation	138	142	151	145	127	130	109	97	84	85	103	122	1433
Upington D73E3 Quinary 2025	28°27'S; 21°25'E 851.6 m	Orange River Brokenveld (#32) Loamy Sand	Daily maximum temperature	29	32	35	35	35	32	28	24	21	21	23	27	29
			Rainfall	12	18	21	28	34	41	26	12	4	3	4	3	204
			A-Pan evaporation	165	189	216	213	177	162	116	91	73	79	101	135	1716
Elsenburg G22G3 Quinary 2700	33°51'S; 18°50'E 181.4 m	Coastal Rhenoster- bosveld (#46) Loam	Daily maximum temperature	22	25	27	28	29	27	24	20	18	17	17	19	23
			Rainfall	49	39	25	17	21	29	81	113	133	116	105	66	796
			A-Pan evaporation	117	145	168	169	142	124	85	60	46	47	61	82	1246
Outeniqua K30B1 Quinary 3307	33°55'S; 22°28'E 965.5 m	Knysna Forest (#04) Loam	Daily maximum temperature	18	19	20	21	21	21	20	18	17	16	16	16	19
			Rainfall	109	94	86	91	91	101	80	66	51	50	84	82	985
			A-Pan evaporation	82	93	103	97	79	80	62	50	43	45	53	64	850
Cedara U20E1 Quinary 4686	29°31'S; 30°17'E 1101.5 m	Natal Mist Belt Ngongoni Veld (#45) Loam	Daily maximum temperature	22	23	25	25	25	25	23	21	19	19	20	22	22
			Rainfall	84	107	131	136	109	101	48	25	12	14	30	45	842
			A-Pan evaporation	109	117	148	130	112	111	87	72	61	66	82	97	1189
Roodeplaat A21A3 Quinary 12	25°55'S; 28°21'E 1541.7 m	Bankenveld (#61) Loam	Daily maximum temperature	26	26	26	27	27	25	23	21	18	18	21	24	24
			Rainfall	74	111	111	126	82	86	45	15	5	4	5	26	689
			A-Pan evaporation	135	140	147	150	126	123	95	80	65	71	91	116	1338

The analysis of hydrological responses shown here is focused on seven strategic locations within South Africa, each represented by its respective Quinary catchment. These seven selected locations are considered to be representative of different climatic regimes and natural vegetation zones in South Africa and have been used as sample locations in previous studies.^{28,29} The selected locations, together with the natural vegetation types in these zones, are shown in Figure 2. Table 1 shows the selected locations' identifiers, elevations, Quinary catchment names and numbers, their dominant natural vegetation and soil types, as well as mean monthly rainfall and potential evaporation, and monthly means of daily maximum temperature for the 50 years of observed and/or infilled data³⁰ (1950–1999), with the different climatic zones, according to the frequently used international Köppen classification³¹ provided in the text.

Roodeplaat is in Köppen Climate Zone Cwb (winters long, dry and cool), with a mean annual precipitation (MAP) of 689 mm, mainly in the

summer months (October to March). Mara is in Köppen Climate Zone BSh (semi-arid, hot and dry), with a low MAP of 375 mm. Upington has a very low MAP of 204 mm (Köppen Climate Zone BWh, arid, hot and dry). Elsenburg is in the winter rainfall region, with a MAP of 796 mm, and is in Köppen Climate Zone Csb (summers long, dry and cool). Outeniqua is in Köppen Climate Zone Cfb (wet all seasons, summers long and cool) and experiences rainfall throughout the year, with slightly lower rainfall in the cool winter months, with a MAP of 985 mm. Cedara is in Köppen Climate Zone Cwb (winters long, dry and cool), with a MAP of 842 mm, mainly in the summer months. Mount Edgecombe has a MAP of 1068 mm and is in Köppen Climate Zone Cfa (wet all seasons, summers long and hot, but wetter in summer than in winter). The locations' MAPs show a wide range from 204 mm to 1068 mm, while the annual mean temperature ranges from 19 °C to 29 °C. There is also a large elevation range, from 83 m to 1542 m.

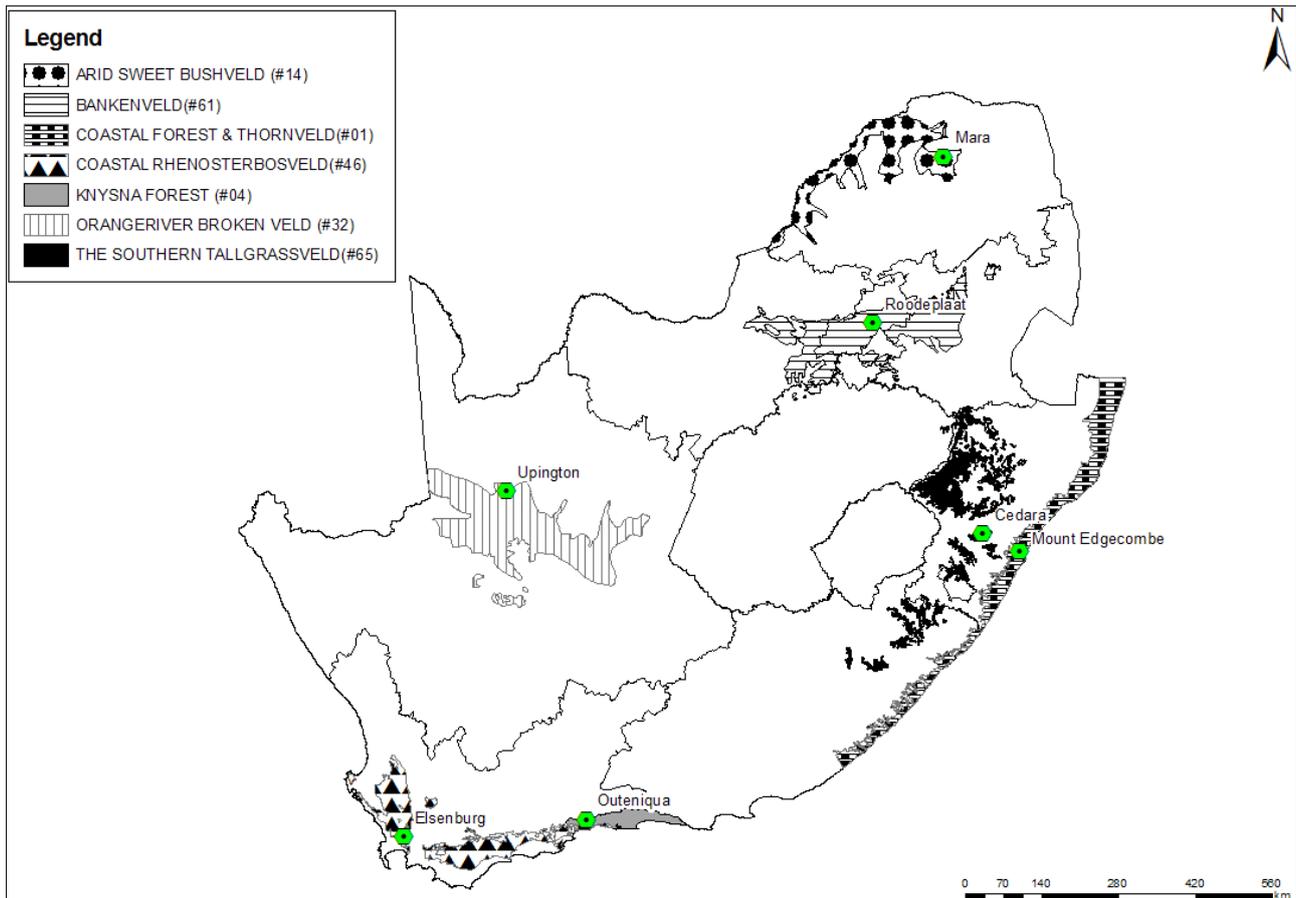


Figure 2: Locations of the seven hydroclimatic zones selected after Schulze²⁹. The vegetation types represented by these zones are labelled according to Acocks³². See also Table 1.

The widely verified process-based daily time-step ACRU Model²⁸ was used first to simulate and explore the baseline hydrological characteristics of the seven hydroclimatic zones assuming naturally occurring vegetation types according to Acocks³². These simulations included volumes and monthly distributions of baseflow and stormflow. The model was then used to simulate the impacts of the various SOC scenarios. The model takes into account the atmosphere–soil profile–plant–water continuum of the landscape. Daily precipitation that reaches the soil surface after interception by vegetation either infiltrates and moves from topsoil horizon to subsoil horizon and possibly groundwater, or the water runs off as stormflow or (slow, delayed) baseflow to discharge into rivers.²⁸

Results

The calculated ACRU input variables changed as a result of SOC changes; for example for Quinary catchment No. 4686, which represents Cedara for the C_1 and C_4 scenarios: the topsoil horizon DUL increased from 0.301 m/m (C_1) to 0.335 m/m (C_4), WP increased from 0.179 m/m (C_1) to 0.181 m/m (C_4) and PO increased from 0.454 m/m to 0.496 m/m.

Figure 3 shows the runoff results for a daily time slice of 5 months for one selected Quinary catchment (No. 4686) representing Cedara for the C_1 and C_4 scenarios. The runoff events are highly dependent on the magnitude and timing of the rainfall events. The C_4 scenario provided evidence that the higher SOC percentages reduced daily peaks compared to the C_1 scenario.

Impacts of the 1%, 2% and 4% SOC scenarios for the same Cedara catchment, for a period of 1 year (Figure 4), show accumulated annual transpiration of 345 mm (C_1 and C_2) and 352 mm (C_3), thus showing an increase in transpiration of 6 mm (2%) from the C_1 to the C_4 scenario. Runoff decreased by 16 mm (equivalent to 13%) from 125 mm (C_1) to

120 mm (C_2) to 109 mm (C_4). The stormflow component of runoff was reduced by 11 mm (11%, for C_1 to C_4) from 106 mm (C_1) to 105 mm (C_2) to 95 mm (C_4), and the baseflow was reduced by 5 mm (or 26%) from 19 mm (C_1) to 15 mm (C_2) to 14 mm (C_4).

Changes in median annual transpiration for the 50 years of modelled daily values at the various locations are shown in Figure 5, representing plant water usage, with large differences, as expected, among the locations, being the lowest in arid Upington (Köppen Zone BWh) and the highest in moist Mount Edgecombe (Köppen Zone Cfa). With an increase in SOC, transpiration hardly changed for Roodeplaat, Mara, Cedara and Upington. However, at Elsenburg, in the winter rainfall zone and with a more temperate climate (Köppen Zone Csb), transpiration increased by 12 mm, equivalent to 9%, for a change in SOC from 1% to 4%, and increased by 6 mm, equivalent to 4%, for a change in SOC from 1% to 2%. Mount Edgecombe (in the Cfa climate zone, wet all seasons, summers long and hot) shows a transpiration increase of 14 mm, equivalent to 3%, for a change in SOC from 1% to 4%, but hardly any change (6 mm or 1%) when changing from 1% to 2% SOC. Generally, however, these locations show an increase in transpiration with increased SOC.

The runoff figures (not shown) in a 1:10 dry year vary from no runoff for all carbon scenarios for arid Upington, to a runoff of 56 mm in the C_1 scenario, 53 mm in the C_2 scenario, 43 mm in the C_4 scenario, and 60 mm, 58 mm and 54 mm, respectively, for the C_{half} , C_{actual} and C_{double} scenarios for Elsenburg. In a year of median responses, the runoff ranges between 1 mm for Upington in the C_4 scenario to 196 mm, 193 mm and 187 mm for Elsenburg (winter rainfall zone, Csb) for, respectively, the C_{half} , C_{actual} and C_{double} scenarios. For a 1:10 wet year, runoff ranges between 21 mm for Upington (dry, BWh) for the C_4 scenario, to 468 mm, 463 mm and 452 mm at Mount Edgecombe (wet, Cfa) for the C_{half} , C_{actual} and C_{double} scenarios (not shown).

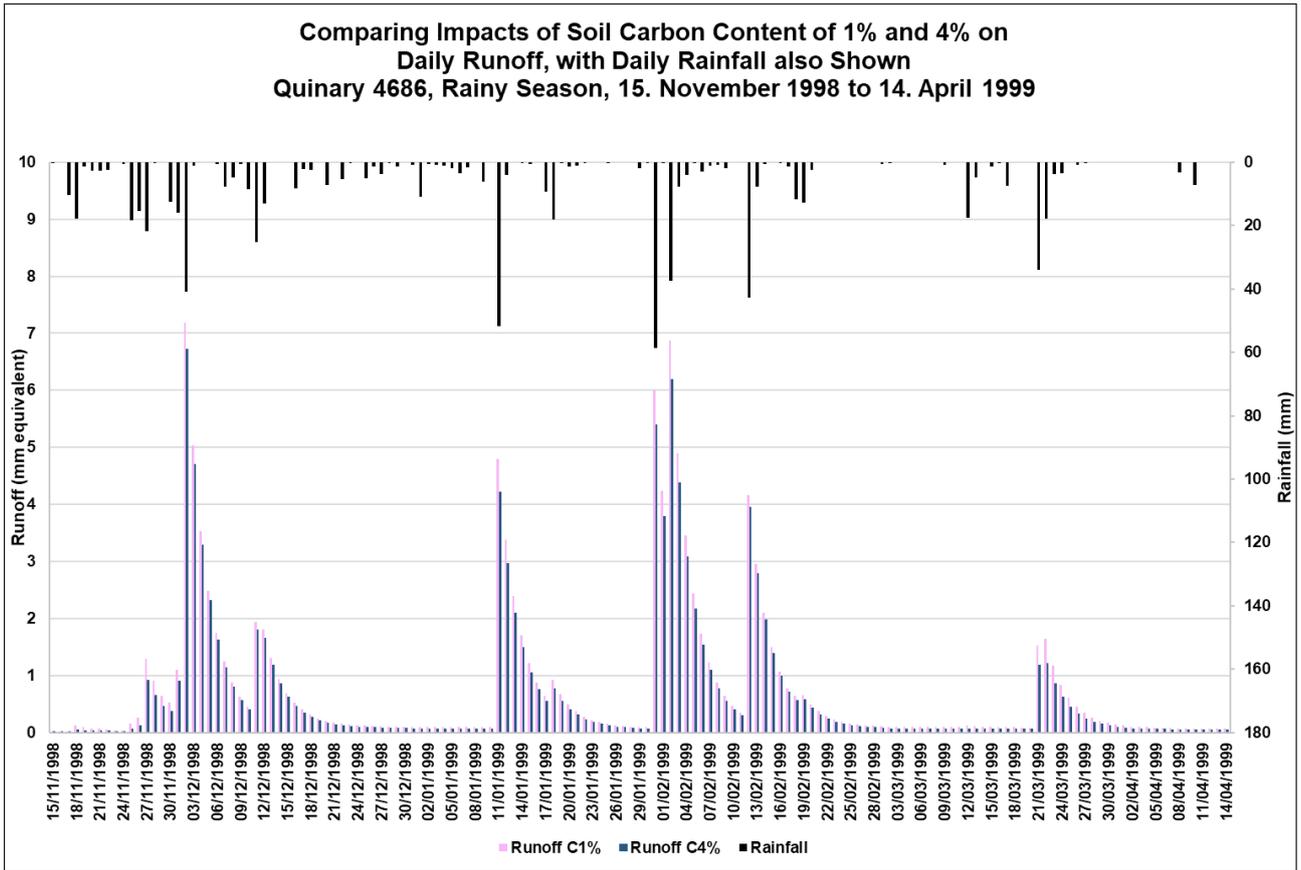


Figure 3: Simulated daily runoff for soil organic carbon of 1% (light pink) and 4% (dark blue), for the Quinary catchment representing Cedara during a 3.5-month period during the rainy season, with daily rainfall shown on the secondary axis.

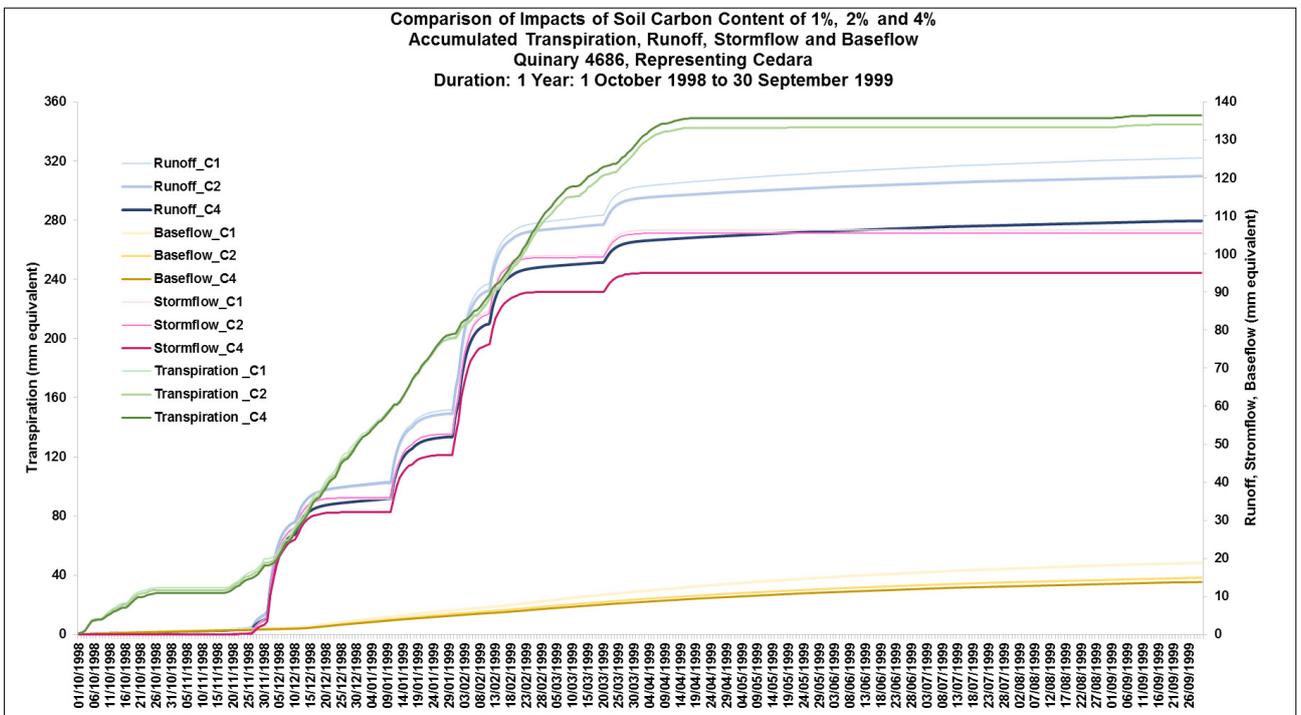


Figure 4: Daily accumulated transpiration (left y-axis), as well as accumulated runoff, stormflow and baseflow (right y-axis, all in mm) for a one-year period for the C₁, C₂ and C₄ scenarios, using Quinary Catchment 4686 representing Köppen Climate Zone Cwb at Cedara.

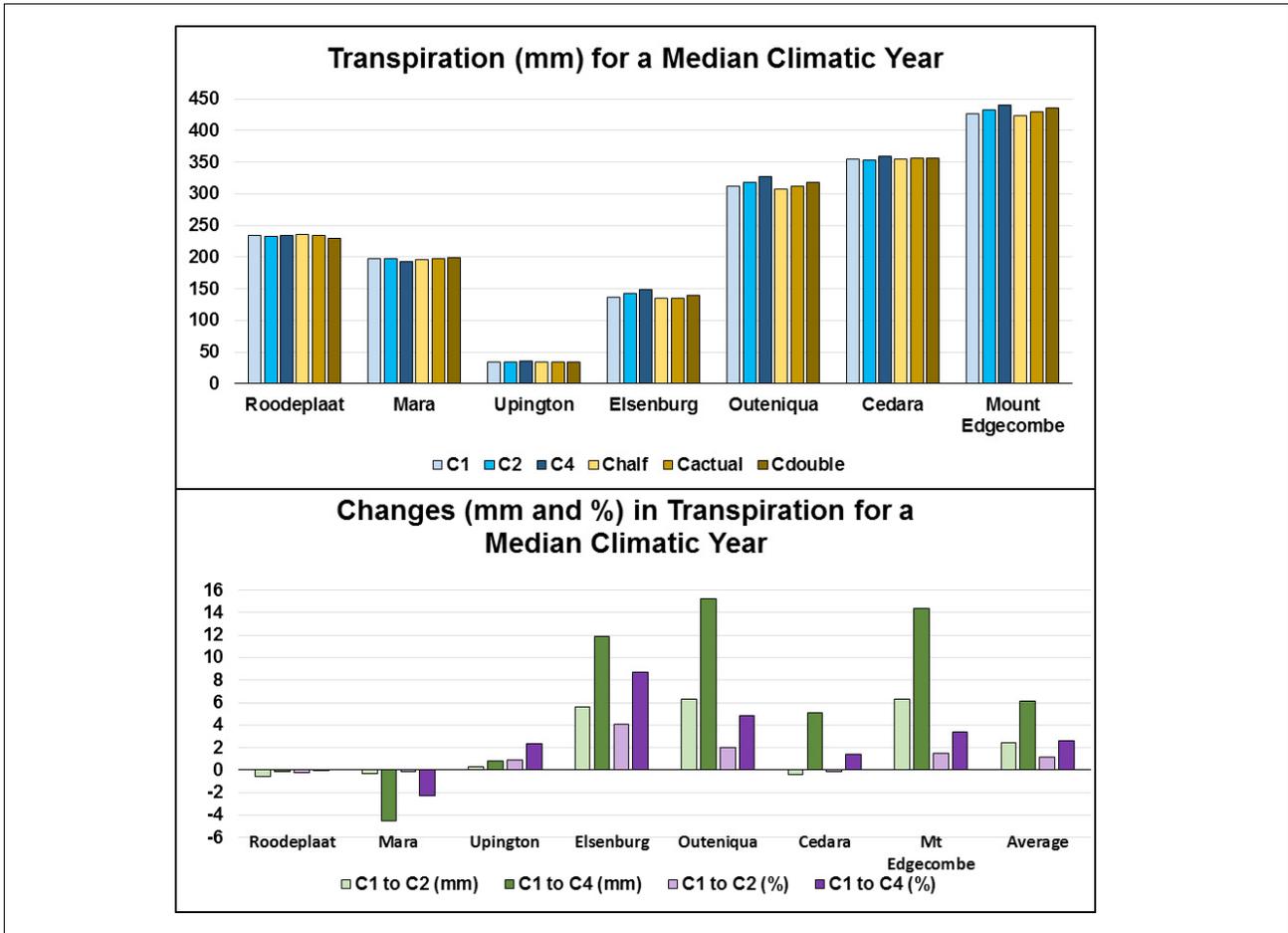


Figure 5: Accumulated transpiration (mm, top) for various soil carbon scenarios at selected locations in South Africa, as well as changes in transpiration from the C_1 to C_2 and from the C_1 to C_4 scenario (% and mm, bottom graph), for a median climatic year.

Selected changes in runoff results (Figure 6) show the impact of SOC to vary. While no impact is seen in Upington in a 1:10 dry year, because there is no runoff anyway, substantial sensitivities to SOC are seen for the other wetter areas. The largest absolute reduction of 24 mm is at Cedara in a 1:10 wet year when changing SOC from 1% to 4% SOC, with the largest relative reduction (but only a small absolute reduction) in runoff for Upington at 44% in a median year with a change in SOC from 1% to 4%.

Stormflows are rapid surface or near surface flows and are generally the major component of total runoff in most parts of South Africa. The highest results are from Mount Edgecombe (wet, Cfa) where stormflows are modelled at 330 mm, 328 mm and 310 mm for the C_1 , C_2 and C_4 scenarios (not shown). Changes (mm and %) in stormflows in a 1:10 dry year, a median year and a 1:10 wet year for changing scenarios from the C_1 to the C_4 scenario (Figure 6) show the biggest absolute change, for a 1:10 wet year at Cedara (wet, Cwb) with a 24 mm reduction for a change from 1% to 4% SOC, while the biggest relative change is for Upington (dry, BWH) with a 27% reduction. In summary, an increase in SOC can lead to significant reductions in stormflows, but this depends on the inherent climate of an area and whether it is a dry, median or wet year.

Baseflows are the slow-release component of runoff and are the only water source in rivers in the non-rainy season while being a major component of runoff in the winter rainfall region. Most important in this sensitivity study are baseflows in the 1:10 dry year, with no baseflows for any of the SOC scenarios generated at Roodeplaat, Mara and Upington and very little at Cedara. The highest annual baseflows are found at Elsenburg (winter rainfall, temperate climate) with respectively 58, 56 and 52 mm for the C_{half} , C_{actual} and C_{double} SOC scenarios (not shown).

In the cases where baseflow occurred, generally, a small reduction in baseflows was evident, although in relative terms this could be high, with up to 99% for Upington for a change of SOC from 1% to 4% in a 1:10 wet year (not shown).

Changes in more extreme runoff design events for 1-day and 3-day accumulated magnitudes for design return periods of 2-, 5-, 10- and 50-year return periods are shown in Figure 7. While the Quinary catchments at Elsenburg (winter rainfall) and Outeniqua (all year rainfall) show no significant changes, the highest absolute reduction was at Mount Edgecombe (wet, Cfa), from 2.9 mm equivalent runoff for a 3-day event for the 2-year return period to 4.4 mm for a 3-day event for the 50-year return period. Relative reductions were highest for Upington (dry, BWH), up to 20% for a 2-day runoff event for a 50-year return period (not shown), with a reduction of 2.2% for 3-day and 2-day runoff events for a 50-year return period.

Overall, it was found that increased SOC content in the topsoil horizon leads to an increase in transpiration, a reduction in runoff, especially in the stormflow component, and to a reduction of extreme runoff events.

Discussion and conclusions

While most soil profile and location specific properties cannot be changed, land use management can influence the amount of carbon in the soil, especially in the topsoil horizon. The sensitivities of hydrological responses such as transpiration, total runoff, the stormflow component, and extreme events to changes in SOC content at a number of diverse locations within South Africa were quantified using a hydrological process modelling approach. Relevant hydrological soil variables of soil water content at DUL (or field capacity), WP and PO, i.e. at saturation, were calculated for the topsoil horizon, using pedo-transfer functions which

include various amounts of carbon representing different soil carbon scenarios. These soil carbon scenarios were then used as inputs to a process-based hydrological model at Quinary catchment resolution, with other soil profile, location and natural vegetation properties remaining as per the standard South African Quinary Catchments Database. Differences in hydrological responses between the scenarios were assessed for a number of climatically diverse areas within South Africa ranging from desert to sub-tropical climates.

Soil water holding capacities impacted by SOC were found to be a link between the carbon and the hydrological cycles as reported in the literature.¹⁻³ For the location studies, SOC was shown to impact hydrological responses, but the magnitude of these changes is strongly influenced by rainfall regimes and varies between the different climatic zones, location and soil properties. In assessing runoff on a daily basis for Cedara, for example, an increase in SOC led to a reduction in the

conversion of rainfall to runoff, with the peak runoff magnitudes generally being reduced. Changes in runoff range between insignificant in very dry areas, to up to 24 mm of absolute reduction for Cedara in a 1:10 wet year, when modelling a change from 1% to 4% SOC, with the largest relative reduction (but only a small absolute reduction) in runoff for Upington at 44% for a median year when SOC is changed from 1% to 4%. The significant reductions in runoff results are mainly from stormflows, but with also more muted reductions in baseflows. An increase in SOC leads to transpiration increases, as was expected and found by others.⁸ With an increase in SOC, shifts from runoff, and especially from the stormflow component, towards transpiration are seen. With increased SOC, the soil holds water more *in situ* in the landscape, with this water being available for plant transpiration and growth, which in turn leads to a reduction in runoff. On the other hand, when there is very little rain, as is in the case of Upington in a 1:10 dry year, then there is no runoff for any of the soil carbon scenarios.

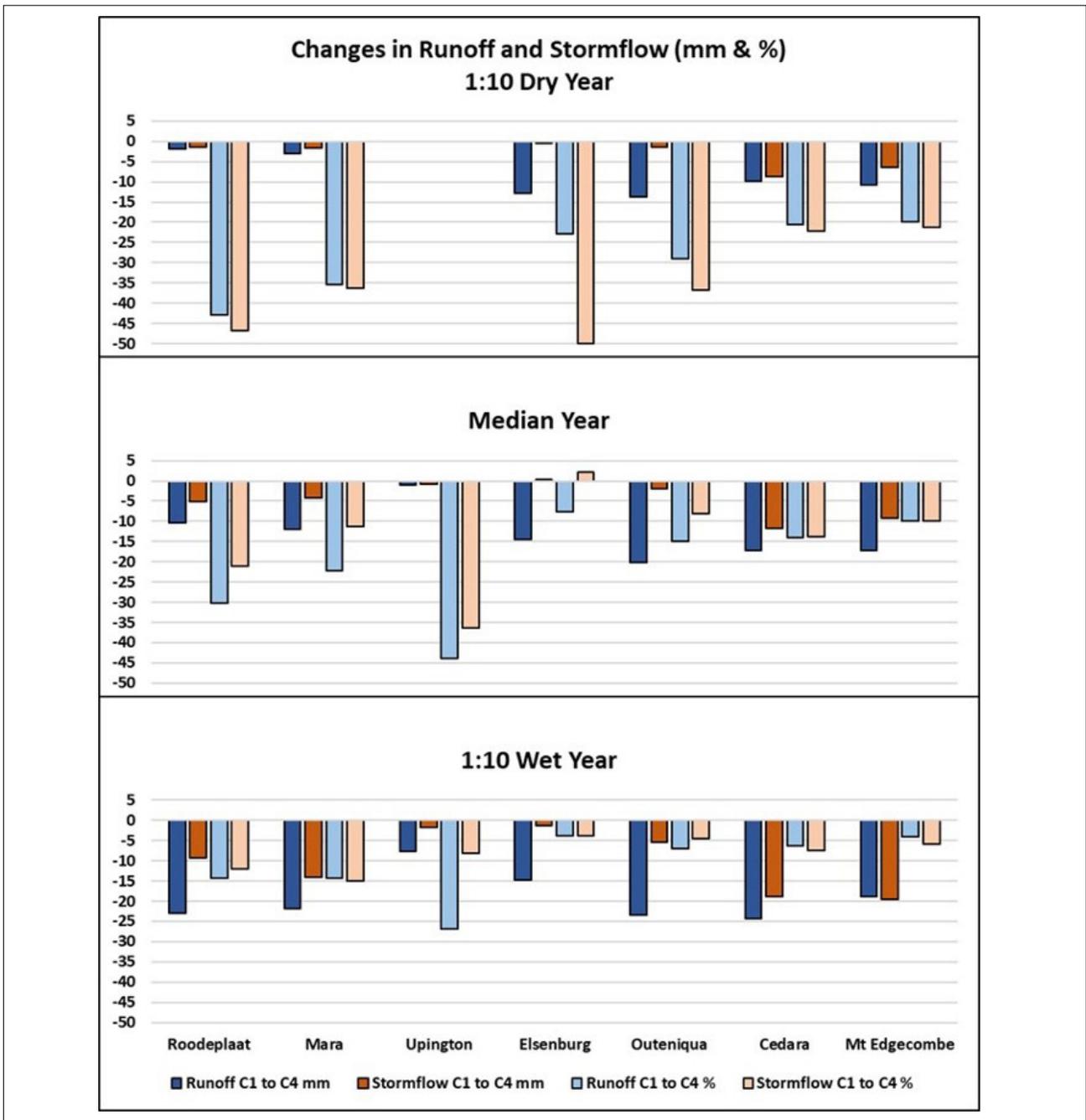


Figure 6: Changes in runoff and stormflow (mm and %) for carbon scenarios of 1% to 4% in a 1:10 dry year, a median year and a 1:10 wet year, for selected locations in South Africa.

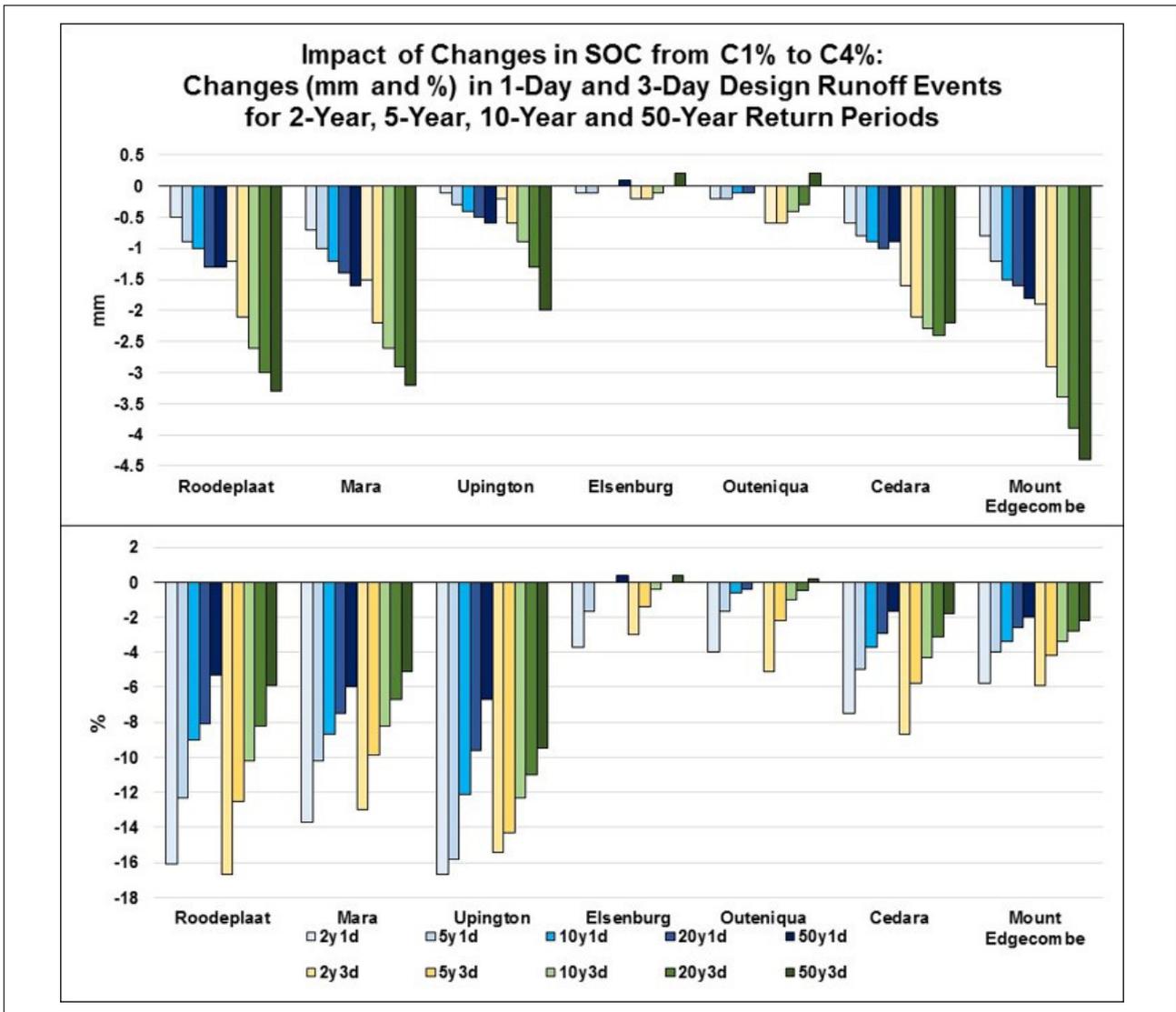


Figure 7: Changes in 1-day and 3-day design runoff events for return periods of 2, 5, 10, 20 and 50 years, with absolute changes (mm, top graph) and percentage changes (bottom graph) shown for selected areas in South Africa.

Not all areas show a change in extreme runoff with SOC changes, but most show a slight reduction in extreme runoff events with an increase in SOC content. When expressed as relative changes, this reduction is higher in smaller floods with shorter return periods compared to changes in larger floods with higher return periods. However, when expressed as absolute changes, the reductions are higher for larger floods with higher return periods compared to smaller floods with shorter return periods. Overall, an increase in soil carbon is shown to reduce extreme runoff events in most areas, but with different magnitudes. Increases in soil carbon should thus help to reduce some flood damage, thereby providing an important ecosystem service.

For the first time in South Africa, sensitivities of hydrological responses to SOC content changes have been calculated for selected locations with widely differing climatic regimes, with the results of this study confirming those in the literature.¹² In this study, a quantification of the overall reduction in runoff, and especially in stormflows, has been presented. Land management practices that increase carbon content would retain more water in the soil profile which would be available for plant use, and would thus usually lead to reduced runoff and flood events, but the impacts are limited and, again, depend on climatic, soil and location factors. Increased SOC, with increased plant water availability, is an additional benefit to climate change mitigation and thus presents a win-win situation.

More research is recommended to update the South African hydrological soil property databases, incorporating the new DUL, WP and plant available water values. While we examined only changes in SOC content in the topsoil, this study could be expanded to the subsoil horizon as well. The methodology developed in this study could also be used for sensitivity studies elsewhere in South Africa. Bearing in mind uncertainties regarding input values of carbon content, climate and soil variables, as well as pedo-transfer functions established elsewhere in the world, further improvements to impact modelling can be made if locally derived equations of WP, DUL and PO, which include a soil carbon factor, and improved model inputs, become available. Further research is also recommended to study the impact of actual changes in SOC on hydrological responses in South Africa over a historical period, as well as on SOC impacts on plant growth in the form of changes to soil water and plant stress-free days, for agricultural crop yield and primary production assessments.

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Competing interests

We declare that there are no competing interests.

Authors' contributions

S.S. devised the methodology, did the modelling and the analyses and wrote the paper. R.E.S. and M.S. provided technical input and provided editing support in their roles as PhD supervisor and co-supervisor, respectively.

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