RESEARCH ARTICLES

Europe's Terrestrial Biosphere Absorbs 7 to 12% of European Anthropogenic CO$_2$ Emissions

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Most inverse atmospheric models report considerable uptake of carbon dioxide in Europe's terrestrial biosphere. In contrast, carbon stocks in terrestrial ecosystems increase at a much smaller rate, with carbon gains in forests and grassland soils almost being offset by carbon losses from cropland and peat soils. Accounting for non–carbon dioxide carbon transfers that are not detected by the atmospheric models and for carbon dioxide fluxes bypassing the ecosystem carbon stocks considerably reduces the gap between the small carbon-stock changes and the larger carbon dioxide uptake estimated by atmospheric models. The remaining difference could be because of missing components in the stock-change approach, as well as the large uncertainty in both methods. With the use of the corrected atmosphere- and land-based estimates as a dual constraint, we estimate a net carbon sink between 135 and 205 teragrams per year in Europe's terrestrial biosphere, the equivalent of 7 to 12% of the 1995 anthropogenic carbon emissions.

Carbon (C) sequestration by terrestrial ecosystems is thought to occur predominantly in the Northern Hemisphere (*1*, *2*), but the exact size and longitudinal distribution of this sink remain uncertain (*3*). We used both land-based and atmosphere-based approaches to constrain the net terrestrial C balance of the European continent (defined as the landmass between the Atlantic Ocean and the Ural, excluding Turkey and the Mediterranean isles) and thus reduce uncertainty in the geographical distribution of the terrestrial C sink. In the land-based approach, C stock changes from the dominant ecosystems (forests, croplands, grasslands, and organic soil wetlands) are evaluated and aggregated over all regions across Europe. This land-based approach,

therefore, provides information on which ecosystems and regions are accumulating C and which are losing C to the atmosphere. Atmosphere-based approaches, in contrast, provide already aggregated information on the regional-scale C balance on a monthly time scale but give no information about which ecosystems are contributing to the sink or the processes involved. These alternative, completely independent approaches are thus complementary and, when used in combination, put a dual constraint on estimates of the integrated C sequestration by European terrestrial ecosystems. This may increase confidence in our estimation of the C balance as compared with estimation by a single method and may also lead to a redefinition of the problem.

Land-Based Analysis

Forest sector C balance. European-wide changes in the C content of European forests (net biome production, NBP) (*4*) have been estimated with models based on national inventories of annual stem-volume increments and harvests (*5–10*). Mean NBP estimated by these models is about 70 g C m^{-2} per year (a^{-1}). In large part, this C sink results from the changing age-class distribution of relatively young European forests and because in most countries the annual cut is less than the increment. On average, about 70% of this sink is attributed to tree

biomass and 30% to soils in these inventory-based models (*6*, *8*, *9*).

Carbon accumulation rates in forest soils derived in this way are small compared to estimates using a more direct method based on ecological measurements. Comparison of annual litter production with heterotrophic respiration (that is, the C inputs to the soil compared to the outputs), in 11 forests along a north-south gradient across Europe (*11*) after correction for soil C losses after disturbance during harvest indicates a mean European forest soil C sink of 110 g C m^{-2} a^{-1}. On the basis of this soil C sink and the value for the biomass C sink given by the inventory models (i.e., 50 g C m^{-2} a^{-1}), current forest NBP amounts to 160 g C m^{-2} a^{-1}. From these two rather different estimates of NBP (70 and 160 g C m^{-2} a^{-1}), it is clear that resolution of the uncertainty in forest-soil C sequestration rates is critical.

Throughout Europe, the net CO$_2$ exchange between forest ecosystems and the atmosphere (net ecosystem production, NEP) (*4*) is measured with the eddy covariance technique (*12*) in a well-developed network of 33 eddy-flux stations encompassing a wide range of European climates and tree species (*13*). Measurements of NEP at these forest sites have been combined with maps of climate and normalized difference vegetation index in a neural network to give an aggregated, European-wide forest NEP estimate of 185 g C m^{-2} a^{-1} (*14*). This mean forest NEP estimate is, however, not directly comparable with the NBP estimates described above because it does not account for C losses from the ecosystem other than the concurrent return of CO$_2$ to the atmosphere. These losses include leaching of particulate and dissolved organic C, emissions of volatile organic compounds, and particularly harvesting of biomass. We have, therefore, multiplied the aggregated mean NEP with the NBP/NEP ratio of 0.47 from the inventory studies (*7*) to give another estimate of forest NBP of 92 g C m^{-2} a^{-1}.

From these three estimates, the overall mean forest NBP is 110 g C m^{-2} a^{-1} (but ranging between 70 and 160 g C m^{-2} a^{-1}). Combining this figure with estimates of forest area (*10*, *15–19*) leads to a mean European C sequestration rate of 363 Tg C a^{-1} (Table 1), suggesting that European forest ecosystems do compose an important C sink.

Whatever the definition of forest, there is always some land that contains trees but does not meet the criteria of a forest, the "other wooded lands" (for example, tree nurseries, young plantations, shrublands, and urban areas). In North America, C uptake by shrublands alone may amount to 120 Tg C a^{-1}, accounting for about 30% of the total North

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American C sink (*20*). However, this large North American shrubland sink mainly results from woody encroachment of grasslands and savannahs after large-scale abandonment of agricultural land and cessation of fire suppression practices. Because these practices are less common in Europe, such woody encroachment is probably much more limited. Furthermore, recent information now suggests that woody plant invasion may not result in increased C sequestration, because C gains in woody biomass may be offset by C losses from soils (*21*). Our rough estimate of the C sink in these other wooded lands (27 g C m^{-2} a^{-1}) resulted in a very small and uncertain European-wide C sink of 14 Tg C a^{-1} (Table 1). Combining the C sinks in forests and other wooded lands suggests that the C balance of the European forest sector (Table 1) is a substantial C sink of 377 Tg C a^{-1}, dominated by forest NBP but with a large uncertainty resulting mainly from inadequate knowledge of the C budget of forest soils.

Aggregated agricultural C fluxes. On the basis of a number of long-term experiments, models have been developed that include the effects of management, climate, soil type, and vegetation on cropland and grassland soil C balances (*22*, *23*). To estimate the European-wide contribution of agriculture to the European C balance, we combined the aggregated country-specific changes in soil organic matter content predicted by the CESAR model (*23*) with estimates of European cropland and grassland areas (*15*, *24*).

To our knowledge, there are only two large-scale (national) and long-term inventories of organic matter in agricultural soils that can be used to validate these model estimates. In a study by Sleutel *et al.* (*25*), repeated sampling of arable soils in Belgium (210,000 samples taken between 1989 and 1999) indicated a mean annual soil C loss of 76 g C m^{-2} a^{-1}. This estimate agrees well with CESAR's prediction of a net loss of 90 g C m^{-2} a^{-1} from cropland soils in Belgium. For Austrian cropland soils, however, the mean C loss predicted by the CESAR model (89 g C m^{-2} a^{-1}) is much larger than the C losses measured in a repeated, large-scale inventory study (24 g C m^{-2} a^{-1}) (*26*). This difference between predicted and observed changes in soil C highlights the uncertainty in predicting soil C losses and again emphasizes the need for a wider range of repeated soil C inventories to constrain modeled soil C losses. Such repeated inventories on croplands of different soil properties, agricultural management practices, and land-use history are essential for evaluating estimates of European soil C balance.

Despite the difference in size, both model estimate and observations suggest a net loss of C from arable soils. This net loss occurs because in arable soils harvest reduces C returns to the soil, whereas C losses may be enhanced because of agricultural practices such as tillage. Thus, land conversion from other land uses to cropland is likely to lead to an overall decline in soil C. Because these losses can continue for a number of years, the current loss of C from cropland soils may be the legacy of conversion of land to cropland during the past 20 to 30 years, as is the case in the United Kingdom (*27*). However, in most European countries the major land-use changes occurred much longer than 20 to 30 years ago, and recent trends are more toward the conversion of arable land to other land uses. Despite this, arable soils are losing C even in these countries where no new cropland has been created, as in the Belgian example discussed above (*25*). These measured soil C losses can therefore not be related to land-use change but are probably because of changes in management practice, such as a decrease in the application of organic manure to cropland (*25*). Another possible hypothesis that could explain why arable soils can lose C without net land use changes is rotation. If the conversion from cropland to grassland equals the conversion from grassland to cropland, national statistics will indicate no land-use change where in reality there is. Under such conditions, arable soils can continue to lose C, and grasslands to gain C. Because national statistics only report net land-use changes, this hypothesis could not be tested.

Our current best estimate of C changes in European agricultural soils indicates that croplands are losing 300 Tg C a^{-1} to the atmosphere (Table 1), thus largely offsetting the sink in the forest sector. The C balance of grassland ecosystems was estimated by following exactly the same methodology as for arable soils. In contrast to arable soils, grassland ecosystems may constitute a net C sink (101 Tg C a^{-1}), although the uncertainty surrounding this estimate is larger than the sink itself (Table 1). This very large uncertainty in the agricultural sector net exchange originates primarily from uncertainty in the modeled NBP estimates but also from our highly simplified aggregation procedure.

C sequestration in organic soil wetlands. Most undisturbed organic soil wetlands accumulate C at rates ranging between 0 and 80 g C m^{-2} a^{-1}, depending on age, climate and the type of wetland ecosystem (for example, mires, fens, and marshes) (*28*, *29*). Because of the relatively small area (*28*–*30*) and predominantly slow accretion rates, undisturbed European peat constitute only a negligible C sink (Table 1).

However, large peat areas have been and are being drained for pasture, cropland, and forestry purposes (*30*, *31*). Drainage of organic soils enhances their aeration and the subsequent enhancement of decomposition results in substantial soil C losses (*31*). Our estimate of the C loss from Europe's drained peat lands indicates that, despite a much smaller area, more C is lost because of drainage than is sequestered in undisturbed peat (Table 1). This situation is further exacerbated by the extraction of peat and its use in horticulture, agriculture, and the energy sector (Table 1), especially in the former Soviet Union (*29*). Overall, European peat ecosystems are a net source of C to the atmosphere of 70 Tg C a^{-1} (Table 1), equivalent to about 20% of the C sequestered by the forest sector.

Integrated land-based estimate. From these considerations, our estimated integrated net C uptake by European forests, croplands, grasslands, and peat lands is a small, very uncertain net C uptake of 111 ± 280 Tg C a^{-1} (Table 1). Within this land-based estimate, forests represent the largest C sink, whereas agricultural soils dominate the large

Table 1. Net biome productivity in forest, agricultural, and peat sectors. Positive fluxes mean net uptake; negative is net loss of C. Numbers within parentheses represent one standard deviation. For each ecosystem, the total area is also given.

	Area (Mha)	NBP (Tg C a^{-1})	Ref. nos.
Forest sector			
Forests	339 (7)	363 (159)	(*10*, *15*–*19*)
Other wooded land	50 (17)	14 (7)	(*10*)
Subtotal		377 (159)	
Agricultural sector			
Croplands	326 (32)	−300 (186)	(*15*, *24*)
Grasslands	151 (36)	101 (133)	(*15*, *24*)
Subtotal		−199 (229)	
Peat sector			
Undisturbed peat lands	39 (6)	13 (7)	(*28*–*30*)
Drained peat lands	16 (4)	−30 (15)	(*29*–*31*)
Peat extraction		−50 (10)	(*29*, *30*)
Subtotal		-67 (19)	
Total		111 (279)	

uncertainty. This large uncertainty is attributable mainly to the lack of data and the simplifications assumed in aggregating fluxes from the mosaic of vegetation types, land-use histories, soil types, climates, and management regimes. If we assume a normal probability distribution, the probability that the land-based sink estimate is positive (i.e., a net C sink) only amounts to 0.66.

Atmosphere-Based Analysis

In the atmosphere-based approach, a global atmospheric tracer-transport model links sources and sinks of CO_2 to atmospheric CO_2 concentrations. Running a transport model in inverse mode, i.e., the use of measured atmospheric CO_2 concentrations to calculate the best fitting set of regional CO_2 sources and sinks, can then give estimates of regional or continental C balances. We selected from the inversion literature those studies in which Europe was either treated as a separate region or further subdivided in subregions and where the time period of analysis was long enough (>5 years) to avoid errors resulting from interannual variability in the fluxes (*32*) (Table 2). All inversions indicate that land ecosystems within geographic Europe have been a net sink during the last decade, but estimates vary between an uptake of 80 to 600 Tg C a^{-1} (*32*, *33*). Because not all the inversion studies selected were assessed over the same time period, interannual variability in the terrestrial fluxes (*32*) could contribute to this range of results. Furthermore, Europe was defined with different boundaries in the different inversion studies. In the study by Gurney *et al*. (*3*), for example, Europe was defined in the same way as in our land-based approach (from Atlantic Ocean to the Urals, with an area of 1.04 10^{13} m^2), whereas Bousquet *et al*. (*32*, *34*) defined Europe more broadly and included the Mediterranean area and part of the Middle East (1.55 × 10^{13} m^2). In addition to different time periods and different boundaries, each of the inverse model studies used a different set of atmospheric observation stations, so the results are not directly comparable one with another.

Although the selected inverse model estimates vary considerably, they all indicate a net terrestrial European C sink with an overall mean of 290 Tg C a^{-1} (Table 2). However, uncertainties within each of the individual inversion studies are very large, typically in the order of magnitude of the flux itself. Inverse-flux estimates of carbon sinks are often credited with two types of associated uncertainties: internal uncertainty, resulting from the inverse procedure itself, and, if provided, external uncertainty, accounting for nonexplicit errors such as variability among the networks of atmospheric stations used, different transport models, or different regularization procedures and given as the standard deviation derived from the results of different sensitivity tests with different inversion settings. On the basis of only internal errors, the statistical probabilities that the simulated C sinks are significantly larger than zero range between 0.74 and 0.99 (Table 2). However, external uncertainty can also be very large (Table 2), often as large as the internal errors, with the consequence that individual inverse modeling studies cannot lead to the unambiguous conclusion that C sequestration in European terrestrial ecosystems is significantly different from zero.
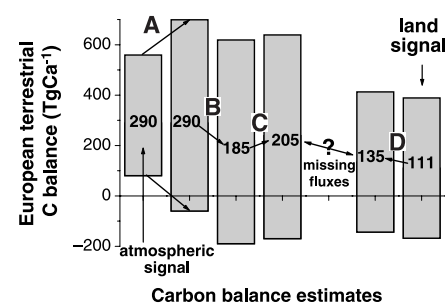
Furthermore, in the final step these atmospheric models need to subtract fossil-fuel emissions from the inversely modeled net CO_2-balance to obtain an estimate of the terrestrial C sink. Because these emissions are much larger than the calculated net terrestrial fluxes, this approach is very sensitive to small errors in the fossil-fuel emissions, both in the annual totals and in their resolution in space and time. Uncertainty in the European fossil-fuel emissions is about 5% to less than 10% (*35*, *36*). Assuming a 7.5% uncertainty in the fossil-fuel emissions increases the uncertainty of the atmospheric models by about 140 Tg C a^{-1} (Fig. 1, arrow A).

Discussion

Both approaches to the estimation of net C uptake by Europe's terrestrial biosphere suggest a net sink, but uncertainties in both approaches are extremely large. To reduce uncertainties in the inverse atmospheric model approach, fossil fuel–derived CO_2 emissions will need to be better resolved. Also, inclusion of more atmospheric monitoring stations and/or more constraints by land-based approaches such as those presented here could represent a major step forward. In the land-based approach, uncertainty could be reduced considerably by placing a stronger focus on the effects of land-use history and management on soil C gains and losses. Implementation of ecosystem models, when constrained by both flux and stock data, may give better spatial integration and better temporal resolution than the currently used approach and could reduce uncertainty originating from current aggregating procedures.

Despite these large uncertainties, the result that two completely independent approaches suggest a European C sink does enhance the probability that such a sink does exist. The mean atmosphere-based estimate of 290 Tg C a^{-1} is much larger than the land-based estimate (111 Tg C a^{-1}). Although this difference is not statistically significant, it does imply that either one or both approaches could be incorrect and, furthermore, that we cannot conclusively relate changes in atmospheric CO_2 concentrations over Europe to the activity of the terrestrial biosphere. Hence, the dual constraint ap-

Table 2. Carbon sink estimates (Tg C a^{-1}) of the European terrestrial biosphere as estimated by inverse atmospheric CO_2-transport models. The investigated time period (Period), the internal error of the inverse model results (Error), and the statistical probability that the reported C sink is larger than zero are given. Numbers in parentheses represent the external error. External errors correspond to the standard deviation among different inversion settings, such as different transport models, different prior settings, or different networks of atmospheric monitoring stations. Dashes indicate unavailable information.

	Period	C sink	Error	Probability sink >0
Bousquet *et al*. (*34*)	1985–95	200 (150)*	470*	0.76
Bousquet *et al*. (*32*)	1980–98	410 (330)*	540*	0.90
Rayner *et al*. (*49*)	1980–96	200	–	–
Kaminski *et al*. (*33*)	1980–86	80	200	0.74
Gurney *et al*. (*3*)	1992–96	560 (400)	340	0.99
Overall mean		290		
Range		80–560		

*Results from Bousquet *et al*. (*32*, *34*) studies were originally reported for an area of 1.55 × 10^{13} m^2. We interpolated these results and associated uncertainties linearly to a similar European surface area as the other inversion studies and the land-based estimate (10^{13} m^2).

Fig. 1. Estimates of the carbon balance of the European terrestrial biosphere obtained by inverse atmospheric CO_2-transport models (atmospheric signal) and by aggregating stock changes in terrestrial ecosystems. Numbers give best estimates obtained by different scenarios, and box sizes give an indication of their uncertainty. Arrow A, inclusion of uncertainty in fossil fuel emissions. Arrow B, correcting atmospheric signal for C losses in non-CO_2 gaseous compounds (CO, CH$_4$, and NMVOCs). Arrow C, correcting atmospheric signal for CO_2 release bypassing the ecosystem stocks (intercontinental trade in food and wood products). Arrow D, correcting land-based signal for C accumulation in the wood products pool.

proach appears at first not to resolve the issue of C sequestration in European terrestrial ecosystems. However, the net CO_2 exchange between land and atmosphere as inferred by the atmospheric inversion models and by the changes in C stocks as estimated with the land-based approach do not measure exactly the same flux.

For example, inverse atmospheric models infer only CO_2 fluxes, but C is also emitted into the atmosphere in other compounds: carbon monoxide (CO), methane, or nonmethane volatile organic compounds (NMVOCs). Because the land-based estimates are calculated from changes in C pool sizes, they do also take into account C losses as methane and NMVOCs, whereas the inverse model estimates do not. Biospheric methane emissions (mainly from enteric fermentation, landfills, waste-water treatment, and rice cultivation) amount to 20 Tg C a^{-1} [recalculated from Olivier (37)], whereas emissions of NMVOCs across Europe amount to 50 Tg C a^{-1} [recalculated from Günther et al. (38)], of which about half escapes oxidation to CO_2 before leaving the continental boundaries. In addition, atmospheric models assume all fossil-fuel C is combusted to CO_2. This is not the case, with about 2 to 5% of fossil fuel (35 to 85 Tg C a^{-1}) being emitted as CO. Correcting the inverse model estimates for these unaccounted C losses reduces the difference between the land-based and atmosphere-based estimates by more than 50% (Fig. 1, arrow B).

Conversely, there are C fluxes that are detected by the atmosphere-based approach but bypass the terrestrial C pools. For instance, in terms of C, Europe had negative intercontinental food and wood trade balances during the 1990s. Europe imports more C to feed its dense populations of humans and livestock than it exports [16 Tg C a^{-1} (24)] and also imported slightly more C via wood products than it exported [4 Tg C a^{-1} (39)]. This food and wood is respired or burned, and its C content released into the atmosphere, where it is taken into account by the inverse atmospheric models. Although relatively small, correcting the atmospheric signal for this food and wood trade balance enlarges the difference between both approaches (Fig. 1, arrow C). In contrast to the small net import of wood product, much larger quantities are harvested and used within the continent. Unlike food products, wood products can have a relatively long life-span, and changes in the pool of wood products (for example, in building construction and in landfills) could also contribute to the discrepancy between atmosphere-based and land-based approaches. With the use of wood harvest and wood trade balance as an input to wood life-cycle analysis models (6, 7, 40), the annual sink in wood products within Europe has been estimated at 24 Tg C a^{-1} (Fig. 1, arrow D).

Including the wood products pool in the land-based approach and the non-CO_2 transfers in the atmosphere-based approach reduces the discrepancy between both estimates (Fig. 1). Nonetheless, it is still possible that other, unidentified C flows are missing from the land- or atmosphere-based approaches. One such potentially important source of error is the restriction of the land-based approach to only the four dominant ecosystems: forests, grasslands, croplands, and organic soil wetlands. Several other C sinks and sources that contribute to the atmosphere-based flux estimate are not accounted for in our land-based approach. For example, emissions from volcanoes and diffuse outgassing of CO_2 produced during metamorphism release C into the atmosphere. These natural geological fluxes may or may not be in equilibrium with the CO_2 consumption during the chemical weathering of silicate and carbonate rocks and the precipitation of hydrocarbonates in groundwater aquifers. If CO_2 consumption is larger than its release, the atmosphere-based approach would overestimate the terrestrial C sink.

Another continental C sink that is detected by the atmosphere-based approach but not included in the land-based approach, productivity of freshwater ecosystems, has probably gained in importance in recent decades because of eutrophication of already existing water bodies and the creation of new, artificial water bodies. This may have increased C sequestration in the sediments of rivers, lakes, reservoirs, and river impoundments (41), as well as river discharge of organic and inorganic C to the oceans (42). River estuaries, on the other hand, emit considerable amounts of C to the atmosphere (43) that are also detected by the atmosphere-based approach. However, a large fraction of the C respired there either was not accounted for as an inland C sink (e.g., freshwater productivity) or was assumed to be completely respired inland. Agricultural produce, soil C losses through erosion or leaching, and imported feed and food products were all assumed to be fully respired and not partly exported to the estuaries as dissolved or particulate organic C. To avoid double counting of these respiratory fluxes, we have not included them in our present land-based approach. More information is needed to constrain better the C balance of inland waters, estuaries, and coastal seas.

Although uncertainty in the individual land-based and atmosphere-based approaches is still very large, the dual constraints imposed by these two completely independent techniques do suggest that the European terrestrial biosphere is a net C sink between 135 and 205 Tg C a^{-1}. Relative to the 1995 anthropogenic C emissions [about 1870 Tg C a^{-1} (44)], this European biospheric C sink accounts for 7 to 12% of the emitted C. As could be expected for such an industrialized region, this compensation is below the global mean of 11 to 33% (2).

The Marrakech accords set a cap on forest management activities accountable under the Kyoto protocol of 11.7 Tg C a^{-1} (Europe excluding Russia) plus 33 Tg C a^{-1} (Russia). This cap originated from the postulate that 15% of the sink in managed forests should be accountable. Given that most European forests are managed, the cap for European countries is extremely conservative, equivalent to 12% (including Russia) of the sink strength estimated in this study.

There is a substantial potential to widen the accounting for biospheric uptake such that the current uptake and C-sink stimulating management practices are awarded as such. The current terrestrial sink strength could be preserved for extended periods or even further enhanced by increasing the sink capacity of forests (45) and reducing the loss in agriculture and peat lands by applying new management techniques specifically aimed at preserving C (46). Stimulating measures to preserve or enhance terrestrial C uptake would retard the increase in atmospheric CO_2 and may therefore gain some time in these times, when increasing temperatures threaten the precarious balance of the global C cycle [for example, (47)].

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Sensing DNA Damage Through ATRIP Recognition of RPA-ssDNA Complexes

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The function of the ATR (ataxia-telangiectasia mutated– and Rad3-related)–ATRIP (ATR-interacting protein) protein kinase complex is crucial for the cellular response to replication stress and DNA damage. Here, we show that replication protein A (RPA), a protein complex that associates with single-stranded DNA (ssDNA), is required for the recruitment of ATR to sites of DNA damage and for ATR-mediated Chk1 activation in human cells. In vitro, RPA stimulates the binding of ATRIP to ssDNA. The binding of ATRIP to RPA-coated ssDNA enables the ATR-ATRIP complex to associate with DNA and stimulates phosphorylation of the Rad17 protein that is bound to DNA. Furthermore, Ddc2, the budding yeast homolog of ATRIP, is specifically recruited to double-strand DNA breaks in an RPA-dependent manner. A checkpoint-deficient mutant of RPA, *rfa1-t11*, is defective for recruiting Ddc2 to ssDNA both in vivo and in vitro. Our data suggest that RPA-coated ssDNA is the critical structure at sites of DNA damage that recruits the ATR-ATRIP complex and facilitates its recognition of substrates for phosphorylation and the initiation of checkpoint signaling.

The ATR (ATM- and Rad3-related) protein kinase plays a central role in the cellular response to replication stress and DNA damage such as double-strand breaks (DSBs) (*1*, *2*). In response to these events, ATR phosphorylates substrates such as p53, Brca1, Chk1, and Rad17. The phosphorylation of ATR substrates collectively inhibits DNA replication and mitosis and promotes DNA repair, recombination, or apoptosis. Despite the identification of many effectors of ATR, the mechanism by which ATR is activated by replication stress or DNA damage remains unsolved.

In human cells, ATR exists in a stable complex with ATRIP (ATR-interacting protein), a potential regulatory partner (*3*). Mec1 and Rad3, the budding and fission yeast homologs of ATR, respectively, also form similar complexes with Ddc2 (also called Lcd1 or Pie1) and Rad26, respectively (*4–7*). In budding yeast, the Mec1-Ddc2 complex is recruited to DSBs induced by the HO endonuclease (HO) or single-stranded DNA (ssDNA) at telomeres caused by a mutation in Cdc13. The recruitment of Mec1-Ddc2 to sites of DNA damage is independent of the replication factor C (RFC)–like protein Rad24 and the proliferating cell nuclear antigen (PCNA)–like proteins Ddc1, Mec3, and Rad17 (*8*, *9*). Likewise, ATR localization to DNA damage–induced foci does not require human Rad17, the homolog of yeast Rad24 (*10*). Thus, the ATR-ATRIP and Mec1-Ddc2 complexes might recognize certain DNA or DNA-protein structures at damage sites in the absence of the RFC-like and PCNA-like checkpoint complexes.

Many distinct DNA damaging agents can elicit the DNA damage or stress response that is mediated by ATR. Thus, a central question in checkpoint signaling is whether there is a sensor for each type of damage or whether all of these are converted to a common intermediate that is detected by a single sensor. A plausible candidate for a common intermediate is ssDNA. In yeast, ssDNA is present at telomeres because of the loss of function of Cdc13 and at the sites of damage caused by HO-induced breaks (*11*, *12*). It has been proposed as a requirement for strong and sustained activation of the checkpoint (*13*).

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